PLANT-SOIL AND BIOTIC INTERACTIONS IN TROPICAL FORESTS

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Candidate Statement of Originality

I hereby certify that the work embodied in this thesis is the result of original research, is free of plagiarised materials, and has not been submitted for a higher degree to any other University or Institution. I confirm that the investigations were conducted in accord with the ethics policies and integrity standards of Nanyang Technological University and that the research data are presented honestly and without prejudice.

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I have reviewed the content and presentation style of this thesis and declare it is of sufficient quality and grammatical clarity to be examined. To the best of my knowledge, it is free of plagiarism and the research and writing are those of the candidate except as acknowledged in the Author Attribution Statement. To the best of my knowledge, the investigations were conducted in accord with the ethics policies and integrity standards of Nanyang Technological University and that the research data are presented honestly and without prejudice.

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This thesis contains material from one paper from the following peer-reviewed journal where I was the first and corresponding author.

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The contributions of the co-authors are as follows:

- I analyzed the data and prepared the manuscript drafts. The manuscript was revised by Asst Prof Kelly Andersen and Prof David Wardle.
- Asst Prof Kelly Andersen designed and carried out the study and helped in statistical analysis.
- All authors read and approved the submitted version.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to the thesis:

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Contents

Abstract

Tropical forests are vital for biodiversity conservation and carbon sequestration. This dissertation examines the ecological dynamics of Brunei’s waterlogged peat and kerangas forests and Panama’s lowland forests, focusing on aboveground and belowground properties. Field transplant experiments, paired plot experiments, and measurements across degradation gradients were employed to study soil nutrient dynamics, seedling performance, tree diversity, forest structure, and decomposition rates. Key findings include waterlogged conditions affecting soil nutrient availability without slowing leaf litter decomposition in peat forests, and plants showing species-specific responses to soil nutrient and water variations. These impacts, while not altering tree diversity or forest structure, lead to important community composition changes. Shifts in species like *Shorea albida* significantly impact ecosystem processes, notably aboveground carbon storage. These results highlight the necessity for further research into factors influencing the role of these ecosystems as carbon sinks and underscore the importance of conserving and restoring them.

Keywords: peatlands; kerangas forest; home-field advantage (HFA); functional traits; dipterocarps; forest degradation

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Chapter 1

Introduction

Tropical forests support an immense portion of the Earth's biodiversity and they play an important role in the global carbon cycle (Dirzo and Raven, 2003; Mitchard, 2018). However, today most tropical forests are impacted at an unprecedented scale by anthropogenic factors (Wright and Muller, 2006). This dissertation investigates the ecological dynamics of tropical forests, with a focus on leaf traits, soil nutrient dynamics, and forest composition, to understand their role in biodiversity conservation and carbon sequestration and their responses to environmental degradation.

The tropical forests of Brunei and Panama provide contrasting environments that can aid our understanding of the complex dynamics of plant-soil interactions in tropical ecosystems. In Brunei, peat forests (Figure 1.1A), are characterized by carbon-dense, waterlogged soils, that play an important role in carbon storage and sequestration (Page and Baird, 2016; Page et al., 2011; Kobayashi et al., 2016). However, these forests face significant risks from deforestation and drainage, threatening their ecological integrity and carbon storage capacity (Murdiyarso et al., 2010; Hooijer et al., 2012). Adjacent to these forests are the 'kerangas' forests (Figure 1.1B), a term from the Iban language for the heath forests in Borneo, which are characterized by their nutrient-poor, free-draining sandy soils, and which offer a stark contrast to the peat forests (Brunig, 1974; Becker et al., 1999; MacKinnon et al., 2013). Similarly, the lowland tropical forests in Panama are shaped by diverse soil nutrients and climatic conditions (Engelbrecht et al., 2007; Condit et al., 2013). These varied forest types provide ideal natural settings for comprehensive studies of both aboveground and belowground plant-soil interactions that are crucial for understanding the broader ecological mechanisms at play in tropical forests.

The study of the ecology of tropical forest can be aided by an understanding of leaf and litter functional economic traits of the component species, and these traits are critical in deciphering plant-environment interactions. Economic traits, such as specific leaf area (SLA), leaf area ratio (LAR), light-saturated photosynthetic rate (A_{sat}), dark respiration rate (R_{dark}), leaf dry matter content (LDMC), and leaf nitrogen and phosphorus concentrations directly relate to how plants interact with and influence their environments. These traits contribute to understanding species resource allocation, growth rates, and survival strategies, and to comprehending community assembly processes (Laughlin and Laughlin, 2013; Kumordzi et al., 2015). These traits encompass a spectrum of strategies ranging from ‘resource acquisitive’ marked by rapid resource uptake and growth, to ‘resource conservative’ characterized by resource retention and longer lifespans (Diaz et al., 2004; Wright et al., 2004). In addition, plant attributes such as root mass ratio (RMR) and traits related to plant size offer insights into a plant’s nutrient acquisition capabilities and overall composition of forest communities (Tilman and Wedin, 1991; Aerts and Chapin, 2000).

This dissertation aims to advance our understanding of tropical forest ecology by exploring how these tropical forest ecosystems function under varying environmental conditions and stressors. Through examining leaf traits, soil nutrient dynamics, and forest composition, we gain critical insights that inform conservation strategies and enhance our understanding of the global carbon cycle. Such an understanding becomes particularly crucial when considering the fragility of these ecosystems, especially in the face of anthropogenic habitat degradation.

1.1 Background of peatland degradation

Tropical peatlands are experiencing rapid and ongoing degradation primarily driven by two human-induced factors, i.e., drainage and fire (Dohong et al., 2017). In Southeast Asia, these carbon-rich environments are frequently drained for agricultural and other land uses, primarily oil palm and pulp plantations (Miettinen et al., 2016). Drainage lowers the water table, allowing the peat to dry out, which in turn promotes belowground processes that lead to increased release of CO_2 and N_2O, and that increases their susceptibility to fires (Cochrane et al., 2009; Prananto et al., 2020). These fires can be particularly devastating, as they not only burn the surface vegetation but also smoulder (through slow, low-temperature, flameless burning) both horizontally and vertically through the peat itself (Usup et al., 2004; Rein, 2013).

Figure 1.1: Forest structure of **(A)** mature peat forest in the Badas Forest Reserve, Belait District, Brunei Darussalam and **(B)** mature kerangas forest in the Labi Hills Forest Reserves, Belait District, Brunei Darussalam.

This cycle of drainage and fire has transformed extensive areas of tropical peatlands from carbon sinks into sources of greenhouse gas emissions, particularly in Southeast Asia, potentially contributing to global climate change and loss of unique habitats.

The burning of tropical peatlands in Southeast Asia causes significant health and economic impacts in surrounding regions. The resulting haze, which is a dense toxic smoke containing harmful particulate matter and toxins like benzene and hydrogen cyanide, can affect air quality across national borders, impacting areas tens or hundreds of kilometers away from the source of the fires (Marlier et al., 2015; Page and Hooijer, 2016). Prolonged exposure to this air pollution is linked to serious health issues such as respiratory and cardiovascular diseases, contributing to an estimated 110,000 additional deaths annually, particularly among children and the elderly (Johnston et al., 2012). Economically, haze events disrupt transportation and reduce tourism, leading to hundreds of millions of dollars in losses (Quah, 2002). The transboundary nature of haze strains international relations, as neighbouring countries grapple with the shared burden of air pollution originating from peatland fires. Effective management and restoration strategies for tropical peatlands are thus essential not only for ecosystem preservation but also for safeguarding public health and economies in the region.

Following degradation, tropical peatlands are frequently converted to agricultural land, particularly for oil palm plantations and pulp, to match rising global demands for food and biofuels (Yule, 2010; Miettinen et al., 2016). This conversion drastically reduces habitat heterogeneity, leading to an increase in non-native invasive and generalist species along with a significant decline in the diversity of flora, fauna, and fungi (Petrenko et al., 2016; Shuhada et al., 2020). For example, the conversion of peatlands to oil palm plantations by the 2000s resulted in the likely local extinction of 16 forest-dwelling bird species in Sumatra and 46 species in Peninsular Malaysia (Koh et al., 2011). Moreover, oil palm cultivation has predominantly negative impacts on ecosystem services, including flood regulation, air quality, and food provision (Lupascu et al., 2020a; Ayompe et al., 2021). The shift from biodiverse peatlands to monoculture plantations (e.g., of oil palm) represents a critical threat to conservation efforts and highlights the urgent need for sustainable land-use practices that balance economic interests with ecological preservation and restoration.

Given the significant environmental, health, and biodiversity issues associated with the degradation of tropical peatland forests, further research is imperative to inform effective conservation and restoration strategies for these ecosystems. There is a critical need to conduct comparative studies between peat forests and surrounding forest ecosystems to understand the ecological distinctions and similarities that can guide restoration efforts. Additionally, investigating processes that potentially impact the carbon sequestration processes in these ecosystems, such as through plant litter decomposition, is essential for understanding their role as a global carbon sink. Research into degradation in tropical forested peatlands resulting from fire and reduced water table levels is also vital because they can illuminate the extent of damage caused by these factors and help develop targeted interventions to mitigate further degradation. By addressing these research needs, we can gain a more comprehensive understanding of tropical peatland ecosystems, which is crucial for developing effective strategies to conserve and restore them.

1.2 Methodological approach and study areas

This dissertation employs a comprehensive methodological framework to investigate ecological properties and processes across various tropical forest ecosystems. The research span's distinct geographical locations, through its primary focus on peat and kerangas forest in Badas and Labi Hills Forest Reserves in Brunei and lowland tropical forests along the Panama Canal.

Field studies and site selection

The core of the research is centered around the Badas and Labi Hills Forest Reserves. Plots were established in these forest reserves to facilitate a direct comparison of two highly contrasting forest types (peat and kerangas) as they consist of a mosaic of both ecosystem types. In addition, transects were established along existing fire and drainage degradation gradients in the Badas Forest Reserve. In Panama, existing forest plots along a soil nutrient and moisture gradient were utilized.

Experimental design

The research design across chapters incorporated a mix of experimental and observational approaches. In Brunei, a paired plot design along with a reciprocal litterbag experiment was utilized to compare adjacent patches of peat and kerangas forests. In addition, soil sampling, floristic surveys, and biomass estimations, were used to address the complexities along the degradation gradient in the Badas forest reserve. In Panama, shade-house and field transplant experiments were conducted to assess seedling performance in varying soil and moisture conditions that represent the range of conditions that characterize tropical forests in that region.

Hypothesis and statistical testing

Hypothesis testing was integral to this research and testing these hypotheses involved utilizing a variety of statistical tools. Two-way ANOVAs, generalized linear mixed effect models, principal component analysis (PCA), and non-metric multidimensional scaling (NMDS) were employed to test hypotheses related to soil nutrient effects on seedling traits, forest structure, and decomposition processes. The methodology incorporated both linear mixed models and non-parametric tests, depending on the data distribution and research questions being addressed. Overall, this research utilized a methodologically diverse and geographically comprehensive approach to provide insights into tropical forest ecology. The selection of study areas, combined with experimental design, allowed for a multifaceted examination of ecological interactions within these ecosystems.

1.3 Outline and aims of the individual chapters

Chapter 2: Palm species traits determine soil nutrient effects on seedling performance

In lowland tropical forests, the complex interplay of climate, soil nutrients, and light significantly impacts seedling performance and species distribution. High precipitation and temperatures in these regions often result in nutrient-poor soils, posing challenges for seedling regeneration. Additionally, soil moisture availability during dry seasons further influences species composition. This study focuses on understory palm seedlings in Panama, where high spatial variability in soil properties and a pronounced rainfall gradient present an ideal opportunity for investigating how soil nutrient and moisture availability affect understory palm seedling performance and, consequently, species distribution patterns. In doing this it aims to enhance understanding of the ecology of palms and their role within tropical forest ecosystems. We tested the following hypotheses to accomplish this aim:

> (H1) To maximize returns of investment in leaf resources, leaf traits such as SLA, LAR, photosynthesis rates (A_{sat}), and dark respiration rates (R_{dark}) will decline as soil fertility declines. Furthermore, we expected the palm species most associated with low nutrient, phosphorus and base cation depleted soils (i.e., *Geonoma congesta*) to have higher leaf resource-use efficiency, and the species most associated with intermediate nutrient soil (i.e., *Chamaedorea tepejilote*) to have leaf traits that maximize carbon gains when grown in their home soil compared to species not associated with those soils.

(H2) Root mass ratio (RMR) should increase as soil fertility declines to meet nutrient demands, at the expense of leaf mass ratio (LMR), stem mass ratio (SMR), and growth potential. Those species that are specialists for particular environments are expected to maximize allocation to leaf biomass to increase growth potential in their home soils compared to other species absent from those soils.

(H3) Due to increased resource-use efficiency (H1) and optimal biomass allocation patterns (H2), specialists growing in the soil that they are naturally associated with will achieve higher RGR compared to species not occurring in those soils.

(H4) Since specialist species have higher resource-use efficiency (H1), higher nutrient/water uptake efficiency biomass allocation patterns (H2), and higher RGR (H3), they will have higher seedling survival rates when growing at the sites where they naturally occur than will species not occurring at those sites.

Chapter 3: Comparative analysis of floristic composition, leaf traits, and soil dynamics in coexisting peat and kerangas forest ecosystems

The research presented in this study addresses a significant gap in understanding how the waterlogged conditions in tropical peat forests influence both aboveground and belowground ecosystem properties relative to other forest types. Our study region in Brunei’s tropical forest landscape involves extensive intact peat forests characterized by waterlogged conditions, juxtaposed alongside free draining kerangas forests in which peat does not accumulate (Figure 1.2). The primary aim of this research is to examine how contrasting environmental conditions between the peat and kerangas forest environments affect floristic composition, leaf traits, and soil nutrient characteristics, using a paired plot experiment in adjacent peat and kerangas forests. This comparative approach is essential for gaining a comprehensive understanding of the functionality and dynamics of tropical peat ecosystems within a broader ecological framework. To achieve this aim, we tested the following hypotheses:

(H1) Total nutrients will be higher in peat soil compared to kerangas soil because the former has more organic matter. However, available nutrients will be higher in kerangas due impaired mineralization in the anoxic environment of the peat.

(H2) The nutrient poor conditions and additional adaptations needed for plants to survive in the waterlogged environment of peat forest will promote a greater

Figure 1.2: Treefall reveals the contrasting soil conditions of **(A)** waterlogged peat of peat forest in the Badas Forest Reserve, Belait District, Brunei Darussalam and **(B)** free-draining kerangas-sand which is overlaid with a layer of kerangas-humus in the Labi Hills Forest Reserves, Belait District, Brunei Darussalam.

diversity of trees (as a result of greater coexistence through reduced competition; Grime, 1979), a higher frequency of trees with a larger diameter (which will be better anchored and more stable in deep peat), and more taxa with nutrient strategies needed to cope with lower levels of available nutrients (such as nitrogen fixing and ectomycorrhizal associations), when compared to kerangas forest.

(H3) Due to differences in nutrient availability, leaf economic functional traits and nutrient resorption will differ between peat and kerangas plots. Specifically, plants from peat plots will demonstrate more conservative economic traits and higher resorption since they are in a more nutrient limited environment.

Chapter 4: No home-field advantage in the decomposition of leaf litter in the tropical peat forests of Brunei

The mechanisms of peat accumulation in tropical peat forests, including those involving how the waterlogged and nutrient-poor conditions of these forest affect plant litter decomposition, are poorly understood. Specifically, the ‘home-field advantage’ (HFA) hypothesis, which proposes that litter decomposition rates are accelerated in the environment from which the litter is sourced due to prior adaptation of the decomposer community, has been little studied in waterlogged forests. This research aims to compare plant litter decomposition rates between peat and kerangas forest environments by using a using leaf litter transplantation experiment (in which leaf litter from both peat and kerangas forest is decomposed in both environments). In doing this it examines the influence of litter quality, decomposition environment, HFA, and soil nutrient status on litter decomposition rates. The ultimate aim of this study is to enhance our understanding of peat accumulation processes in tropical peat forests, and thus contribute to the broader ecological knowledge of these vital carbon reservoirs. We tested two hypotheses to accomplish these aims:

> (H1) Decomposition and nutrient release will overall be faster for litter placed in kerangas because soil biological activity will be impaired less by waterlogging and nutrient limitation. Further, litter from kerangas vegetation will decompose and release nutrients faster regardless of where it is placed.
>
> (H2) Home field advantage will mean that litter from both peat and kerangas vegetation will decompose more rapidly than expected in the environment that it was collected (i.e., in peat and kerangas environments respectively). However, this advantage will be stronger in peat and for plant taxa that produce poorer quality litter because the microbes in the peat are better adapted for decomposing more recalcitrant litter.

Chapter 5: Peatland degradation: examining impacts on soil, plant diversity, forest structure, and biomass

The effects of tropical peat forest degradation, particularly in terms of how fires and drainage impact both aboveground and belowground ecosystem properties, remain poorly understood. In Brunei’s Belait District, the Badas Forest Reserve showcases a clear degradation gradient within its peat dome, which provides an ideal study system for exploring the consequences of fire and drainage on forest stand characteristics, biomass, and carbon loss (Figure 1.3). The primary aims of this research are to enhance understanding of how intensification of peat forest degradation resulting from fire and water drainage influence the ecological characteristics of these forests, and to provide key insights that may benefit the restoration of these vital ecosystems. We tested the following hypotheses to accomplish this aim:

> (H1) Available nutrients will be highest in heavy degraded and most degraded plots due to lower water table levels which allows for increased mineralization.
>
> (H2) Plant diversity and community structure will shift significantly along the degradation gradient, with lower diversity and greater domination by resource-acquisitive plant taxa in the intermediate to most degraded areas (due to the increased mineralization and canopy openness) as compared to higher diversity and domination by resource-conservative plant families in lightly degraded and pristine areas.
>
> (H3) As forest degradation intensifies, tree abundance, stand basal area, canopy height and emergent layer height, will decrease due to the loss of mature trees and the consequent reduction in canopy complexity. Meanwhile ground cover will increase due to increased light and nutrient availability favouring fast-growing plant species.

Chapter 6: Discussion

The aims of this chapter are to synthesize and contextualize the main findings of this research, particularly focusing on soil nutrients, soil water content, and plant traits, and their interplay in tropical forest ecology. It seeks to highlight how the work reported in Chapters 2-5 bridge gaps in current ecological knowledge and contribute to a deeper understanding of tropical forest dynamics. Additionally, the discussion will explore the broader implications of these findings for climate change mitigation and outline directions for future research, emphasizing areas that require further investigation to enhance conservation and management strategies in tropical forests.

1.4 Unified research aims

The unified aim of this research is to enhance our understanding of the interactions between plants and soils in tropical forests, with a particular focus on factors that drive both the aboveground and belowground subsystems and how their effects vary across both time and space. These key factors, each playing a crucial role in ecosystem dynamics, are as follows:

Figure 1.3: Peatland fire and drainage degradation gradient viewed from the extensive drainage canal alongside the Jalan Badas road in the Badas Forest Reserve, Belait District, Brunei Darussalam. In the foreground is the drainage canal. The middle ground features the most degraded areas, which have been repeatedly burned and are now dominated by ferns and sedges. In the background, the forest edge transitions into a *Shorea albida* - dominated peat forest.

Soil nutrients

Chapters 2-5 all investigate the ecological impact and significance of soil nutrients, including both total and available nutrients, across various tropical forests. The research in total investigates how plant species respond to differing soil nutrient levels, by examining the implications for plant growth, survival, and the overall composition of forest communities. The studies span a range of soil conditions, from nutrient-rich to nutrient-poor soils, and provides insights into how soil fertility influences ecological patterns and processes over time.

Soil water content

The role of water is thoroughly examined throughout the thesis, with a particular focus on soil moisture gradients (in Panama) and waterlogged conditions (in the Brunei peat forests). These chapters explore how varying soil water content affects ecological processes, ranging from the physiological functioning of individual plants to broader ecosystem processes such as plant litter decomposition. The research covers diverse environments, from well-drained to water-saturated soils, and highlights the significant influence of water availability on forest properties and processes across different landscapes and degradation intensities.

Species-specific responses

The chapters explores species-specific responses and the role of plant functional traits, including leaf economic traits and nutrient contents, to the spatial variation in soil properties, including nutrient availability and moisture. By examining plant traits in a variety of forest types and environmental conditions, the research sheds light on the adaptive strategies of plants and how these traits contribute to shaping forest structure, community composition and ecosystem functioning.

Together, these chapters present a comprehensive picture of several key aspects of the aboveground and belowground ecology of diverse and carbon-dense tropical forests, and in doing so provide fundamental information which is essential for understanding the functioning and shaping the conservation and management of these ecosystems.

Chapter 2

Palm species traits determine soil nutrient effects on seedling performance

2.1 Abstract

Environmental gradients influence plant establishment, survival, and functional traits. Along the Panama Canal Isthmus there is a strong rainfall gradient with an underlying mosaic of soil types ranging in soil nutrient availability. In this region, tree species distribution patterns are correlated with soil phosphorus availability and rainfall patterns, but how understory plant species such as palms relate to these factors is less clear. We hypothesized that due to greater resource use efficiency and optimal biomass allocation, specialist species will have greater seedling performance growing in home soil and sites compared to species not occurring there. To test this hypothesis, we used two specialist species (*Chamaedorea tepejilote* and *Geonoma congesta*) and two generalist species (*Geonoma cuneata* subsp. *cuneata* and *Chamaedorea pinnatifrons*), and for these four species we measured traits on seedlings and assessed their performance in shade house and field transplant experiments using five soils. Soils were sourced from five sites which varied in nutrient availability and rainfall, and were distributed along lowland tropical forests of the Panama Canal Isthmus. In the shadehouse experiment, leaf functional traits were determined by species rather than soil nutrient availability. However, in the shadehouse experiment, seedling biomass allocation, and relative growth rate were determined by interactions between species and soil, with weak support for home-site advantage for one of the species. In the field

transplant experiment, seedling survival was strongly related to dry season water availability. However, species tended to have high survival at home sites and other sites with higher dry season rainfall. Together, results from these experiments suggest that understory palm species seedling performance are determined by species-specific responses to the combination of soil nutrient and water availability. This indicates that while soil nutrients influence seedling biomass allocation, dry season water availability determines both specialist and generalist seedling survival and therefore distributions along the soil nutrient and moisture gradient.

2.2 Introduction

Abiotic environmental factors, including climate, soil nutrients, and light are drivers of seedling performance, including their survival, growth, and functional traits, and consequently influence species distribution patterns (Grubb, 1977; Grime, 2006; Engelbrecht et al., 2007). These abiotic factors do not operate independently of each other. For example, in lowland tropical forests, high mean annual precipitation (MAP) and temperatures leads to high rates of leaching of labile cations and phosphorous from the parent material during soil formation (Vitousek and Sanford, 1986; Sollins, 1998), and therefore result in nutrient limitation of rock-derived nutrients necessary for successful seedling regeneration (Alvarez-Clare et al., 2013). In addition to nutrient limitation, dry season soil moisture availability can also impose a filter on seedling regeneration and species composition (Baltzer et al., 2005; Engelbrecht et al., 2007; Condit et al., 2013). However, disentangling the effects of different abiotic drivers such as soil nutrient availability and dry season water deficit on seedling performance may reveal different mechanisms that drive habitat associations and ultimately species distribution patterns along environmental gradients (Fortunel et al., 2016).

Plants show trade-offs between ‘acquisitive’ strategies aimed at rapid resource uptake driving fast growth rates, and ‘conservative’ strategies aimed at the retention of resources and longer life spans (Diaz et al., 2004; Wright et al., 2004; Díaz et al., 2016). The traits underpinning these strategies are responsive to environmental gradients, including soil nutrient (Richardson et al., 2004; Peltzer et al., 2010), and moisture availability (Maharjan et al., 2011; Pollock et al., 2012; McLean et al., 2014). For example, plants growing in fertile soils allocate biomass aboveground and are associated with high relative growth rates (RGR), leaf-area ratios (LAR), specific leaf area (SLA; Aerts and Chapin, 2000; Palmiotto et al., 2004; Dent and Burslem, 2009), and height (Yavitt and Wright, 2008; Ali and Yan, 2017), whereas those growing in low-nutrient soils allocate more biomass belowground and are associated low RGR and SLA (Tilman and Wedin, 1991; Aerts and Chapin, 2000). Together, plant functional traits govern how species both influence and respond to their environment (Diaz et al., 2004) and can drive community assembly (Laughlin and Laughlin, 2013; Kumordzi et al., 2015). Among plant groups, monocots and particularly, palms, produce leaves with high leaf toughness (Dominy et al., 2008) and lignin (Santiago, 2007), slow decomposition rates, and low SLA and nutrient content compared to dicots, suggesting palms may have conservative plant economic strategies. However, despite the high species diversity and abundance of palm species in lowland tropical forests, we know little about how functional traits vary among palm species or the ecological significance of this variation compared to the breadth of information for their woody counterparts.

Understanding drivers of palm species distributions is central to understanding whole forest community ecology in lowland tropical forests because palms act as filters that affect tree seedling growth and survival (Farris-Lopez et al., 2004; Wang and Augspurger, 2004). Palms reduce seedling establishment by modifying microsite conditions through increasing leaf litter depth and decreasing light availability (Farris-Lopez et al., 2004). Therefore, it is important to better understand drivers of palm species distribution patterns. Palm species distribution patterns, phylogenetic structure, and ecological interactions are all influenced by soil conditions, such as nutrient and moisture availability (Clark et al., 1995; Emilio et al., 2013; Cámara-Leret et al., 2017; Muscarella et al., 2019). For example, palm species distribution patterns are strongly correlated with soil phosphorus and base cations across landscape scales in lowland Amazonia (Cámara-Leret et al., 2017) and soil nitrogen availability in lower montane forests in western Panama (Andersen et al., 2010a,b). Although there have been many studies examining the relationship between soil parameters and palm species distributions, fewer studies have experimentally tested the mechanisms responsible for driving these patterns along soil gradients or examined plant functional traits.

The Panamanian Isthmus presents an ideal study system for exploring species habitat specialization because of its mosaic of environmental conditions. The complex environmental variation in this region is due to a strong rainfall gradient which ranges from 1,500 to 3,000 mm MAP from the Pacific to Caribbean sides of the 60 km Isthmus (Paton, 2020a,b), as well as a diverse geology resulting in a range of soil properties (Turner and Engelbrecht, 2011; Cusack et al., 2018). Soil nutrients and moisture are the main abiotic factors that drive a near complete floristic turnover of woody species in the lowland tropical forests across the 60 km Panama Isthmus (Pyke et al., 2001; Engelbrecht et al., 2007; Condit et al., 2013). In addition to shifts in species composition, there are large changes in fine root biomass driven by variation in soil base cation availability (Cusack et al., 2018), and changes in community-level leaf trait values, such as SLA and leaf thickness, driven by variation in both soil moisture and phosphorus (Umaña et al., 2021). This demonstrates strong species selection and trade-offs along multiple resource gradients for trees, but it is unclear whether understory plant species follow the same patterns.

One of the most extensively studied understory palm communities occurs in the Fortuna Forest Reserve (Fortuna) and surrounding lower montane forests of western Panama, a hot spot for palm species diversity and endemism (Andersen et al., 2010a; Prada et al., 2017). In Fortuna, understory palm species community composition and functional traits are related to shifts in soil nitrogen, cation, and aluminum availability (Andersen et al., 2010a, 2012), whereas tree (woody and palm) species composition is related to soil phosphorus availability and rainfall (Prada et al., 2017). Furthermore, seedling transplant experiments of understory palm species have revealed that whole-plant functional strategies of low nutrient specialist species give them a performance advantage at low soil nutrient sites (Andersen et al., 2010b, 2014; Andersen and Turner, 2013). These findings suggest that functional traits and seedling performance drive understory palm species distribution patterns across the soil nutrient gradient at Fortuna, where species show ‘home-site advantages’ when growing in soils they are associated with compared to species absent from the site. Here, we expand on these studies by using seedling experiments to test the effects of soil nutrient and moisture availability on seedling performance of four contrasting understory palm species along soil nutrient availability and rainfall gradient in lowland tropical forests of the Panama Canal Watershed.

To specifically examine the effects of soil nutrient availability on understory palm seedling performance and functional traits, we conducted a shadehouse experiment growing seedlings of four species in soil collected from five sites varying in soil nutrient availability along the Panama Canal (Table 2.1), (Turner and Engelbrecht, 2011; Cusack et al., 2018). Nutrient availability varied from ‘low nutrient’ soil that is depleted in phosphorus and base cations to ‘high nutrient’ soil that is rich in phosphorus. We included two site specialist species (*Chamaedorea tepejilote*), from site Pipeline Road Plot 15 (an intermediate nutrient site), and *Geonoma congesta*, from site Fort Sherman (a low nutrient site). We also included two site generalist species (*Geonoma cuneata* subsp. *cuneata* and *Chamaedorea pinnatifrons*) from the lower montane Fortuna sites which have soils that range in nutrient availability (Table 2.1). In this study, a species was defined as a specialist if it is found at one site, i.e., that is has a single soil nutrient ranking. A species was classified as a generalist if it is found at multiple areas which vary in soil nutrient availability. While the ratio of generalist to specialist palm species across these sites is poorly understood, in western Amazonian lowland rainforests generalist species have wide tolerances to differences in soil fertility and outnumber specialist species (Ruokolainen and Vormisto, 2000). To further understand how abiotic factors (including both soil nutrients and moisture availability) influence seedling survival of the four palm species, we also transplanted seedlings of all four species into the five field sites. We expected that, due to higher resource use efficiency and optimal biomass allocation, the specialist species (*C. tepejilote* and *G. congesta*) would show greater seedling performance in the soil and at the site that they are associated with compared to species not occurring at those sites. On that basis we tested the following four hypotheses:

> (H1) To maximize returns of investment in leaf resources, leaf traits such as SLA, LAR, photosynthesis rates (A_{sat}), and dark respiration rates (R_{dark}) will decline as soil fertility declines. Furthermore, we expected the species associated with low nutrient, phosphorus and base cation depleted soils (*G. congesta*) to have higher leaf resource-use efficiency and the species associated with intermediate nutrient soil (*C. tepejilote*) to have leaf traits to maximize carbon gains when grown in their home soil compared to species not absent from those soils.
>
> (H2) Root mass ratio (RMR) should increase as soil fertility declines to meet nutrient demands at the expense of leaf mass ratio (LMR), stem mass ratio (SMR), and growth potential. The specialist species are expected to maximize allocation to leaf biomass to increase growth potential in their home soils compared to other species absent from those soils.
>
> (H3) Due to increased resource-use efficiency (H1) and optimal biomass allocation patterns (H2), specialists growing in the soil they are associated with will achieve higher RGR compared to species not occurring in those soils.
>
> (H4) Since specialist species have higher resource-use efficiency (H1), higher nutrient/water uptake efficiency biomass allocation patterns (H2), and higher RGR (H3), they will have higher seedling survival rates when growing at the sites where they naturally occur than will species not occurring at those sites.

By simultaneously examining the above hypotheses, we aim to advance our understanding of the mechanisms that influence establishment, survival, and functional traits of seedlings of understory palm species, and thus their distribution patterns along soil nutrient and moisture gradients in lowland tropical forests.

Table 2.1: Environmental conditions and plot locations of five sites along a soil nutrient gradient in lowland tropical forests of the Panama Canal Watershed. Soil samples were collected 10 cm below the soil surface from each plot (N = 90 samples).

Watershed	**Fort Sherman**	**La Laguna**	**Pipeline Road Plot 9**	**Pipeline Road Plot 15**	**Campo Charges**
Site code	SH	M25	P9	P15	CCH
Environmental variables					
Soil nutrient ranking	low	low	intermediate	intermediate	high
Geology[a]	Chagres sandstone	Rhyolite	Pre-Tertiary basalt / Gatuncillo	Gatunocillo formation	Alhajuela formation
Soil order[a]	Oxisol	Ultisol	Inceptisol	Alfisol	Alfisol (Mollisol)
Latitude (degrees)	9.281	9.079	9.169	9.162	9.211
Longitude (degrees)	-79.975	-79.799	-79.741	-79.745	-79.600
Elevation (m)	140	110	160	70	109
Topography	irregular	sloping	irregular	level	sloping
Succesional status	primary	secondary	primary	mature	mature
Soil variables					
pH	4.63 ± 0.03^{c}	4.51 ± 0.03^{c}	5.90 ± 0.09^{b}	6.02 ± 0.08^{b}	6.51 ± 0.07^{a}
Al (g cm^{-3})	20.78 ± 0.99^{c}	12.04 ± 0.39^{b}	7.31 ± 0.58^{a}	6.82 ± 0.44^{a}	7.86 ± 1.2^{a}
Ca (g cm^{-3})	1.04 ± 0.2^{c}	0.21 ± 0.02^{c}	8.18 ± 0.46^{b}	6.19 ± 0.45^{b}	18.42 ± 1.47^{a}
Fe (g cm^{-3})	1.48 ± 0.12^{a}	1.11 ± 0.11^{a}	1.13 ± 0.07^{a}	1.38 ± 0.05^{a}	1.35 ± 0.09^{a}
K (g cm^{-3})	0.12 ± 0.01^{b}	0.07 ± 0.01^{b}	0.12 ± 0.01^{b}	0.27 ± 0.03^{b}	1.20 ± 0.12^{a}
Mg (g cm^{-3})	1.27 ± 0.17^{c}	0.68 ± 0.07^{c}	4.77 ± 0.27^{b}	2.55 ± 0.16^{bc}	11.38 ± 1.5^{a}
P (µg g dry soil^{-1})	4.59 ± 0.42^{bc}	2.95 ± 0.15^{c}	10.74 ± 0.51^{b}	7.35 ± 0.32^{bc}	32.68 ± 4.01^{a}
CEC (%)	24.85 ± 1.07^{b}	14.39 ± 0.28^{d}	21.78 ± 0.76^{bc}	17.59 ± 0.40^{cd}	40.37 ± 3.67^{a}
NO_3^- (µg g dry soil^{-1})	3.28 ± 0.50^{cd}	1.8 ± 0.15^{d}	6.43 ± 1.23^{bc}	8.34 ± 0.62^{ab}	11.65 ± 1.31^{a}
NH_4^+ (µg g dry soil^{-1})	30.47 ± 1.08^{c}	48.86 ± 3.16^{b}	50.08 ± 1.19^{b}	66.40 ± 3.79^{a}	27.37 ± 1.18^{c}
Nitrification (g cm^{-3} day^{-1})	1.30 ± 0.16^{a}	0.96 ± 0.07^{a}	1.15 ± 0.12^{a}	1.12 ± 0.12^{a}	1.06 ± 0.21^{a}
N mineralization (g cm^{-3} day^{-1})	3.24 ± 0.22^{c}	1.75 ± 0.14^{a}	2.31 ± 0.2^{a}	0.59 ± 0.2^{b}	2.35 ± 0.3^{a}
Base saturation (%)	10.29 ± 1.11^{d}	8.70 ± 0.63^{d}	61.12 ± 2.25^{b}	53.03 ± 2.72^{c}	77.31 ± 1.68^{a}
Moisture					
Annual precipitation[a] (mm)	2848.2	2176.9	2344.7	2330.1	2481.2
Dry season moisture deficit[b] (mm)	-491.7	-553.6	-545.4	-549.4	-570.8
Soil water content (dry season; % dry mass)	70.8 ± 3.0^{c}	32.2 ± 1.2^{b}	50.3 ± 1.8^{a}	35.8 ± 1.2^{b}	46.7 ± 3.9^{a}
Soil water content (wet season; % dry mass)	89.7 ± 2.3^{d}	44.1 ± 1.7^{c}	67.7 ± 2.2^{a}	51.5 ± 1.7^{b}	73.1 ± 3.3^{a}
Soil water content (% dry mass)	81.2 ± 3.3^{c}	39.1 ± 2.1^{b}	60.5 ± 3.0^{a}	45.0 ± 2.6^{b}	62.5 ± 4.5^{a}
Combined PCA axes					
PC1 environmental	-1.88 ± 0.06^{b}	-2.01 ± 0.03^{b}	0.18 ± 0.13^{c}	0.03 ± 0.11^{c}	3.68 ± 0.31^{a}
PC2 environmental	1.86 ± 0.21^{d}	-0.22 ± 0.17^{b}	-0.46 ± 0.17^{b}	-1.89 ± 0.19^{c}	0.72 ± 0.26^{a}
PC3 environmental	-0.12 ± 0.28^{d}	-0.55 ± 0.16^{b}	0.31 ± 0.21^{b}	0.60 ± 0.19^{c}	-0.23 ± 0.44^{a}

Geology, soil order, and annual precipitation is based on Cusack et al. (2018). Dry season moisture deficit is based on ForestGEO data portal (www.forestgeo.si.edu). Cation exchange capacity is abbreviated as CEC. All means are shown ± SE and different letters among sites indicate statistically significantly different means after a Bonferroni correction ($P < 0.05$).

2.3 Material and methods

The present study was conducted at five one-hectare sites in lowland tropical forest along the Panama Canal (Pyke et al., 2001; Engelbrecht et al., 2007; Condit et al., 2013; ForestGEO data portal). These sites following nomenclature from Pyke et al. (2001) and Cusack et al. (2018), and ForestGEO data portal include the Fort Sherman/San Lorenzo crane site (SH), La Laguna/Rio Paja (M25), Pipeline Road plot 9 (P9), Pipeline Road plot 15 (P15), and Campo Charges (CCH). Mean annual precipitation of these sites range from 2,177 mm at site M25 to 2,848 mm at site SH, with dry seasonal precipitation deficit ranging from 570 mm at site CCH to 492 mm at site SH (Condit et al., 2013; ForestGEO data portal). In general, soil nutrient availability and dry season water deficit increase as MAP decreases among sites (Condit et al., 2013; Cusack et al., 2018; Umaña et al., 2021). The M25 site represents a low nutrient site with low MAP, however, the fine texture soil allows it to maintain high soil available water capacity for a given gravimetric soil moisture content (Kursar et al., 2005).

To quantify the soil nutrient gradient, soil samples were collected in May 2004. At each site, three subsamples were collected from the top 10 cm of the soil, representing the main rooting zone (Cavelier, 1992), and bulked at eighteen locations in each of the 1-ha plots. Each of the eighteen composite samples per site were divided into four subsamples to measure soil moisture content, nitrate and ammonium, pH, and cation (Al, Ca, Fe, K, and Mg) and phosphorous concentrations. In addition, nitrogen mineralization and nitrification rates were estimated using *in situ* PVC incubation tubes at each of the soil sampling locations. After 30 days, soil from the tubes was collected and processed for ammonium and nitrate concentrations. For nitrate and ammonium analyses, 2.0 *g* of fresh soil were extracted with 2M KCl and analyzed colormetrically on a Latchat QuikChem flow injection analyzer (Hach Company, Loveland, CO, United States). Soil pH was measured in a 1:3 fresh soil solution with distilled water. Soil cation and phosphorus analyses were conducted by extracting 2.5 *g* fresh soil with Mehlich III extractant (Mehlich, 1984) and the filtrate analyzed by inductively coupled plasma optical emission spectroscopy on a Perkin-Elmer Optima 2000 (Perkin Elmer Inc., Shelton, CT, United States). Soil water content was measured by weighing fresh soil and soil samples dried at 100°C for 72 h to enable the calculation of the amount of dry soil used in all measurements. We used principal components analysis (PCA, see statistical analyses for details) to rank the sites by soil nutrient availability. The sites with the lowest nutrient availability were SH and M25, with sites P9 and P15 being intermediate, and site CCH having high soil fertility, with the main soil nutrient gradient driven by soil P and cation concentration and soil pH (Figure 2.1A).

2.3.1 Species selection and seed collection

We focused on four common understory palms species within the subfamily, Arecoideae (Table 2.2): *C. pinnatifrons* (Jacq.) Oerst, *C. tepejilote* Liebm., *G. congesta* H. Wendl. ex Spruce, and *G. cuneata* subsp. *cuneata* (H. Wendl. ex Spruce; Baker et al., 2011; Henderson, 2011). All species are Neotropical long-lived perennials that differ in general morphology, life history, habitat association, and spatial distribution (Henderson et al., 2019). We define soil-based habitat associations on occurrence within the Panama Canal Watershed region. Preliminary surveys suggest that two of the four species are site specialists: *C. tepejilote* occurs at intermediate soil nutrient sites and *G. congesta* occurs at a low soil nutrient sites in the lowland tropical forests of the Panama Canal Watershed (Table 2.2). The other two species are generalist species in the lower montane forests of Fortuna Forest Reserve in western Panama, including the most abundant species in the lower montane forests of Fortuna, *G. cuneata*, as well as *C. pinnatifrons* (Andersen et al., 2010a). *Geonoma congesta*, ranges from Honduras to Panama and occurs locally at the SH site where the seeds for the experiments were collected from. *Chamaedorea tepejilote*, ranges from Mexico to Colombia and occurs at the P15 site and seeds of this species were collected along the Pipeline Road forests. *Geonoma cuneata*, ranges from Nicaragua to Ecuador and contains a complex of subspecies (Henderson, 2011) including several within Panama. *Geonoma cuneata* subsp. *indivisa* Henderson, occurs locally at SH, P9, and P15. However, the seeds used in the experiments were collected from *G. cuneata* subsp. *cuneata* “Fortuna morphotype” (Henderson, 2011), which occurs across the soil nutrient gradient at the Fortuna Forest Reserve (Andersen et al., 2010a,2014). *Chamaedorea pinnatifrons*, spans from Mexico to northern South America (Henderson et al., 2019). However, this species did not occur at any of the five sites used in our study and seeds were collected from the Fortuna Forest Reserve where it occurs across the soil nutrient gradient (Andersen et al., 2010a, 2014). We collected seeds for all four species from the field between July and September 2005.

All seeds for the experiments were germinated at the Santa Cruz Experimental Site, Panama. Soils were collected from the five sites and mixed with washed sand in a 30:70 sand: soil ratio. Seeds were sowed into germination trays containing the soil type that the seedlings would be transplanted to for the shadehouse and field experiments.

Table 2.2: List of species and their general morphology and associated habitats. Abbreviations used: Pipeline Road Plot 15 (P15) and Fort Sherman (SH).

Genus and species	***Chamaedorea pinnatifrons***	***Chamaedorea tepejilote***	***Geonoma congesta***	***Geonoma cuneata***
Authority	(Jacq.) Oerst.	Liebm.	H. Wendl. ex Spruce	(H. Wendl. ex Spruce) Skov
Growth habit	aerial	aerial	aerial	acualescent
Life form	treelet	treelet	treelet	shrub
Leaf shape	pinnate	pinnate	pinnate	bifid
Habit	Solitary	Solitary or Clumped	Solitary or Clumped	Solitary or Clumped
Elevational range	0 to 2700m	0 to 1600m	0 to 1000m	0 to 1200m
Site associations	Fortuna Forest Reserve	P15	SH	Fortuna Forest Reserve
Seed collection location	Fortuna Forest Reserve	Pipeline Road forests	SH	Fortuna Forest Reserve

2.3.2 Shadehouse experiment

To determine the effect of soil nutrient availability on seedling performance and functional traits, we conducted a completely randomized, factorial design shadehouse experiment by growing seedlings of the four species in soil from the five field sites. Once the seedlings had germinated with one fully expanded leaf, one seedling was transplanted per pot which contained freshly collected soils from the field sites that had been mixed with sand in a 30:70 sand:soil ratio. Ten seedlings per species * soil combination were planted in pots, resulting in a total of 200 plants. Pot size ranged from 0.5L for the smaller *Geonoma* species to 2L for the larger *Chamaedorea* species. Seedlings were watered during the dry season (January–April) and as needed to supplement natural rainwater during the wet season. Temperature was maintained at ambient conditions while light levels were maintained at 2% light conditions to simulate natural understory conditions within the shadehouse. Seedlings were moved around continuously during the experiment to avoid any bias in growing conditions.

Seedling survival was monitored for the experiment over 416 days, as at this time all the seedlings had produced multiple leaves and had started to reach the size limits of their pots. Light saturated photosynthetic capacity (A_{sat}) and dark respiration (R_{dark}) were measured on the youngest fully mature leaf of all individuals surviving to the end of the experiment using a Li-Cor 6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, United States). Measurements were made with the following chamber conditions: < 75% relative humidity, temperature of 25–28°C, air flow rate of 500 $\mu mol \cdot s^{-1}$ and CO_2 of 400 ppm. Light saturation curves were performed to determine saturating light conditions for a subset of individuals of each species (data not shown), after which light levels were set to 400 $\mu mol \cdot m^{-2}\ s^{-1}$ for the A_{sat} measurements (Chazdon, 1986). For R_{dark}, leaves were left for 15 min to stabilize with the light source turned off. The mean values of five-point measurements over 60 s were recorded for gas exchange measurements. After the gas exchange measurements were complete, all surviving seedlings were destructively harvested to measure leaf area and biomass allocation patterns. Seedlings were separated into leaf, stem, and root components and dried for 72 h at 65°C. Prior to drying, fresh leaves were digitally scanned using a Cannon CanoScan LiDE 100 flatbed scanner (Cannon, Melville, NY, United States) and leaf area was estimated using ImageJ software. Harvest data were used to calculate SLA (leaf area per leaf mass; $mm^2 \cdot mg^{-1}$), LAR (leaf area per whole plant mass; $mm^2 \cdot mg^{-1}$), LMR (leaf mass divided by whole plant mass; LMR), SMR (stem mass divided by whole plant mass; SMR), and RMR (root mass divided by whole plant mass; RMR), and RGR (biomass at harvest subtracted by initial biomass divided by number of days since planting; RGR; $mg \cdot g^{-1} \cdot day^{-1}$). These parameters are indicative of resource use and acquisition, carbon allocation, and overall seedling performance. All seedlings of *G. cuneata* died before traits were measured at the end of the experiment.

2.3.3 Field transplant experiment

To examine seedling survival under field conditions, we conducted a split-plot transplant experiment with ten gardens of paired exclosure and open (control) subplots randomly located at each field site. Transplant locations were chosen to represent closed canopy forest locations for all field sites. A regional study suggests that light transmittance to the understory of these forests are generally around 1–2% annually throughout the Panamanian Isthmus (Brenes-Arguedas et al., 2011). In November 2005, twenty seedlings of each of the four species were transplanted at each of the five sites, resulting in 400 seedlings in total. Within each site we set up ten randomly located gardens and established paired 50 cm x 50 cm subplots, i.e., a control subplot and a treatment subplot. One seedling per species was transplanted into each paired subplot (i.e., two seedlings per garden). Paired subplots were <1 m from each other and gardens were at least 20 m from each other. Exclosure subplots were covered by 1 mm transparent mesh to exclude herbivores, while control subplots were completely open to herbivores. Soil cores were taken adjacent to the experimental subplots at every census to monitor gravimetric soil moisture. Seedlings were monitored on average every 63 days on eight occasions, or 505 days in total. Seedling performance did not differ between the paired control and exclosure subplots and data was pooled prior to analysis by calculating the mean survival rate (%) per species per garden (N = 10 per site).

2.3.4 Data analysis

To examine how soil nutrients affect seedling leaf functional traits, biomass allocation and RGRs in the shadehouse experiment, we conducted two-way ANOVAs to test for differences in mean values among species, soil, and their interaction. We assessed whether model assumptions were met using graphical diagnostics. We used a backward elimination model simplification approach based on Akaike Information Criterion values and reported the statistics from the final (best fit) models. Tukey's post hoc tests were then used to identify significant differences between means at $P = 0.05$, using the R package emmeans (Lenth, 2021).

To examine seedling survival in the field transplant experiment, we used generalized linear mixed effect models using the glmer function in the R package lme4 (Bates et al., 2015). Mean seedling survival rates per garden were fitted using binomial distribution and log link families with species, site, and their interactions as fixed effects and garden as a random effect. To examine species specific survival rates at the end of the field transplant experiment, generalized linear models (GLM) were performed for each species separately followed by Tukey's post hoc tests at $P = 0.05$ to examine differences in the mean survival among sites.

We conducted two separate PCA. The first analysis was performed on the soil nutrient data, to enable us to rank the five sites by overall soil nutrient availability. The second analysis was performed on the seedling trait and RGR data from the shadehouse experiment to examine whole-plant trade-offs among species and soil type. The PCA were conducted using the R package FactoMineR (Lê et al., 2008). The data was centered and standardized to one unit of variance, but not transformed prior to analysis.

2.4 Results

2.4.1 Shadehouse experiment

Leaf functional traits

In the shadehouse experiment, the mean and standard error for SLA across all the seedlings was 306 ± 9.5 $\mathrm{mm}^2\ \mathrm{g}^{-1}$. The best fit model for SLA showed that only species differed significantly ($F_{2,86} = 70.91$, $P < 0.0001$). Across all soil sources, *C. tepejilote* a significantly higher mean SLA (362 ± 7.9 $\mathrm{mm}^2\ \mathrm{g}^{-1}$) than the other species, and *G. congesta* had a significantly higher SLA (276 ± 12.5 $\mathrm{mm}^2\ \mathrm{g}^{-1}$) than *C. pinnatifrons* (187 ± 12.8 $\mathrm{mm}^2\ \mathrm{g}^{-1}$; Figure 2.2A).

The mean LAR across all the seedlings was 138 ± 4.1 $\text{mm}^2\ \text{g}^{-1}$. The best fit model for LAR retained both species ($F_{2,82} = 38.5$, $P < 0.0001$) and soil ($F_{4,82} = 3.99$, $P < 0.01$), but not their interaction. *Chamaedorea pinnatifrons* had a significantly lower mean LAR (86.6 ± 6.35 $\text{mm}^2\ \text{g}^{-1}$) than either *C. tepelijote* (154.0 ± 3.88 $\text{mm}^2\ \text{g}^{-1}$) or *G. congesta* (143.0 ± 6.13 $\text{mm}^2\ \text{g}^{-1}$; Figure 2.2B). In addition, LAR was higher across all species growing in soil from P15 (143 ± 10 $\text{mm}^2\ \text{g}^{-1}$) and CCH (150 ± 9.97 $\text{mm}^2\ \text{g}^{-1}$) than M25 (122 ± 7.62 $\text{mm}^2\ \text{g}^{-1}$), with intermediate values for SH and P9.

The mean light-saturated photosynthesis (A_{sat}) across all seedlings was 2.29 ± 0.115 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthetic rates significantly differed among species ($F_{2,46} = 8.03$, $P < 0.001$) but were unaffected by soil or its interaction with species. Photosynthetic rate was significantly higher for *C. tepejilote* (2.90 ± 0.131 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than *C. pinnatifrons* (1.73 ± 0.131 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), with intermediate rates for *G. congesta* (2.21 ± 0.157 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Figure 2.2C).

The mean R_{dark} for all seedlings was 0.54 ± $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The best fit model for R_{dark} showed a significant difference between species means ($F_{2,42} = 7.19$, $P < 0.01$) with a non-significant soil effect retained in the model ($F_{4,42} = 2.29$, $P = 0.08$). Leaf respiration was significantly greater for *G. congesta* (0.74 ± 0.11 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than for *C. pinnatifrons* (0.34 ± 0.035 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), with intermediate R_{dark} rates for *C. tepejilote* (0.61 ± 0.042 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Figure 2.2D).

Biomass allocation

In the shadehouse experiment, the mean LMR across all seedlings was 0.463 ± 0.009. LMR was significantly influenced by the interaction between species and soil ($F_{8,74} = 2.38$, $P < 0.05$; Figure 2.3A). Among species and soil combinations, LMR was highest for *G. congesta* in soil from P15 (0.58 ± 0.03) and lowest for *C. tepejilote* in soil from M25 (0.33 ± 0.02). We found that LMR for *C. tepejilote* was lower than *C. pinnatifrons* when growing in the M25 site soil ($t = 5.89$, $P < 0.001$). Furthermore, *C. tepejilote* LMR differed among soils, with lower LMR when growing in low nutrient site soils compared to high nutrient soils and had an intermediate LMR in the P9 soil, although LMR in P9 soil was significantly higher than in M25 soil ($t = 5.26$, $P < 0.001$).

The mean SMR across all seedlings was 0.330 ± 0.009. SMR was significantly influenced by the interaction between species and soil ($F_{8,74} = 2.78$, $P < 0.01$; Figure 2.3B). For all soil and species combinations, *C. tepejilote* in soil from M25 had the highest SMR (0.47 ± 0.02) while *G. congesta* in soil from CCH had the lowest SMR

(0.21 ± 0.03). *Chamaedorea tepejilote* had higher SMR compared to the two other species when growing in the M25 site soil. Further*more*, for *C. tepejilote*, SMR was higher when growing in the M25 site soil compared to all other soil sources.

The mean RMR across all seedlings was 0.197 ± 0.005. There was no significant interactive effect between species and soil, but root mass was significantly influenced by the main effects of species ($F_{2,74} = 13.58$, $P < 0.001$) and soil ($F_{4,74} = 7.45$, $P < 0.0001$). RMR of *C. tepejilote* (0.21 ± 0.01) was higher than that of the other two species Figure 2.3C). Across all species, RMR of seedlings growing in soils from SH (0.23 ± 0.01) was higher than for the other four soils Figure 2.3C).

Relative growth rate

In the shadehouse experiment, the mean RGR across all species and soils was 11.5 ± 0.25 $\text{mg}\cdot\text{g}^{-1}$ day^{-1}. There was a significant interaction between soil and species ($F_{8,74} = 3.01$, $P < 0.01$), and significant differences among the species ($F_{2,74} = 9.76$, $P < 0.0001$) and soil ($F_{4,74} = 7.16$, $P < 0.0001$) on RGR. For all soil and species combinations, *C. tepejilote* in soil from P15 had the highest RGR (14.5 ± 0.58 $\text{mg}\cdot\text{g}^{-1}$ day^{-1}) while *G. congesta* in soil from CCH had the lowest RGR (9.41 ± 0.92 $\text{mg}\cdot\text{g}^{-1}$ day^{-1}; Figure 2.4). When growing in the P15 soil, *C. tepelijote* had significantly higher RGR than *G. congesta* ($t = 3.77$, $P = 0.05$). Furthermore, *C. tepejilote* had significantly higher RGR growing in P15 soil, where it naturally occurs, than in lower nutrient soils, whereas RGR in the highest nutrient soil (CCH) was similar to all soils Figure 2.4).

Principal components analysis of traits

For the PCA of the seedling trait data for the shadehouse experiment, the primary ordination axis (PC1) explained 30.8% of the total variation and represented increasing values of LAR and SLA, and more acquisitive leaf traits Figure 2.1B). Species aligned along PC1. The second axis (PC2) explained 27.1% of the total variation and represented a shift from high leaf investment (LMR) to high stem investment (SMR). Soils aligned along PC2. As soil fertility increased (from soils from sites SH and M25 to soils from sites P9, P15, and CCH), there was an increase in seedling LMR and a decrease in SMR.

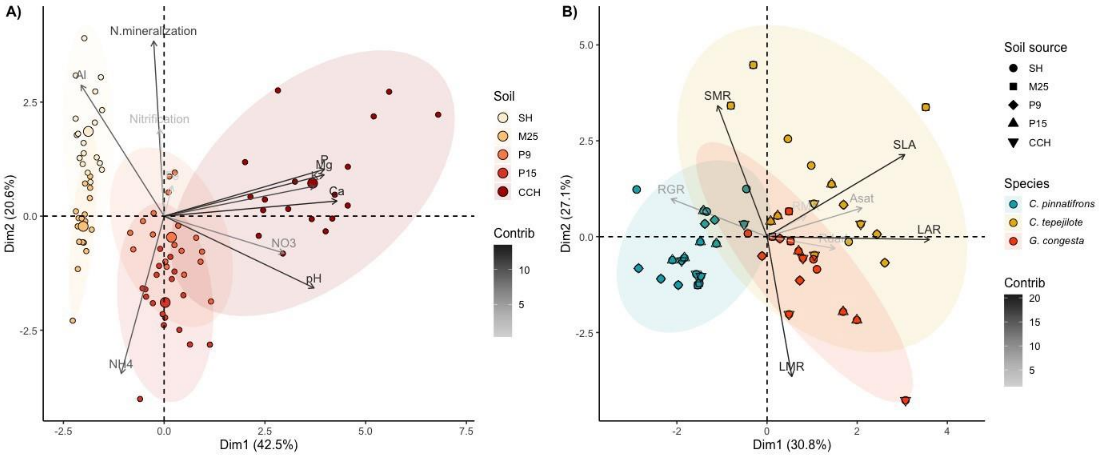

Figure 2.1: **(A)** Principal component analysis of soil data for each of the five sites, SH, M25, P15, P9, and CCH. Each point represents a separate sample (N = 90) and shading represents increasing soil nutrient availability from SH to the CCH site. Contribution of soil properties, Al, Ca, Fe, K, Mg, P, NH_4^+, NO_3^-, N mineralization, Nitrification, and pH, are indicated by arrow shading. Concentration ellipses are displayed for each of the five soils. **(B)** Principal component analysis of seedling trait data for three species at each of the five sites, with each point representing a separate sample (N = 59). Contribution of seedling traits are indicated by arrow shading. Concentration ellipses are displayed for each of the three species. The primary seedling trait ordination axis (PC1) represents a shift from high relative growth rate (RGR) to investment in high leaf quality, specific leaf area (SLA), leaf area ratio (LAR), root mass ratio (RMR), maximum photosynthetic rate (A_{sat}), and dark respiration rates (R_{dark}). The secondary seedling trait ordination axis (PC2) represents a shift from high leaf mass ratio (LMR) to high stem mass ratio (SMR).

2.4.2 Field experiment

Seedling survival

Seedling survival by the end of the field experiment was significantly influenced by the interaction between site and species (χ^2 = 214, df = 12, P < 0.0001). After 505 days, overall survival across all species except *C. tepejilote* was highest at SH (low-nutrient, high-rainfall site; mean ± SE = 57.5 ± 5.23%), and lowest at CCH (high-nutrient, low-rainfall site; 0.0% ± 0.0) where all seedlings of all species died after 120 days during the first dry season Figure 2.5). Among species, survival rates across all sites were highest for *C. tepejilote* (40.2 ± 5.69%) and lowest for *C. pinnatifrons* (26.3 ± 3.71%). For the species that naturally occurs at the P15 site (*C. tepejilote*), survival rates were 80.0 ± 2.83% at that site and did not differ from survival at the P9 or SH sites, but survival at these three sites were higher than that for M25 (45 ± 2.12%; *z*-ratio = 9.89, P < 0.0001) and for CCH (with zero seedlings surviving). For the species that naturally occurs at the SH site (*G. congesta*), survival was higher at its “home-site” (65 ± 2.5%) than at the other four sites, i.e., P15 (*z*-ratio = 2.89, P < 0.05), P9 (*z*-ratio = 11.36, P < 0.0001), M25 (*z*-ratio = 17.68, P < 0.0001), and CCH (*z*-ratio = 25.5, P < 0.0001; Figure 2.5C).

2.5 Discussion

We used seedling experiments to better understand how four understory palm species respond to gradients of soil nutrients and rainfall in lowland tropical forests of Panama. In the shadehouse experiment, leaf functional traits were determined by species, whereas RMR was highest at the lowest nutrient site and with generally biomass allocation and RGR shifting with species-specific responses to soil source. By contrast, in the field transplant experiment seedling mortality was largely determined by dry season water availability rather than soil nutrient availability among the sites. Together, these results suggest that seedling performance is responsive to soil fertility when there is sufficient soil moisture. Thus, by pairing controlled and field experiments, we determined that seedling survival, and hence potentially species distribution, are strongly constrained by dry season water availability, whereas soil nutrient availability shapes subsequent seedling biomass allocation and RGRs.

2.5.1 Species identity is driving leaf functional traits

In contrast to the predictions of our first hypothesis, we did not find that leaf morphological traits such as SLA and LAR, or physiological traits, such as A_{sat} and

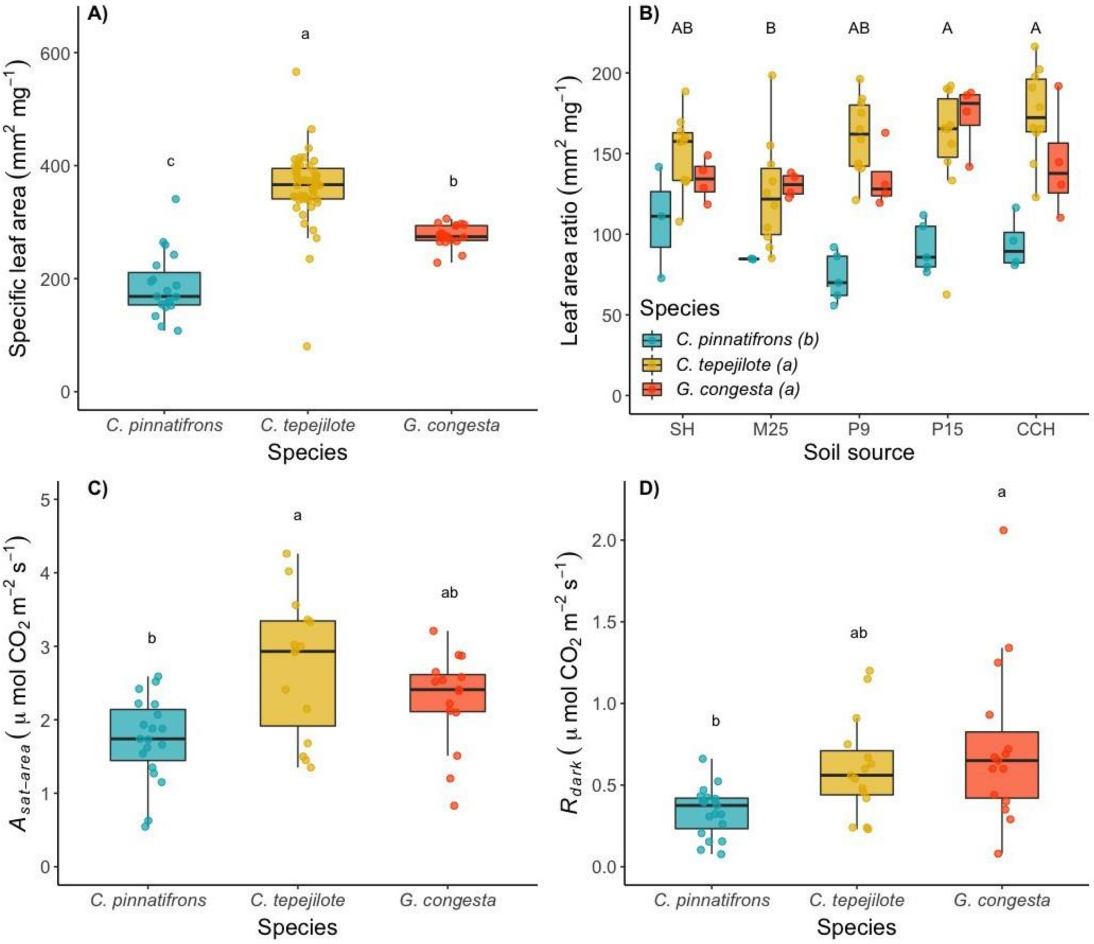

Figure 2.2: **(A**) Specific leaf area (SLA), **(B)** leaf area ratio (LAR), **(C)** photosynthetic rates (A_{sat}), and **(D)** dark respiration rates (R_{dark}), in a greenhouse transplant experiment. Boxplots represent median shown by the solid black horizontal line in the middle of each box and bounds represent 25th and 75th percentiles and individual values. Soil is sourced from five sites across a soil nutrient gradient and sites are ranked and listed in order of increasing overall soil nutrient availability. Different letters above the bars and boxplots indicate statistically significant different means according to Tukey's test ($P < 0.05$), with lower case letters representing species differences and capital letters representing soil differences.

R_{dark}, responded to soil fertility, and these traits were instead mainly determined by species identity. The only trait that differed among soils was LAR which was lower for seedlings growing in one of the low nutrient soils compared to high nutrient soils. In addition, we did not find any differences between generalist and specialist species leaf trait responses to soil fertility. Among the three species, the species associated with the intermediate fertility P15 site (*C. tepejilote*) had the most acquisitive leaf trait strategy whereas the generalist species found throughout the lower montane Fortuna sites in western Panama (*C. pinnatifrons*) had the most conservative leaf trait strategy. Our findings contrast experiments where leaf traits of seedlings grown in contrasting soil types follow the leaf economic strategy with higher SLA and LAR when growing in high resource environments (Baltzer et al., 2005; Dent and Burslem, 2009). Our findings also contrast with a parallel shadehouse experiment of five *Chamaedorea* species across the Fortuna soil gradient, where seedlings of *C. pinnatifrons* had higher photosynthetic rates than *C. tepejilote* and all species showed strong soil-driven shifts in photosynthetic rates (Andersen, 2021). One possible explanation for the discrepancy between these experiments is that soil nitrogen, a key nutrient for photosynthesis, is generally high across the lowland soil gradient (Figure 2.1A, PC2), whereas soil nitrogen partly drives the lower montane soil gradient (Andersen et al., 2010b, 2014). This suggests that soil phosphorus and cations, the main drivers of the lowland soil nutrient gradient, do not strongly influence palm seedling leaf traits. However, evidence from tree species along the lowland Panama Isthmus shows changes in community-level leaf trait measures such as SLA and thickness are driven by variation in both soil phosphorus and moisture (Umaña et al., 2021). Thus, it is possible that understory palm leaf traits are more responsive to variation in soil nitrogen than phosphorus availability, while tree species are more responsive to variation to soil phosphorus among sites.

2.5.2 Biomass allocation responds to soil nutrient availability

Our second hypothesis predicted that RMR for each species would increase as soil fertility declines to meet nutrient demands at the expense of LMR, SMR and overall growth potential. While palms use roots to access water and nutrients, in this shadehouse experiment, nutrient availability varied by soil source while water availability remained constant for all soil and species combinations. This suggests that root mass seems to increase in response to nutrient availability. In line with this we found that RMR was greatest at the least fertile SH site, suggesting that seedlings increased investment in roots to acquire limiting nutrients when grown in the lowest

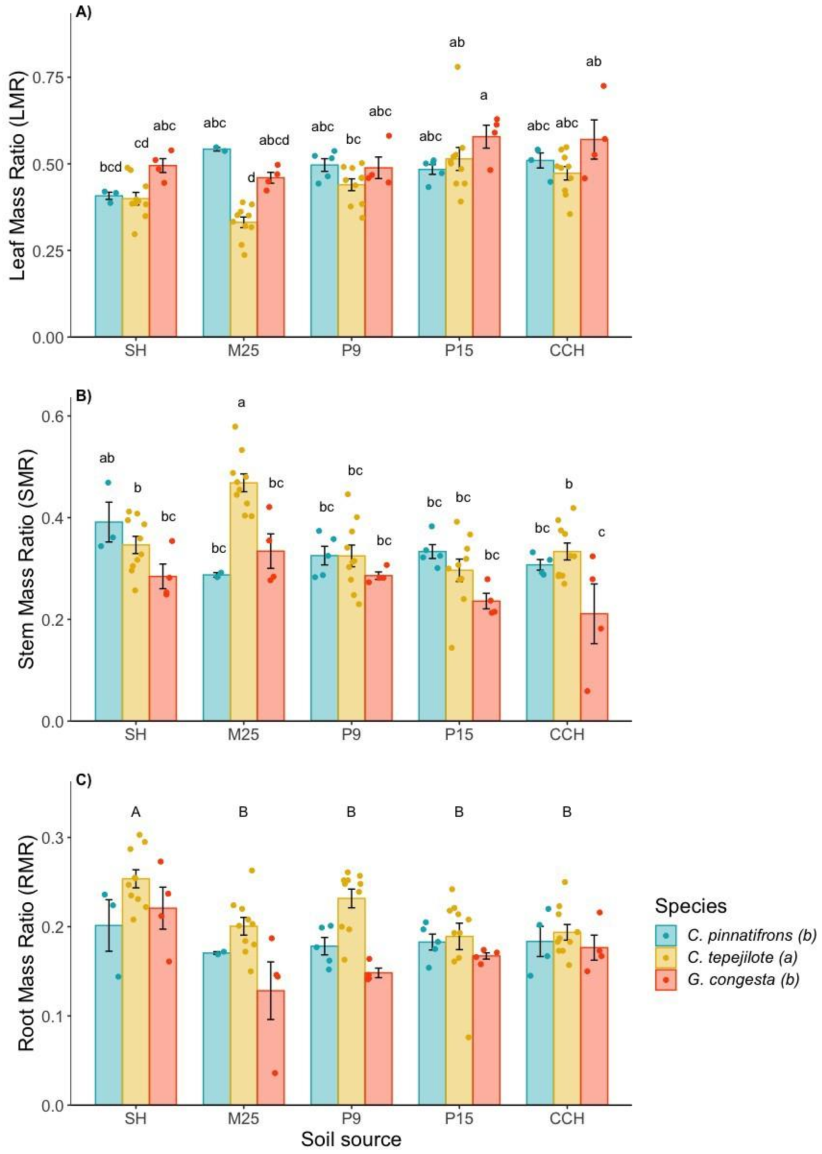

Figure 2.3: Biomass allocation (mean ± SE) of seedlings growing in soil from five sites along a soil nutrient gradient. **(A)** Leaf mass ratio (LMR), **(B)** Stem mass ratio (SMR), and **(C)** Root mass ratio (RMR). Soil is sourced from five sites across a soil nutrient gradient and sites are ranked and listed in order of increasing overall soil nutrition. Different letters above the bars indicate statistically significant different means according to Tukey's test ($P < 0.05$), with lower case letters representing differences among species*soil source combinations and capital letters representing differences among soil sources. The legend represents species fill color for all panels and the letters represent species differences for RMR only. *Represents the interaction between species and soil.

nutrient soil at the expense of allocation to leaf biomass. Both LMR and SMR had interactions between species and soil source. However, LMR generally increased with increasing soil nutrient availability, whereas SMR tended to decrease. This is in line with optimal allocation theory which predicts that allocation to belowground and support tissue increases with decreasing soil nutrient availability (Chapin, 1980; Poorter et al., 2012). In shadehouse experiments in French Guiana and Malaysia, seedlings of tree species showed similar trade-offs between above and belowground allocation with soil nutrient availability (Baraloto et al., 2005; Dent and Burslem, 2009). In palm seedling field experiments in Fortuna, RMR did not respond to nitrogen addition (Andersen et al., 2010a) but did increase as soil nutrient availability decreased (Andersen et al., 2014), suggesting that RMR and biomass allocation trade-offs for palm seedlings are driven by rock-derived nutrients such as soil P and cations. Furthermore, in the Fortuna transplant experiment, seedlings of species associated with the lowest nutrient site showed biomass allocation patterns that would promote growth compared to species not occurring at that site. However, here we found that despite the influence of soil source on biomass allocation, there was no indication that species were able to optimize their biomass allocation to promote growth in the soils they were associated with compared to species not occurring in that soil type.

Home site advantage for relative growth rate

Our third hypothesis predicted that specialist species growing in the soil they are associated with should have a higher RGR compared to species not occurring in those soils. We found that *C. tepejilote* had higher RGR when growing in the soil for which it is associated with compared to the low nutrient specialist species (*G. congesta*) but not the Fortuna generalist species *C. pinnatifrons*. Furthermore, *C. tepejilote* had higher RGR at higher nutrient soils compared to lower nutrient soils, suggesting that *C. tepejilote* may have adaptations that enhances growth and performance in higher fertility soils. Similarly, in a seedling transplant experiment in Fortuna, *C. tepejilote* was one of the species associated with the intermediate soil nutrient site Palo Seco and also had a growth advantage at home (Andersen et al., 2014), further supporting the hypothesis that this species is able to maximize its growth in soils where it occurs naturally. However, the mechanism for the enhanced growth performance of *C. tepejilote* in intermediate nutrient soils in lowland shadehouse experiment remains unclear as we did not observe greater resource use efficiency or optimal biomass allocation of this species compared to others. Our findings corroborate an Amazonian transplant study, where growth rates of habitat specialists were often but not always highest when growing in the soil they are associated with (Fortunel et al., 2016).

In contrast to *C. tepejilote*, the low-nutrient specialist, *G. congesta*, did not differ in RGR compared to other species when growing in the soil it is associated with. This contrasts with the general trends from the Fortuna transplant experiment, where species associated with low nutrient soils had strong growth advantages when grown at home (Andersen et al., 2014). Furthermore, *G. congesta* did not show significant differences in RGRs across the soil nutrient gradient, suggesting that *G. congesta* has a highly constrained and low RGR that may help it survive in low nutrient soils but may be outcompeted at higher nutrient sites as it had significantly lower RGR than *C. tepejilote* in the P15 soil. Alternatively, RGR of *G. congesta* may also be driven by other factors such as light and soil moisture, which may vary among sites in the field, but which were kept constant in the shadehouse experiment.

Soil and rainfall gradients influence seedling survival

Our fourth hypothesis predicted that specialist species will have higher seedling survival rates at sites where they occur naturally compared to other species and compared to their survival at sites where they do not occur. In line with this, we found that the low nutrient specialist, *G. congesta*, had higher seedling survival rates growing at its home site compared to the other sites. However, *C. tepejilote* tended to have higher survival compared to other species regardless of lowland site. Nonetheless, for the site specialist *C. tepejilote*, survival rates were highest at its home site P15, and at sites P9 and SH, all of which have a lower dry season moisture deficit compared to the other sites. We also found that seedling survival for all species was high at the low nutrient site SH which has the highest annual rainfall (2,848 mm) and the highest soil water content during the wet season (89.7 ± 2.3 mm) and dry season (70.8 ± 3.0). Across all species, seedling survival rates were lowest at lowland site CCH which has the highest nutrient soil and dry season water deficit (571 mm). In the Fortuna seedling transplant experiment in lower montane forests, species showed strong home-site advantages in survival at low and high nutrient sites, but not intermediate nutrient sites (Andersen et al., 2014). However, the mechanisms driving home site survival advantages in the Fortuna lower montane experiment and this lowland experiment are expected to differ due to differences in MAP and seasonality. The lower montane soil gradient has a rainfall gradient of 4–10 m MAP with no substantial dry season compared to the 1.5–3 m MAP gradient and strong 4-month dry season at sites in this lowland experiment (Andersen et al., 2014). Furthermore, the lower montane experiment found that survival was mediated by herbivores, whereas protection from

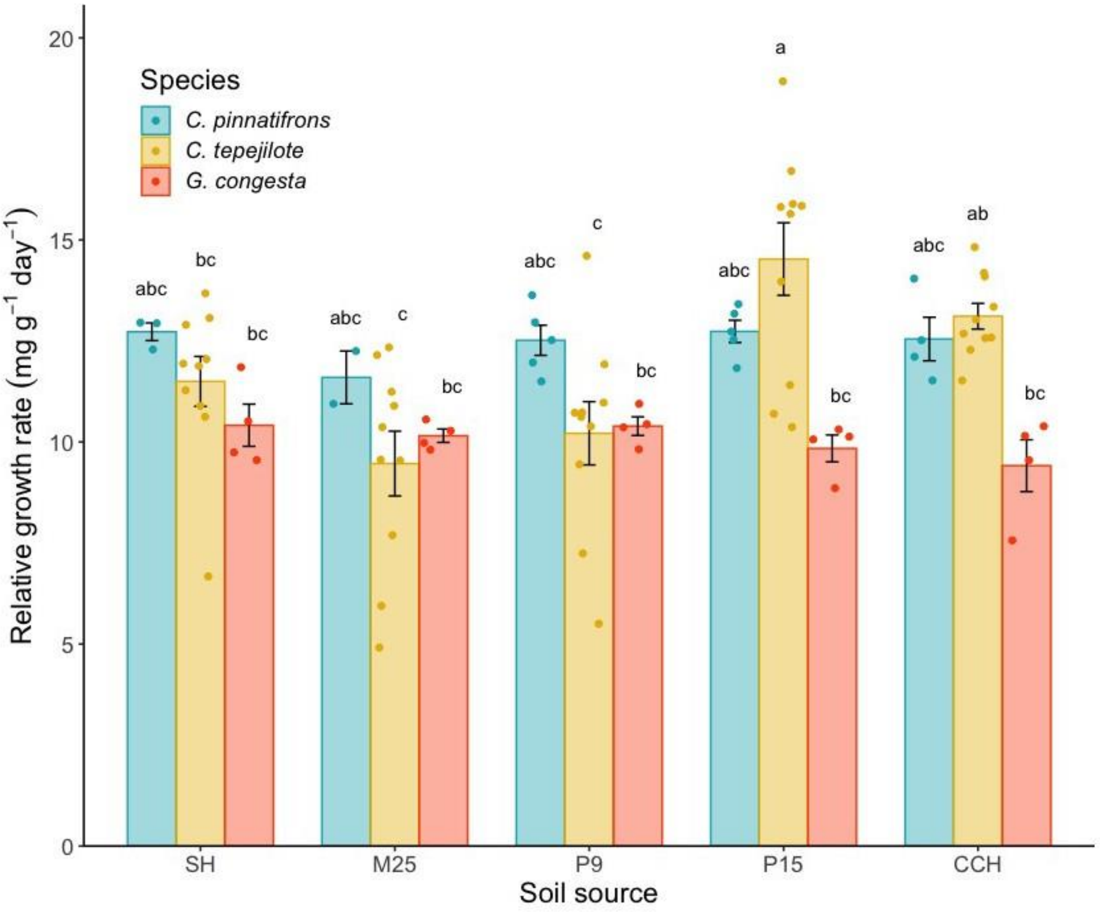

Figure 2.4: Relative growth rate (RGR; mean ± SE) of seedlings growing in soil from five sites along a soil nutrient gradient. Soil sources are ranked and listed in order of increasing overall soil fertility. Bars are shaded by species. The statistical analysis compares species within sites and between sites. We conducted two-way ANOVAs to test for differences in mean values among species, soil, and their interaction. Different letters above the bars indicate statistically significant differences among means according to Tukey's test ($P < 0.05$).

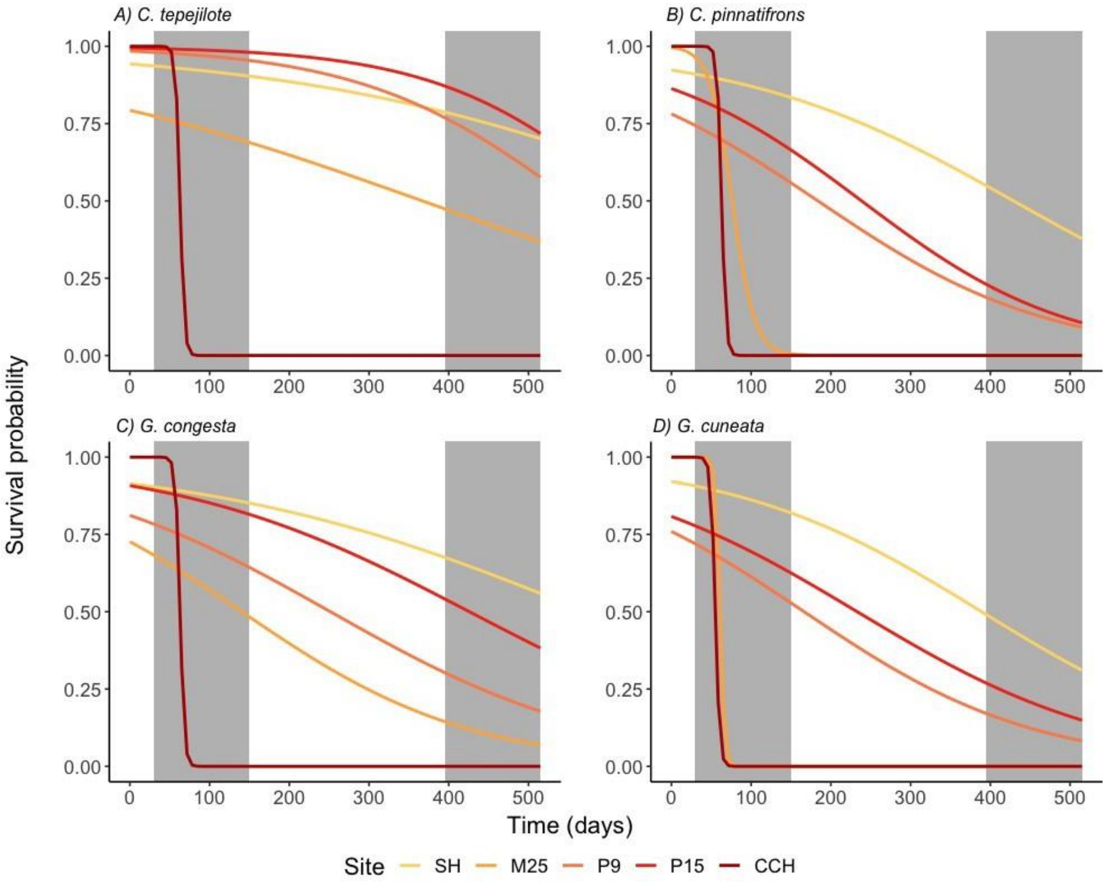

Figure 2.5: Field transplant experiment of seedling survival of four understory palm species, **(A)** *Chamaedorea tepejilote*, **(B)** *C. pinnatifrons*, **(C)** *Geonoma congesta*, and **(D)** *G. cuneata*. Seedlings of each species were grown at each of five sites that differed in soil fertility. Percent survival is based on the species mean per garden per site. Curves for each species are the outputs from generalized linear models (Survival rates ∼ Site). Shading of the curve increases intensity with soil nutrient availability from SH to CCH. Gray shaded boxes represent dry seasons in year 1 and 2 of the field experiment.

herbivores had no effect on survival in the lowland experiment. Similarly, our findings corroborate a transplant study where home-site survival advantages across lowland tropical forests in Amazonia were related to moisture and soil gradients, but not herbivory for seedlings of habitat specialist tree species (Fortunel et al., 2016).

Although the focus of this study was on belowground environmental variation, light availability can also influence seedling survival (Cintra and Horna, 1997; Record et al., 2016). Field transplant locations were chosen to represent closed canopy forest locations across all field sites. We do not have field light data, but a regional study suggests that light transmittance at the understory layer in these forests is generally around 1–2% annually throughout the Panamanian Isthmus (Brenes-Arguedas et al., 2011), and this is in line with previous measurements at two of our study sites, i.e., P9 (Gaviria et al., 2017) and SH (Brenes-Arguedas et al., 2011). Together, our results suggest that the main driver of seedling survival is dry season water availability, thus drought tolerance or avoidance may be important mechanisms, especially with more frequent droughts associated with extreme El Niño events, that determine species distributions along the Panama Canal Isthmus (Engelbrecht et al., 2007; Browne et al., 2021).

2.6 Conclusion

In this study, we found that although soil nutrient availability was an important driver of seedling biomass allocation and RGR in a controlled shadehouse setting, dry season water availability determines seedling survival in the field. This work demonstrates the necessity of transplant experiments to disentangle resource-based and climatic factors in understanding species pre-adaptions and response to environmental change. If lowland tropical forests in Panama are driven by soil nutrient and rainfall gradients, then changes in soil fertility due to nitrogen deposition (Hietz et al., 2011) and soil moisture availability caused by climate change have the potential to alter species distributions and forest dynamics (Engelbrecht et al., 2007). Conservation and restoration efforts of forests across the isthmus of Panama will need to consider the responses of individual species to such changes. Here, we observed the effects of limiting resources on four palm species. These understory species act as filters that affect seedling growth and survival in forest (Farris-Lopez et al., 2004; Wang and Augspurger, 2004). Therefore, factors that affect the growth and distribution of these palm species will indirectly impact tree seedling recruitment and forest regeneration. Further research on additional species is needed to obtain a more comprehensive view of forest dynamics in relation to spatial variation in the landscape of soil nutrient availability and rainfall patterns.

Chapter 3

Comparative analysis of floristic composition, leaf traits, and soil dynamics in coexisting peat and kerangas forest ecosystems

3.1 Abstract

Tropical peatlands are important global carbon sequestration sinks, and they differ greatly from other tropical forest ecosystems in terms of environmental conditions and ecological functions. Our study investigated the floristic and belowground differences between adjacent paired patches of intact tropical waterlogged peat forests and kerangas (free-draining heath) forests in Brunei Darussalam. We hypothesized higher total nutrients in peat soils due to organic matter, but higher available nutrients in kerangas due to impaired peat mineralization. We also predicted greater tree diversity, larger trees, more taxa with nitrogen-fixing and ectomycorrhizal associations, and more conservative leaf traits with higher nutrient resorption in peat forests. For each of these forest patches we examined total and labile nutrient concentrations in soils, forest tree stand diversity and structural characteristics, functional traits of live leaves and leaf litter, and nutrient resorption by leaves during senescence. We found 28 times as much total nitrogen in peat compared to kerangas-sand, while dissolved nitrogen was 4 times higher in kerangas-humus than in peat, suggesting that anoxic conditions in peat soils may impair nutrient mineralization into available forms but do not result in nutrient capital loss. Despite this, tree diversity and structural characteristics,

including tree abundance and stand basal area, did not differ between the forest types. However, stem density of Dipterocarpaceae which has an ectomycorrhizal strategy, was 2.7 times higher in kerangas than in peat, while Sapotaceae and Clusiaceae, which both have arbuscular mycorrhizal strategies, were respectively 3.2 and 4.0 times higher in peat than in kerangas. Leaf and litter functional traits and nutrient resorption processes were invariant across the two forest types, reflecting low plasticity in leaf characteristics, which suggests consistent nutrient use strategies despite large differences in local environmental conditions and belowground carbon storage. This suggests that belowground carbon accumulation in peatlands is largely disconnected from plant community characteristics and is likely instead driven by other processes operating in the belowground environment. These findings emphasize the need for further research on the drivers of carbon storage in tropical peatlands relative to other adjacent forest types, to better understand their ecological functioning.

3.2 Introduction

Tropical peatlands are forested ecosystems that are amongst the worlds' most carbon dense terrestrial ecosystems (Page and Baird, 2016). Peat in these ecosystems is derived from woody plant material, which makes them distinct from temperate peatlands that are derived from Sphagnum moss. Tropical peatlands are characterized by waterlogged conditions that slow the decomposition of wood, leaf and root litter, leading to the accumulation of organic material over thousands of years, and which eventually form carbon-rich deposits up to 20 meters thick (Anderson, 1983). An estimated 105 Gt of organic carbon, equivalent to 30% of the carbon that is held in tropical rainforests globally (Page et al., 2022), is stored in tropical peatlands, even though tropical peatlands only occupy around 0.25% of the global land surface area (Page et al., 2011). Tropical peatlands are therefore substantive long-term stores of carbon that play an important role in the global carbon cycle (Ribeiro et al., 2021). However, in Southeast Asia, which hosts about half of the world's tropical peatlands, there has been extensive deforestation, drainage, and fires in tropical peatlands over the past 30 years, meaning that less than 30% of the region's original peat forest still remains. These changes are changing these ecosystems from carbon sinks to greenhouse gas emitters (Murdiyarso et al., 2010; Hooijer et al., 2012; Mishra et al., 2021).

Despite the pivotal role of tropical peat forests in carbon sequestration, the biological implications arising from peat accumulation and the near-continual waterlogging of peatland soils for community and ecosystem properties in these forests are not well understood either aboveground or belowground. However, in peat forest in Malaysia it was shown that plants growing in waterlogged sites demonstrate an increased presence of stilt roots, pneumatophores, and knee roots, along with thicker roots, than do the same species in drier sites (Pahang Forestry Department, 2005). In southern Thailand, waterlogged peat forests were found to have a diverse microbial community capable of versatile metabolic processes (Kanokratana et al., 2011). In Indonesia, near-intact peat swamps had a significantly greater microbial biomass than did degraded and drained peatland, with water drainage profoundly impacting CO_2 flux rates (Jauhiainen et al., 2008; Könönen et al., 2018). However, our understanding of how tropical peat forest's function, particularly in comparison to other free draining tropical forests in the same region, is limited (Miyamoto et al., 2016). The shortage of comparative studies between peat and adjacent non-peat forests hinders our ability to understand the dynamics and functioning of tropical peat ecosystems within a broader ecological context.

Brunei features extensive areas of both intact and semi-pristine forests, which unlike the forests elsewhere in Southeast Asia, have not been heavily cleared or degraded. The forested areas consist of a mosaic of forest types, including both peatlands and 'kerangas' forests, the latter being a term from the local Iban language for the free-draining heath forests in Borneo with sand-based soils that are too infertile for rice cultivation (Brunig, 1974). Brunei's peatlands cover about 17% (1,015 km^2) of the country's landmass (Wong et al., 2015), and its largest peat swamp forest, the Badas Peat Dome, stores approximately 1,535 tonnes (t) of carbon per hectare (Cobb et al., 2017). Brunei peat forests are established on waterlogged accumulated organic matter that frequently range in thickness from 8 m to 15 m (Kobayashi et al., 2016). In contrast, kerangas forests are established on free-draining white-sand soils, overlaid with a layer of humus that is up to 0.7 m thick (Brunig, 1974; Katagiri et al., 1991; MacKinnon et al., 2013; Din et al., 2015). The vegetation within each of these two forest types has evolved distinct adaptations to cope with their specific environments. Many trees in peatlands are tall growing and grow buttresses for stability as well as knee roots and pneumatophores for gaseous exchange in waterlogged conditions (Yule, 2010). Many trees in kerangas forest are typically shorter, unbuttressed, and exhibit sclerophylly, which is characterized by small, thick leaves with low nitrogen content, as an adaptation to the water stress and nutrient-poor conditions (Whitmore, 1984; Becker et al., 1999; Turner et al., 2000). While these individual adaptations are recognized, a more comprehensive understanding of the ecological differences between peat and kerangas forest is lacking, and we therefore know little about the functional contrasts between these two forest types.

In this study system, we set up a paired plot experiment to assess above ground and below ground properties in adjacent patches of peat and keragans forest. The main aim of our research was to unravel how the contrasting environmental conditions of peat and kerangas influence their floristic composition, leaf traits, and soil nutrient characteristics. We tested the following hypotheses to accomplish this aim:

> (H1) Total nutrients will be higher in peat soil compared to kerangas soil because the former has more organic matter. However, available nutrients will be higher in kerangas due impaired mineralization in the anoxic environment of the peat.
>
> (H2) The nutrient poor conditions and additional adaptations needed for plants to survive in the waterlogged environment of peat forest will promote a greater diversity of trees (as a result of greater coexistence through reduced competition; Grime, 1979), a higher frequency of trees with a larger diameter (which will be better anchored and more stable in deep peat), and more taxa with nutrient strategies needed to cope with lower levels of available nutrients (such as nitrogen fixing and ectomycorrhizal associations), when compared to kerangas forest.
>
> (H3) Due to differences in nutrient availability, leaf economic traits and nutrient resorption will differ between peat and kerangas plots. Specifically, plants from peat plots will demonstrate more conservative economic traits and higher resorption since they are in a more nutrient limited environment.

We address these hypotheses by measuring the soil and floristic characteristics in peat and kerangas forest. By testing them in combination, we aim to better understand how local-scale variation among coexisting forest types that differ fundamentally in the degree of waterlogging impacts both aboveground and belowground components in tropical forests.

3.3 Methods

3.3.1 Study system, plots and soil sampling

The plots were established in the Badas and Labi Hills Forest Reserves, Belait District, Brunei Darussalam, Northwest Borneo. These forest reserves provide an ideal system for direct comparison of two forest types (peat and kerangas) as they consist of a mosaic of both ecosystem types. While there are areas of the Badas Forest Reserve that have been severely disturbed by anthropogenic drainage and fire, our study included areas that have been subjected to minimal human disturbance. We established nine pairs of plots, each pair consisting of a plot in kerangas forest and one in peat forest, providing a total of 18 plots. Within a pair, the typical distance between peat and kerangas plots was 100 m, while the distance between each pair and the next nearest pair was always at least 300 m. A total of 12 (i.e., six pairs) plots were established in the Badas Forest Reserve while six plots (i.e., three pairs) were established in the Labi Forest Reserve (Figure 3.1). Forest patches were selected based on advice from Brunei Forestry Department. Soil cores were taken to ensure that peat plots have waterlogged peat soil and kerangas plots have a top humus layer and bottom sand layer. We marked the centre of each plot with a center pole, and using a range finder, we flagged trees of at least five cm diameter at breast height (DBH) within 11.3 m from the center pole to set up a 400 m^2 circular plot, and trees of at least one cm diameter at breast height (DBH) within 5.65 meters from the center pole to set up a 100 m^2 circular subplot. Plots were set up between 18 and 30 September 2022, and all measurements and sampling were performed over the following three months.

Within each peat plot one composite soil sample was collected to 15 cm depth. Within each kerangas plot two composite soil samples were collected; the first was collected to the depth of the humus layer (the typical depth was six cm) and the second was collected in the sand layer from immediately below the humus layer to 15 cm deeper. For all plots, composite samples were collected by selecting eight points (two in each quadrant of the plot) and sampling soil at each point. All eight soil samples within each plot were bulked and homogenised manually by thorough mixing in a sealed plastic bag forming a composite. Peat samples and the sand samples from the kerangas were sampled using a Russian peat corer while the humus from the kerangas was collected as cubes of 715 cm^3 at each point using a hand spade. All samples were packaged in the field in double zip-loc bags and kept cool until analyses were performed. At the University of Brunei Darussalam (UBD), samples were weighed to measure wet weight, oven dried at 60°C for three days, then weighed again to record dry weight. Bulk density was determined using the oven dry weights and known volume of each sample. Potassium chloride (KCl) extraction (Øien and Selmer-Olsen, 1980; Gianello and Bremner, 1986) was performed on fresh subsamples of each composite sample (10 g with 50 ml 1M solution KCl) for subsequent analysis of mineral nutrients. All samples were sent by courier to Singapore for nutrient analysis.

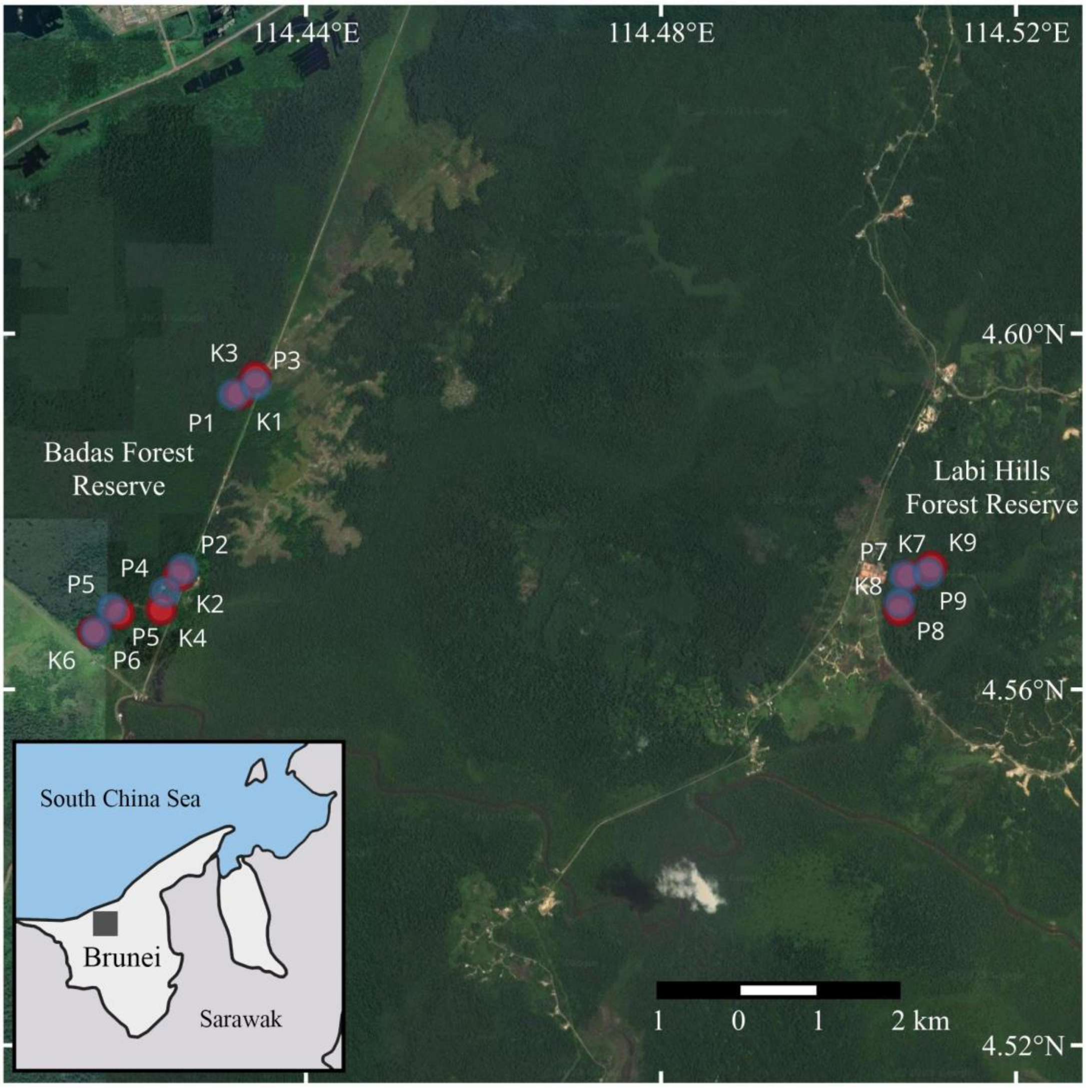

Figure 3.1: Location of the study sites in the Badas and Labi Hills Forest Reserves, Belait District, Brunei Darussalam. Eighteen 400 m^2 plots were established, i.e., nine pairs with each pair consisting of a plot in intact peat forest (blue circles with the letter P) and a plot in kerangas forest (red circles with the letter K). Pairs are indicated by the same number. The location of the forest reserves within Brunei Darussalam are shown in the inset.

3.3.2 Soil properties

A subsample of each plot's fresh soil composite was measured for available nutrients. KCl extractions were used to measure nitrate (NO_3^-) and ammonium (NH_4^+) using a SEAL AutoAnalyzer (SEAL Analytical, USA, model AA500). Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in the KCl extracts using a Total Organic Carbon analyzer (Shimadzu Scientific Instruments, Japan, model TOC-LCPH).

An oven-dried subsample of each soil composite was measured for total nutrients. Total N and total C concentrations were measured using the Dumas method determined by CHNS elemental analyzer (Elementar, Germany, model Vario El Cube). Total P was determined using the molybdenum blue method with ascorbic acid (Murphy and Riley, 1962). This involved sample ignition (550°C for 1 h) and extraction in 1 M H_2SO_4 (1:50 soil/solution ratio, 16 h), with PO_4 detection by automated molybdate colorimetry using a Tecan Spark Multimode Microplate Reader (Tecan Group, Switzerland). Soil C to N, C to P, and N to P ratios were determined from these values.

3.3.3 Floristic variables

For each plot, the diameter at breast height (DBH) of each stem with a DBH greater than five cm was measured and identified to at least the family level. For each subplot, each stem with a DBH greater than one cm was measured and identified to at least the family level. The stem diameter and frequency data were used to determine tree abundance and stand basal area, as well as the Shannon-Weiner diversity index (family level), Simpson's diversity index (family level) and total family richness. Further, for each subplot, the percentage of ground cover of all plants occupying space on the forest floor were visually estimated and identified to at least the family level.

We conducted trait analyses at the family level, as species-level characterization was not feasible due to the substantive biodiversity in these tropical forests. For each plot, a list was compiled to identify families that occur in all peat and kerangas plots. From this, five tree families and three ground cover plant families were selected. For each family in each plot, we sampled among all the plant individuals present to collect an average of 12 fully expanded live leaves and collected at least eight recently senesced dead leaves from the top of the litter layer. Photographs were captured of each live leaf with a ruler as a scale, and the area of that leaf was calculated using the image analysis software ImageJ (Schneider et al., 2012). For each family in each plot, leaf samples were weighed while fresh to determine the mean wet weight per live leaf and per dead leaf. Leaf samples were then oven dried at 60°C for three days and then weighed to determine the mean oven-dry weight per live leaf and per dead leaf for each family in each plot. Using these values, for each family in each plot leaf mass area (LMA) was calculated as LMA = dry weight/leaf area and leaf dry matter content (LDMC) was calculated as LDMC = (wet weight – dry weight)/dry weight.

For each family in each plot, the total N and total C concentrations of both the live and senesced leaves were measured as described above for total nutrients in the soils. Although we measured total P in the same way as for soils, we performed extraction in 1 M HNO_3 instead of H_2SO_4. Foliar and litter C to N, C to P, and N to P ratios were determined from these values. Percent resorption for both foliar and litter N and P was calculated as:

$$\text{percent resorption} = 100 \text{ X } ((CL-CD)/CL),$$

where CL is the concentration of N or P in live leaves and CD is the concentration of N of P in dead leaves.

3.3.4 Data analysis

All soil variables were analysed using one-way ANOVA with plot-pairs as replicate blocks (nine blocks in total) to test for differences between peat soil, kerangas sandy soil, and kerangas-humus. When significant differences were found at $P = 0.05$, Tukey's post hoc test was conducted for pairwise comparisons. Data were log-transformed if needed, based on assessments of normality (using visual inspection of Q-Q plots or Shapiro- Wilk tests) and homoscedasticity (using Levene's test), to conform to the assumptions of normality and homoscedasticity for ANOVA and t-tests. Further, differences in soil variables between peat soil, kerangas-humus, and kerangas-sand were assessed using principal component analysis (PCA).

All forest structure and diversity variables were analysed using paired t-tests with each plot pair as a replicate block to test for differences between peat and kerangas forest; data were transformed if needed to conform to t-test assumptions. Further, overall differences between peat and kerangas plots in community composition of the nine tree families occurring most frequently across all plots were analysed using PCA. We also conducted non-metric multidimensional scaling (NMDS) analysis to explore the dissimilarity patterns in our plots based on the tree abundances of 28 families. A Bray-Curtis dissimilarity matrix was calculated to quantify the dissimilarity between samples and the stress value was calculated to evaluate the goodness-of-fit of the

NMDS solution. PERMANOVA was then carried out to test the significance of difference between the peat and kerangas plots in the NMDS plot. The PERMANOVA analysis was conducted with the dissimilarity matrix as the response variable and the forest type as the predictor variable. Distance-based redundancy analysis (db-RDA) with Hellinger transformation was used to further investigate species composition differences between peat and kerangas forests.

To test how habitat type and family affected foliar and litter traits, we used linear mixed models (LMM) with habitat type, family, and their interaction as fixed factors. Plot nested within block was included as a random factor, with N = 18 plots and N = 9 blocks to control for non-independence of the five observations within each plot, as well as the non-independence of observations within each block of paired plots. Statistical analyses were performed in “R” (R Core Team, 2021) using the lme4 package for mixed models (Bates and Maechler, 2009), FactoMineR package for PCAs (Lê et al., 2008), vegan package for NMDS (Oksanen et al., 2020), and emmeans package for mean comparison (Lenth et al., 2022).

3.4 Results

3.4.1 Differences in soil variables

Soil variables differed significantly among the three soil types (Table 3.1). Peat had the highest concentrations of total C, total N, and total P, and the highest C:P ratio. Meanwhile, kerangas-humus had the highest N:P ratio and highest concentrations of NH_4^+, TN, and TOC and kerangas-sand had the highest bulk density. Together, the first two axes of the PCA accounted for 80.6% of the total variation in soil nutrients (Figure 3.2). The primary ordination axis (PC1) explained 58.1% of the variation and represented increasing values of total N, TOC, and total C concentrations while the secondary ordination axis (PC2) accounted for 22.5% of the variation and represented a gradient of increasing NH_4^+, total mineral N, and total P. Kerangas-humus and peat soils were separated along PC2. Kerangas-humus is represented by a large cluster and is associated with higher TOC, total mineral N and NH_4^+. Peat is represented by a slightly smaller cluster and is associated with higher total N, total C, and total P. Kerangas-sand is represented by a small cluster and is well-separated from the other two soil types along PC1.

Table 3.1: Soil characteristics of nine peatland and nine kerangas sites in Belait District, Brunei Darussalam. Values given are for the top 15 cm of peat in the peat sites, humus layer to full depth at the kerangas sites ("Kerangas- Humus"), and top 15 cm of underlying sand at the kerangas sites ("Kerangas- Sand"). Nutrient availability was quantified once entering the peak wet season. Data in the table derived from pooled soil samples. Values are means ± SE (N = 9). Different superscript letters and values in boldface indicate significantly different means at *P* < 0.05 (Tukey's post hoc test).

Soil Variables	**Peat**	**Kerangas-humus**	**Kerangas-sand**	**$F_{2,23}$ (*P*)**
C (%)	**54.86 ± 1.14^a**	**40.85 ± 2.09^a**	**2.24 ± 0.33^b**	**329.7 (<0.001)**
N (%)	**1.42 ± 0.08^a**	**1.28 ± 0.04^a**	**0.05 ± 0.01^b**	**887.7 (<0.001)**
P (%)	**0.129 ± 0.009^a**	**0.113 ± 0.015^a**	**0.014± 0.001^b**	**135.3 (<0.001)**
C:N	39.64 ± 2.64	32.07 ± 1.50	41.81 ± 3.80	3.0 (0.072)
C:P	**445.4 ± 33.9^a**	**404.7 ± 43.9^a**	**159.9 ± 21.1^b**	**25.4 (<0.001)**
N:P	**11.30 ± 0.69^a**	**12.87 ± 1.58^a**	**3.73 ± 0.25^b**	**59.7 (<0.001)**
NH_4^+(mg/L)	**2.35 ± 0.52^b**	**12.51 ± 1.08^a**	**1.46 ± 0.18^b**	**56.5 (<0.001)**
NO_3^- (mg/L)	0.36 ± 0.10	0.13 ± 0.10	0.19 ± 0.11	1.2 (0.310)
TN (ppm)	**6.74 ± 1.27^b**	**23.73 ± 2.11^a**	**3.86 ± 0.34^b**	**53.8 (<0.001)**
TOC (ppm)	**25.92 ± 3.27^b**	**36.15 ± 2.77^a**	**14.24 ± 1.45^c**	**19.7 (<0.001)**
Bulk density (g/cm^3)	**0.096 ± 0.015^b**	**0.063 ± 0.018^b**	**0.918 ± 0.049^a**	**55.5 (<0.001)**

Notes: Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in KCl extracts.

3.4.2 Variation in forest structure and diversity

None of the forest structural characteristics (tree abundance, stand basal area and ground cover) and none of the measures of diversity (family, Simpson, Shannon) differed between peat and kerangas (Table 3.2).

3.4.3 Differences in community composition

Significant differences between peat and kerangas were found for three of the 14 families when tree abundance was considered, and one of the 14 families when tree basal area was considered (Table 3.3). Specifically, stem density of Dipterocarpaceae which has an ectomycorrhizal strategy, was 2.7 times higher in kerangas than in peat, while Sapotaceae and Clusiaceae, which both have arbuscular mycorrhizal strategies, were respectively 3.2 and 4.0 times higher in peat than in kerangas. Stand basal area of Myrtaceae which have both arbuscular and ectomycorrhizal strategies was 3.0 times higher in kerangas than peat.

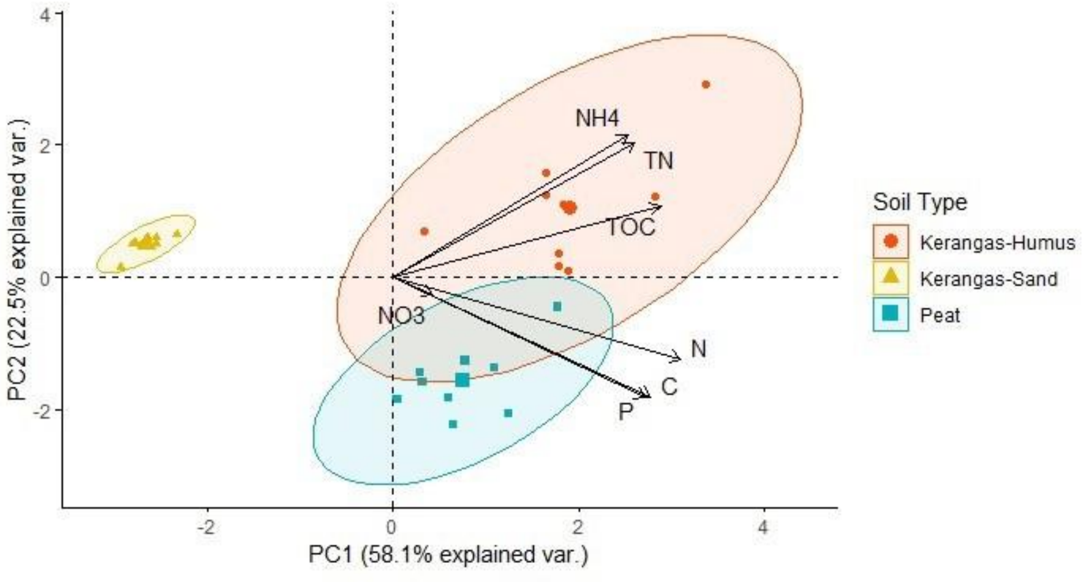

Figure 3.2: Principal component analysis of concentration of total and available nutrients in peat and kerangas plots in the Badas and Labi Forest Reserves, Brunei Darussalam Darussalam. Kerangas soils are composed of a top humus layer and bottom sand layer. Small symbols represent individual plots while large open symbols represent overall means. Ellipses represent the 95% confidence region for each soil type. N, C, and P are total nitrogen, total carbon, and total phosphorus concentrations respectively. NH_4^+ is ammonium while NO_3^- is nitrate. Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in KCl extracts.

Table 3.2: Forest structure and diversity of nine peat and nine kerangas paired plots in Badas and Labi Forest Reserves, Brunei Darussalam Darussalam. Means were not significantly different between habitats at ($P < 0.05$) according to paired t-tests (N = 9).

Forest Characteristics	**Peat**	**Kerangas**	**t (*P*)**
Structure			
Tree abundance (number/ha)	3,450 ± 350	3,175 ± 175	0.7 (0.498)
Stand basal area (m^2/ha)	2,606 ± 427	2,148 ± 328	1.0 (0.367)
Total ground cover (%)	51.1 ± 5.9	37.8 ± 5.7	2.2 (0.063)
Diversity			
Family richness (Families/400 m^2)	22.0 ± 1.5	19.0 ± 1.4	1.5 (0.173)
Shannon's Index	1.14 ± 0.04	1.08 ± 0.04	0.8 (0.435)
Simpson's Index	0.90 ± 0.02	0.89 ± 0.01	0.5 (0.634)

Notes: Shannon’s and Simpson’s indices were computed using plant families.

Table 3.3: Family nutrient strategies, tree abundance (number/ha), and stand basal area (m^2/ha) in peat and kerangas paired plots in Badas and Labi Forest Reserves, Brunei Darussalam. Means are shown ± SE. Values in boldface indicate statistically significantly different means at ($P < 0.05$) determined by paired t-tests (N = 9).

		Tree Abundance (number/ha)			Stand basal area (m^2/ha)		
Family	Nutrient strategies	Peat	Kerangas	t(*P*)	Peat	Kerangas	t(*P*)
<u>All Plots</u>							
Euphorbiaceae	AMF	150.0 ± 31.2	247.2 ± 83.5	1.1 (0.288)	1.3 ± 0.4	8.7 ± 4.3	1.7 (0.125)
Fabaceae	N-fixing, AMF	225.0 ± 85.6	183.3 ± 23.6	0.5 (0.607)	27.7 ± 19.1	6.8 ± 2.5	1.1 (0.300)
Lauraceae	AMF	100.0 ± 22.4	116.7 ± 23.6	0.4 (0.703)	0.6 ± 0.3	1.4 ± 0.4	1.4 (0.191)
Dipterocarpaceae	ECM	**163.89 ± 56.1**	**450.0 ± 98.6**	**3.1 (0.015)**	109.3 ± 31.2	88.2 ± 41	0.4 (0.679)
Myrtaceae	AMF, ECM	388.9 ± 108.3	475 ± 94.9	1.4 (0.200)	**18.5 ± 12.5**	**55.4 ± 15.2**	**2.4 (0.045)**
Rubiaceae	AMF	91.7 ± 13.2	83.3 ± 16.7	0.4 (0.710)	0.4 ± 0.2	0.3 ± 0.1	0.2 (0.810)
Sapotaceae	AMF	**377.8 ± 109.3**	**116.7 ± 35.6**	**2.5 (0.035)**	143.7 ± 70.5	6.1 ± 2.5	2.0 (0.087)
Sapindaceae	AMF	133.3 ± 23.9	233.3 ± 69.6	1.4 (0.198)	4.3 ± 1.9	27.5 ± 15.7	1.6 (0.138)
Anacardiaceae	AMF	100 ± 29.5	75 ± 24.6	1.2 (0.256)	32.4 ± 19.4	3.7 ± 2.5	1.5 (0.176)
Ebenaceae	AMF	113.9 ± 42.3	61.1 ± 21.7	1.1 (0.305)	5.3 ± 2.7	2.8 ± 1.8	0.9 (0.379)
Clusiaceae	AMF	**55.6 ± 13**	**13.9 ± 7.3**	**2.9 (0.020)**	0.4 ± 0.2	0.2 ± 0.2	0.5 (0.607)
Crypteroniaceae	AMF	33.3 ± 12.5	5.6 ± 5.6	1.8 (0.107)	3.0 ± 1.7	0.0 ± 0.0	1.7 (0.129)
Araucariaceae	AMF	2.8 ± 2.8	66.7 ± 35.4	1.8 (0.111)	0.0 ± 0.0	11.6 ± 6.2	1.9 (0.100)
Meliaceae	AMF	19.4 ± 13	27.8 ± 12.8	0.4 (0.710)	0.0 ± 0.0	1.1 ± 0.9	1.1 (0.293)

Notes: AMF = arbuscular mycorrhizal fungi, ECM = ectomycorrhizal fungi, N-fixing = nitrogen fixing

For a PCA of the nine most frequent families (Figure 3.3), the first two axes accounted for 50.7% of the total variation (PC1 = 30.1%, PC2 = 20.6%). The clusters representing the peat and kerangas plots had similar spreads and overlapped predominantly in the middle of the ordination biplot, suggesting considerable similarity in the relative abundance of the nine most frequently occurring tree families between the two forest types.

For a NMDS analysis of all 28 families in the peat and kerangas plots (Figure 3.4), we found a stress value of 0.177, indicating an acceptable fit of the data in the reduced-dimensional space. The NMDS plot showed a clear separation between the peat and kerangas plots, with each forest type forming a distinct cluster. The PERMANOVA confirmed a statistically significant dissimilarity between peat and kerangas in the composition of the tree families (F = 3.0, $P = 0.003$). For the db-RDA we found that while soil variables together explained approximately 52.76% of the variation in species composition, none of the individual soil variables were statistically significant on their own.

3.4.4 Effect of habitat and family on floristic traits

For the eight plant families examined, no significant differences between peat and kerangas were observed for foliar nitrogen content (%N), phosphorus content (%P), or nitrogen to phosphorus ratio (N:P), (Figure 3.5A-C). Similarly, no significant differences between the two forest types were observed for foliar carbon content (%C), carbon to nitrogen ratio (C:N), and carbon to phosphorus ratio (C:P), (Table 3.4). However, there were large differences among the eight families for both %N and %P. Overall the highest foliar N and P concentrations occurred for Fabaceae and Euphorbiaceae while the lowest N and P concentrations were for Myrtaceae and Pandanaceae. Significant differences were observed among families for C:N and C:P ratios (Table 3.4).

There were also no significant differences between peat and kerangas for foliar LMA or LDMC (Table 4, Figure 3.6A-B), but the eight families differed for both traits. Overall, the highest foliar LMA occurred for Myrtaceae while the lowest LMA was for Zingiberaceae. Furthermore, the highest foliar LDMC occurred for Dipterocarpaceae and Arecaceae while the lowest LDMC were for Zingiberaceae and Pandanaceae.

For the eight plant families examined, no significant differences between peat and kerangas were observed in litter nitrogen content (%N), phosphorus content (%P), or

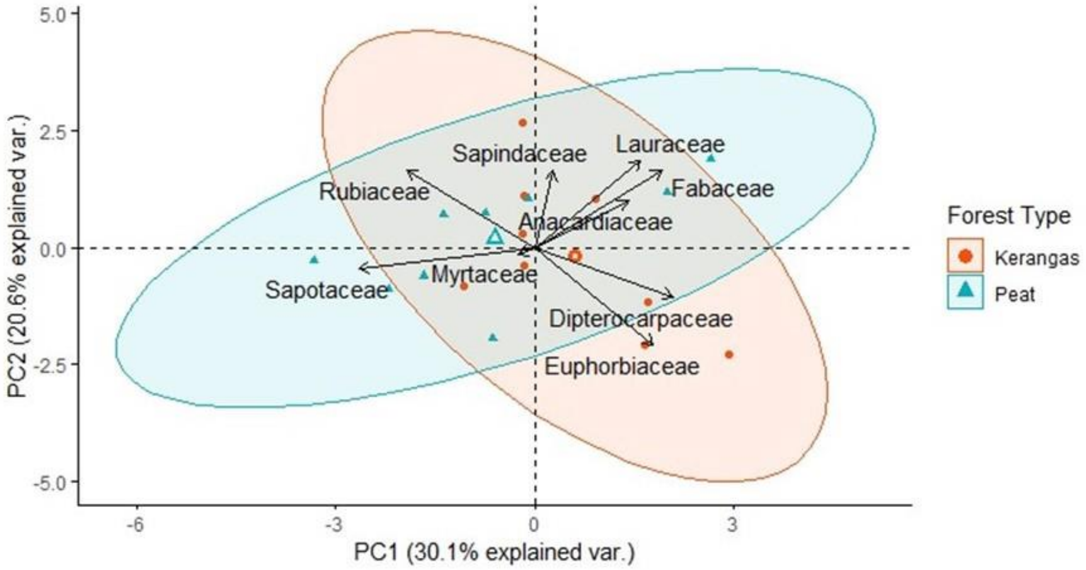

Figure 3.3: Principal component analysis of abundance of the nine tree families occurring most frequently in both peat and kerangas plots in Badas and Labi Forest Reserves, Brunei Darussalam. Small symbols represent individual plots while large open symbols represent means.

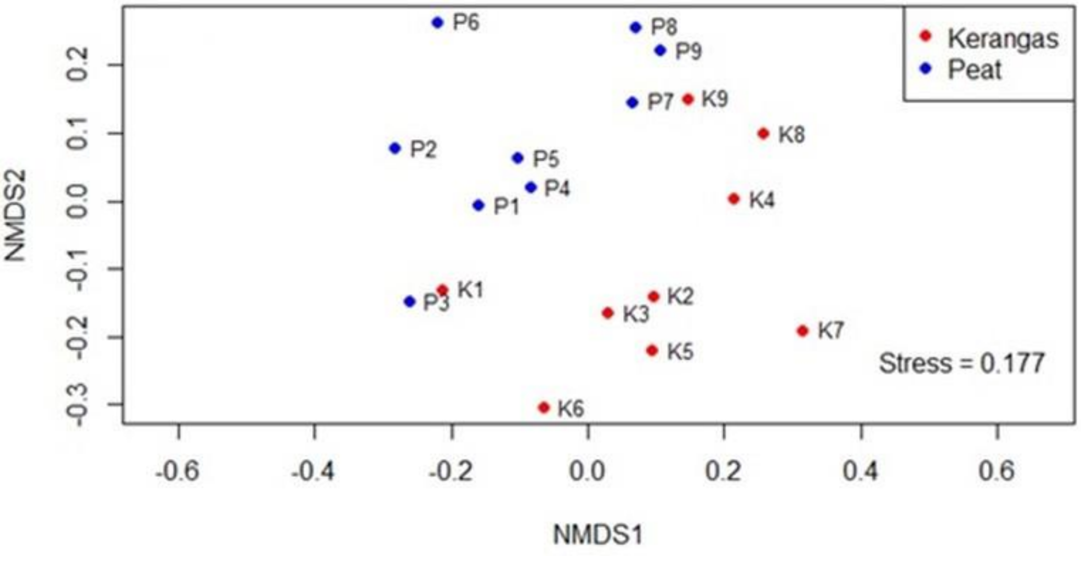

Figure 3.4: Nonmetric multidimensional scaling (NMDS) of plot dissimilarity (Bray-Curtis, stress=0.177) based on abundance of 28 tree families of 18 paired plots (kerangas N = 9, peat N = 9). Plots located in different habitat types are represented by different colors: red (kerangas) and blue (peat). PERMANOVA analysis indicate a significant effect of ‘habitat type’ (*F* = 3.0, *P* = 0.003) on the dissimilarity observed.

Table 3.4: The influence of peat versus kerangas (‘habitat’) and family on foliar, litter, and resorption variables tested in linear mixed models while accounting for random variations within the Block and Plot levels. Values inboldface indicate significant effects with $P < 0.05$.

Response Variables	**Habitat**			**Family**		
	F	**d.f.**	***P***	***F***	**d.f.**	***P***
<u>Foliar</u>						
LMA	0.2	1	0.694	**24.8**	**7**	**<0.001**
LDMC	0.3	1	0.624	**18.0**	**7**	**<0.001**
%N	1.5	1	0.259	**5.1**	**7**	**<0.001**
%P	0.1	1	0.761	**6.4**	**7**	**<0.001**
% C	3.4	1	0.104	1.7	7	0.118
N:P	0.9	1	0.376	1.2	7	0.284
C:N	0.7	1	0.413	**14.2**	**7**	**<0.001**
C:P	1.2	1	0.307	**4.5**	**7**	**<0.001**
<u>Litter</u>						
%N	0.2	1	0.673	**2.2**	**7**	**0.041**
%P	0.3	1	0.571	1.2	7	0.285
% C	0.0	1	0.853	1.0	7	0.424
N:P	0.9	1	0.376	**2.5**	**7**	**0.020**
C:N	1.5	1	0.254	**5.0**	**7**	**<0.001**
C:P	0.0	1	0.960	1.8	7	0.102
<u>Resorption</u>						
%N	1.9	1	0.210	1.3	7	0.244
%P	1.0	1	0.352	**3.1**	**7**	**0.005**

Notes: LMA = leaf mass area (g/m^2), LDMC = leaf dry matter content. For habitatand family, the denominator degrees of freedoms are approximately 8.0 and 118.0, respectively (Kenward-Roger method).

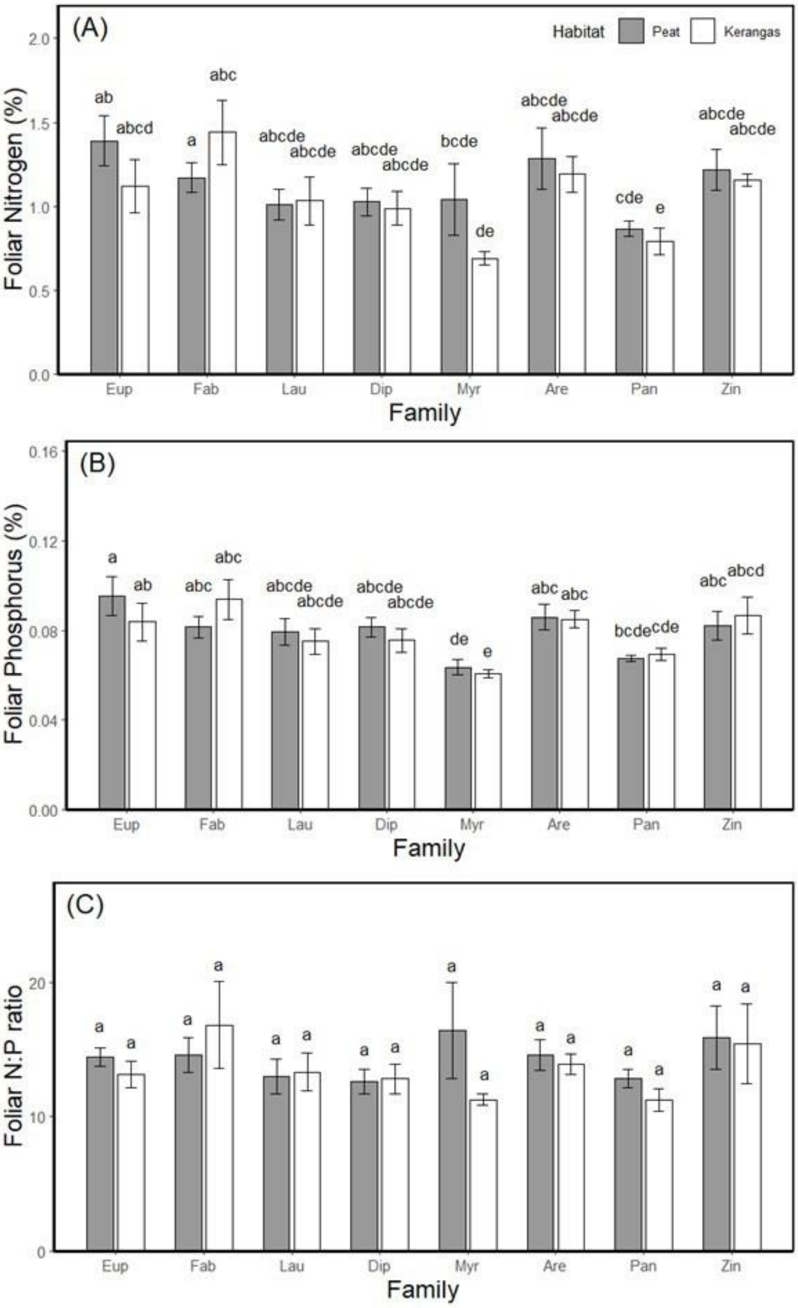

Figure 3.5: Mean ± SE foliar **(A)** nitrogen (%), **(B)** phosphorus (%), and **(C)** N:P ratio for live foliage from each family in peat and kerangas (N = 9). Pooled leaf samples were comprised of an average of 12 leaves from typically 2–4 species per family. Bars topped by the same letter are not significantly different at $P < 0.05$ (Tukey's post hoc test). Peat is represented by gray bars while kerangas is represented by white bars. Family abbreviation: Euphorbiaceae (Eup), Lauraceae (Lau), Fabaceae (Fab), Dipterocarpaceae (Dip), Myrtaceae (Myr), Arecaceae (Are), Pandanaceae (Pan), and Zingiberaceae (Zin).

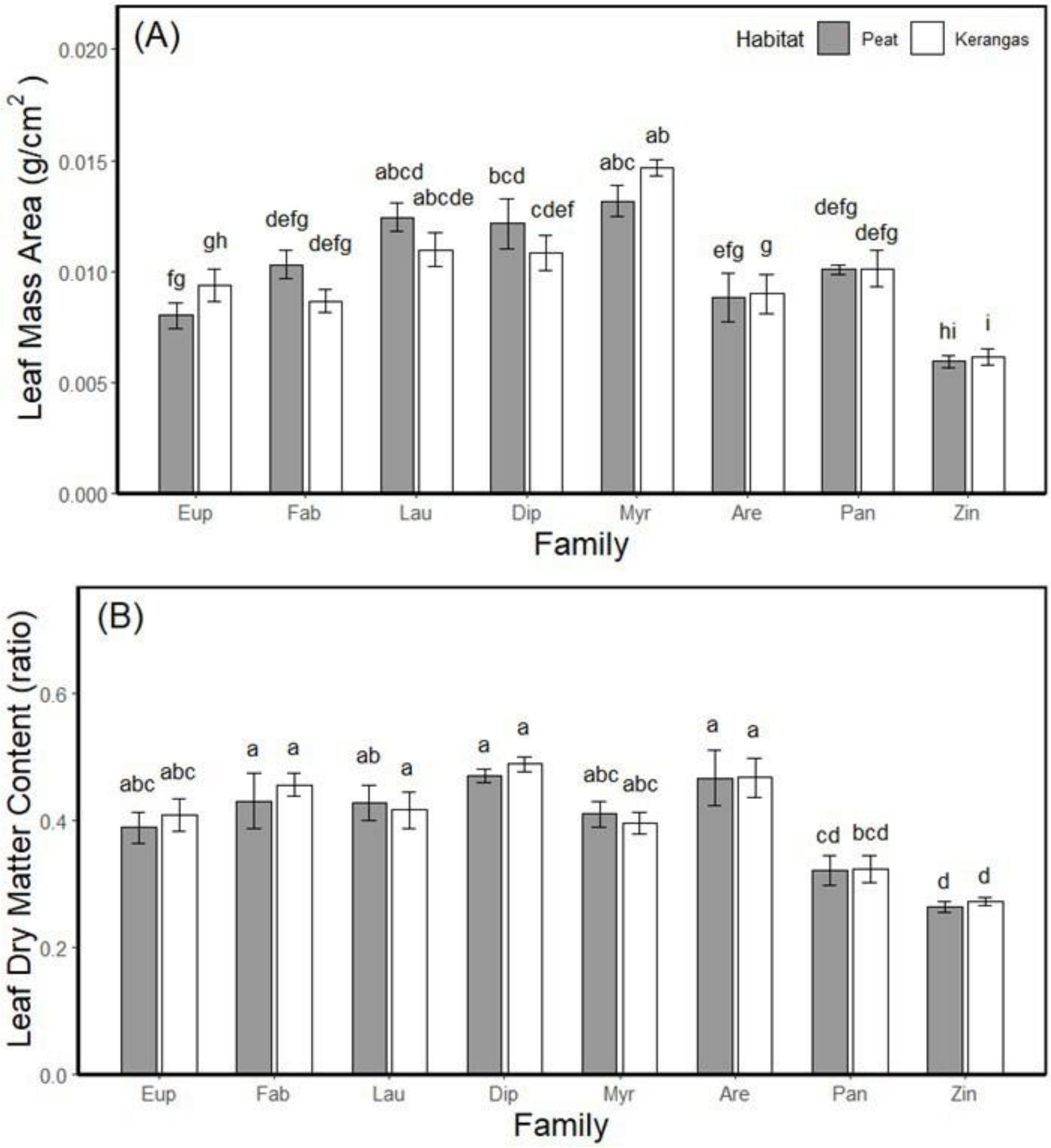

Figure 3.6: Mean ± SE foliar **(A)** leaf mass per area (LMA), (g/cm^3) and **(B)** leaf dry matter content (dry:fresh mass) for each family in peat and kerangas (N=9). Pooled leaf samples were comprised of an average of 12 leaves from typically 2–4 species per family. Bars topped by the same letter are not significantly different at $P < 0.05$ (Tukey's post hoc test). Peat is represented by gray bars while kerangas is represented by white bars. Family abbreviation: Euphorbiaceae (Eup), Lauraceae (Lau), Fabaceae (Fab), Dipterocarpaceae (Dip), Myrtaceae (Myr), Arecaceae (Are), Pandanaceae (Pan), and Zingiberaceae (Zin).

nitrogen to phosphorus ratio (N:P) (Figure 3.7A-C). Similarly, no significant differences between the two forest types were observed for litter carbon content (%C), carbon to nitrogen ratio (C:N), and carbon to phosphorus ratio (C:P), (Table 4). According to the LMM, there were significant differences among the eight families for litter %N. However, the post hoc test did not indicate significant differences for %N. Differences were observed among the eight families for both litter N:P. and C:N (Table 4). Overall, the highest litter N:P occurred for Euphorbiaceae and Arecaceae while the lowest N:P were for Myrtaceae and Pandanaceae (Figure 3.7C). Data for C:N ratios are not presented.

3.4.5 Resorption

For the eight plant families examined, no significant differences between peat and kerangas were observed in nitrogen resorption (Table 4, Figure 3.8A). According to the LMM, there were significant differences among the eight families for phosphorus resorption (Table 4). However, the post hoc test did not indicate significant differences for phosphorus resorption (Figure 3.8B).

3.5 Discussion

We found that total nutrients were more concentrated in peat and in kerangas-humus than in kerangas-sand, while available nutrients were highest in kerangas-humus soil. Despite this, we found no difference in tree diversity or in families with specific nutrient strategies between the forest types. Furthermore, while leaf economic traits and nutrient resorption varied among plant families, they showed no significant differences between peat and kerangas forests. These findings are now discussed to enhance our understanding of the structural and functional differences between adjacent peatland and kerangas ecosystems.

3.5.1 Soil nutrient differences

Contrary to our first hypothesis, we found that the total nutrient content, and nutrient ratios, of the kerangas-humus layer was comparable to that of peat, although the kerangas-sand had lower total nutrients than either humus or peat. However, our first hypothesis was partly supported in that amounts of labile forms of N (i.e., NH_4^+ and total dissolved N) were less in the peat than in kerangas-humus. This is most likely a consequence of anoxic conditions of the peat (Hoyos-Santillan et al., 2019) limiting microbial activity, thus slowing down the decomposition process and impairing of N

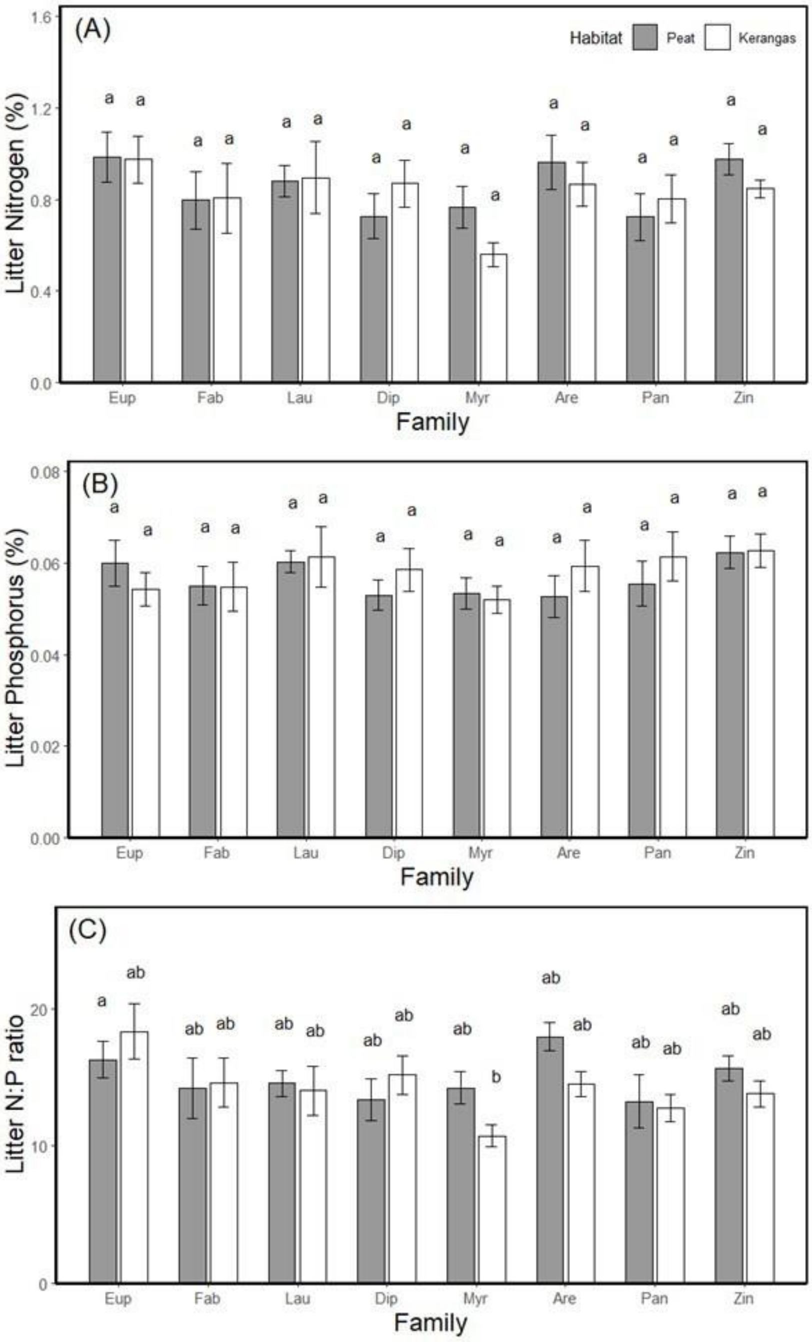

Figure 3.7: Mean ± SE litter **(A)** nitrogen (%), **(B)** phosphorus (%), and **(C)** N:P for each family in peat and kerangas (N = 9). Pooled leaf samples were comprised of an average of eight leaves from typically 2–4 species per family. Bars topped by the same letter are not significantly different at $P < 0.05$ (Tukey's post hoc test). Peat is represented by gray bars while kerangas is represented by white bars. Family abbreviation: Euphorbiaceae (Eup), Lauraceae (Lau), Fabaceae (Fab), Dipterocarpaceae (Dip), Myrtaceae (Myr), Arecaceae (Are), Pandanaceae (Pan), and Zingiberaceae (Zin).

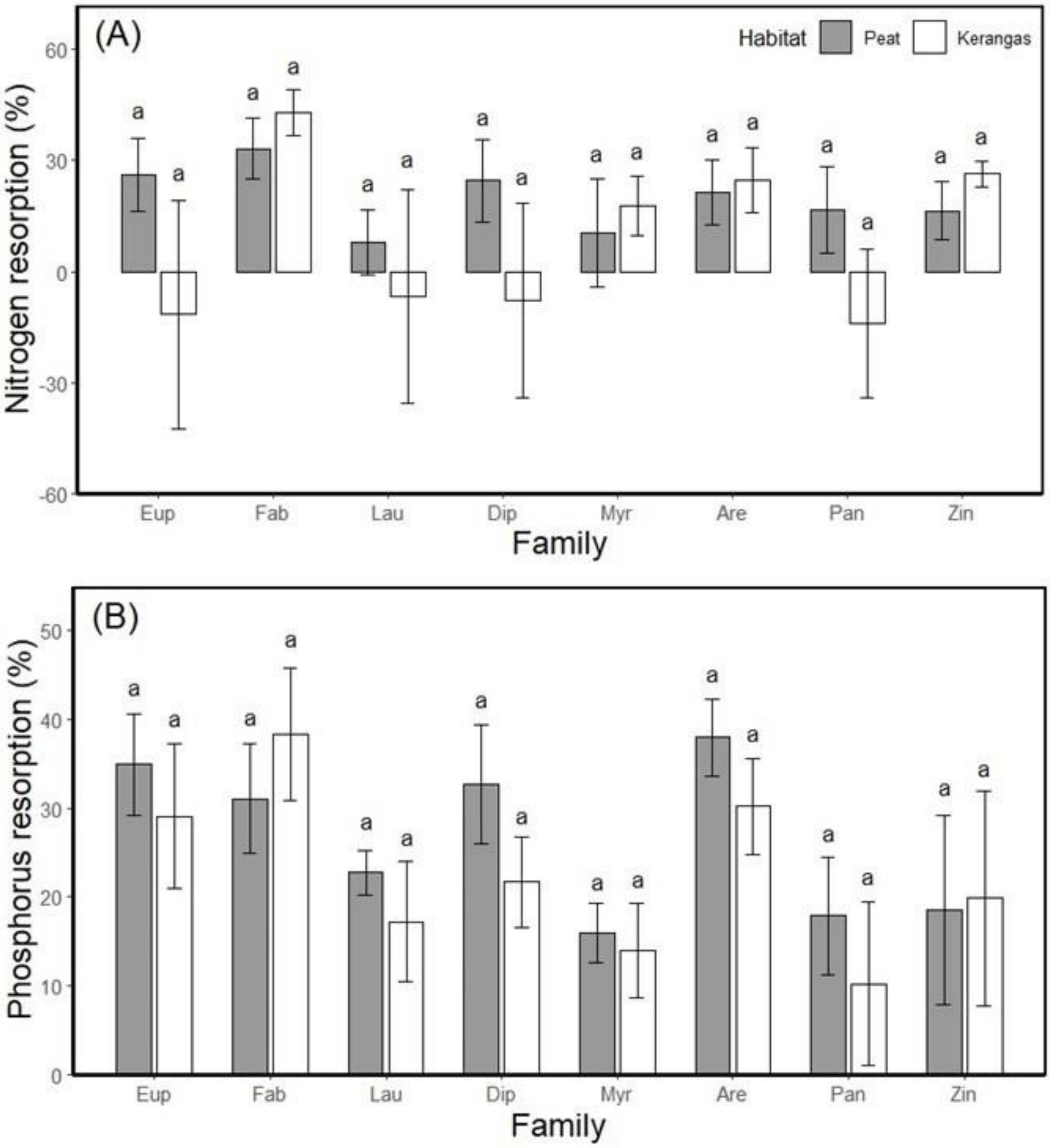

Figure 3.8: Mean ± SE **(A)** nitrogen resorption (%) and **(B)** phosphorus resorption (%) ± SE for each family in peat and kerangas (N = 9), computed as (fresh content – dry content) / fresh content x 100%. Pooled leaf samples were comprised of an average of 8-12 leaves from typically 2–4 species per family. Bars topped by the same letter are not significantly different at $P < 0.05$ (Tukey's post hoc test). Peat is represented by gray bars while kerangas is represented by white bars. Family abbreviation: Euphorbiaceae (Eup), Lauraceae (Lau), Fabaceae (Fab), Dipterocarpaceae (Dip), Myrtaceae (Myr), Arecaceae (Are), Pandanaceae (Pan), and Zingiberaceae (Zin).

mineralization (Jauhiainen et al., 2005). Our findings are consistent with Leng et al. (2019) and Mishra et al. (2021), which underscores the critical role of oxygen availability and hydrological factors in soil nutrient dynamics in tropical peatlands. Both the absolute phosphorus concentrations and nutrient ratios indicate phosphorus limitation in both peat and kerangas forests. Low phosphorus levels, combined with high C:P ratios (around 400–450) and N:P ratios in the range of 11–13, suggest that phosphorus is likely a limiting nutrient, which could constrain plant and microbial productivity in these ecosystems (Troxler et al., 2012; Xu et al., 2022). Although decomposition rates are similar in both forests, and despite the anoxic conditions in peat forests slowing mineralization, total phosphorus levels are similar in peat and kerangas-humus. This could be due to similar litter inputs from dominant tree species across both forest types, along with the kerangas-humus layer retaining nutrients in organic matter that has not yet been fully mineralized. The similarity in total nutrient concentrations between peat and kerangas-humus aligns with the fact that nutrient concentrations in the litter inputs from the eight plant families did not differ between these two habitats. However, impeded mineralization due to anoxia causes large amounts of organic matter to accumulate in peat but not kerangas forest, leading to higher (but less available) nutrient capital in the former. This is also consistent with faster decomposition rates previously observed in kerangas (Rahajoe and Kohyama, 2003). This similarity in total nutrient concentrations in peat and kerangas-humus suggests that, despite their distinct hydrological conditions, both ecosystems may exhibit convergent nutrient dynamics, potentially driven by comparable sources or compositions of organic matter.

Nutrient availability in tropical peat is heavily influenced by seasonal changes in water table levels, microbial activity, and decomposition rates (Marwanto et al., 2018; Girkin et al., 2020). Given that we sampled only once during the year, our study may have missed seasonal variations in nutrient dynamics. Soil nutrient concentrations in peatlands can fluctuate significantly between wet and dry seasons due to shifts in waterlogging and oxygen availability (Macrae et al., 2013). These fluctuations are especially relevant in tropical peat forests, where water table levels and redox potential can vary substantially with rainfall patterns. Future studies should aim to sample during multiple periods across the year to capture these seasonal dynamics, providing a more comprehensive view of nutrient cycling in this ecosystem. This would allow for a deeper understanding of how temporal shifts impact carbon and nutrient cycling along the degradation gradient.

3.5.2 Diversity and structure

In contrast to our second hypothesis, we observed no significant differences in the diversity of trees, their frequency, or stand basal area between the two forest types. Despite the waterlogged and nutrient-poor conditions of peat forests that encourage plant adaptations like buttress roots, stilt roots, and pneumatophores (Pahang Forestry Department, 2005), these factors did not lead to increased tree diversity through mechanisms of coexistence or reduced competition in the manner that may be expected in stressed environments (Grime, 1979). The relative similarity in tree diversity and forest structure between the two forest types, coupled with dominance by the same dominant plant families in both of them, suggests the existence of a shared taxa pool adapted to diverse environmental conditions. These observations are in line with a study by Giesen et al. (2018), which found that over 80% of the known peat swamp forest flora is common to a variety of habitats, including kerangas and montane forests.

Taxa that occur across contrasting environments (such as kerangas versus peat) often exhibit significant phenotypic plasticity (West-Eberhard, 1989). In Southeast Asia this includes the Dipterocarpaceae (a dominant family in both forest types of our study) which has previously been shown to exhibit significant adaptability by varying growth characteristics and traits among habitats (Chan, 2016). This adaptability is reflected in the present study, with Dipterocarpaceae exhibiting lower abundance but a larger average basal area (i.e., fewer but larger and more robust trees adapted to waterlogged conditions) in peat forests. This aligns with previous work in the region by Nishimura and Suzuki (2001), showing that the dipterocarp species *Shorea teysmanniana,* adapts its growth patterns and resource allocation to thrive in both peat and kerangas forest, such as deeper roots and smaller leaves in kerangas, and more lateral root growth in peat forest (Nishimura and Suzuki, 2001).

We did not find evidence to support our hypothesized higher prevalence of taxa with specialized nutrient strategies, such as ECM and nitrogen-fixing associations, in peat than in kerangas forests. This could be attributed to the phenotypic plasticity observed in shared taxa across the two forest types, allowing them to adapt their nutrient acquisition strategies to diverse environmental conditions, as has previously been observed with N uptake in tropical forest (Andersen et al., 2017). Contrary to our predictions, Dipterocarpaceae and Myrtaceae, both of which have ECM associations (Corrales et al., 2018), were more abundant and had a greater stand basal area, respectively, in the kerangas forests despite labile forms of soil N being higher.

ECM fungi are likely to be more adversely affected by waterlogging and anoxia compared to AM fungi (Wang et al., 2010; Usman et al., 2021), so despite less labile N in peat, ECM fungi are likely to have reduced success in these conditions.

3.5.3 Leaf traits and nutrient resorption

In contrast to our third hypothesis, leaf economic traits and nutrient resorption did not differ between peat and kerangas forests. Despite greater nitrogen availability and less anoxia in kerangas, leaf traits and resorption processes that are known to respond to environmental stress and nutrient limitation (Chapin et al., 1986; Brant and Chen, 2015), are relatively invariant across the two forest types. This suggests that the adaptations enabling plants to access unavailable nutrients and tolerate anoxia in peat forest enables them to exhibit similar trait and resorption values in that environment as they do in kerangas. Furthermore, the similarity in nutrient resorption across the significantly different environmental conditions of peat and kerangas suggests that plants in both habitats perceive similar levels of nutrient availability (Chen et al., 2021). Efficient nutrient uptake facilitated by AM fungi, which are associated with most plant taxa in both environments (Table 3.3), may account for the observed invariance in economic traits and resorption in both habitats despite peat having lower concentrations of labile forms of N.

The finding that family-level influences on leaf traits are stronger than site-specific effects suggests that these traits are deeply phylogenetically conserved. Traits like LMA, LDMC, and phosphorus resorption appear to be genetically controlled, showing limited plasticity and making them less adaptable to variations in environmental conditions (Donovan et al., 2011; Wright et al., 2004). These low-plasticity traits may have evolved within plant families to be well-suited to a narrow range of aboveground environmental conditions, which leads to consistency in trait expression across sites.

Aboveground, both forest types are comparable in characteristics such as tree abundance, stand basal area, ground cover, and diversity, despite significant differences in soil conditions between the waterlogged peat and well-draining kerangas sites. This similarity aboveground likely reduces the selective pressure for leaf trait adjustments between sites, thereby further supporting the consistency of family-level traits. These findings highlight how evolutionary history has shaped functional traits within lineages to remain stable across varying conditions (Ackerly, 2003), suggesting that aboveground habitat uniformity can reinforce trait conservation even amid differing soils.

3.6 Conclusions

This study enhances understanding of tropical peatlands and their differences from kerangas forest by showing that they have considerable similarity in forest stand characteristics, and foliar and litter traits, despite large differences in their belowground environment. The invariance within families in functional traits and nutrient resorption among forest types, despite large differences among families, points to a remarkably low level of plasticity in these characteristics across vastly contrasting environments. The lack of large differences in plant communities, and leaf and litter characteristics between peat and kerangas means that it is unlikely that the massive C accumulation in peat is due to plant community factors but rather is driven by soil-related processes, such as the retardation of decomposer activity. Further research is needed to determine if these findings apply to other tropical forests, particularly for forests that are in close proximity and share the same species pool, as this would enhance our understanding of the factors influencing the local-scale aboveground ecology of forest ecosystems. Tropical peat forest plays a critical role in global carbon sequestration and our findings indicate that differences in the producer subsystem between peat and kerangas forests are unlikely to drive C storage in peat forest; there is therefore a research need to instead focus on other drivers that may impact C storage such as what happens in the decomposer subsystem.

Chapter 4

No home-field advantage in the decomposition of leaf litter in the tropical peat forests of Brunei Darussalam

4.1 Abstract

Tropical peatlands have a globally important role as carbon sinks. The issue of how their waterlogged conditions and low nutrient status impact plant litter decomposition is not well-understood, despite decomposition processes often underpinning carbon sequestration. Our study explored leaf litter decomposition between adjacent paired patches of intact tropical waterlogged peat forests and kerangas (free-draining heath) forests in Brunei Darussalam and tested for the ‘home-field advantage’ effect which predicts that litters decompose fastest in the environment that they were sourced from because of pre-adaption of the decomposer community. To do this, a reciprocal transplantation experiment was conducted across paired adjacent peat and kerangas plots using litter from five tree families common to both forest types. Contrary to our expectations, we found no significant difference in rates of mass or nutrient loss from decomposing litter between peat and kerangas forests irrespective of the litter’s origin, despite the large differences in environmental conditions between the two environments. We also found no evidence for home-field advantage for either forest. We did find litter nutrient concentration to operate as a key predictor of decomposition, but this effect was independent of forest type. The study suggests that leaf litter

decomposition processes may not significantly contribute to the substantial amount of organic matter accumulation observed in peat forests, indicating that other factors, such as woody debris, branches, and entire tree trunks must instead be contributing to their substantial levels of belowground carbon sequestration. This emphasizes the need for further research to explore the factors driving organic matter accumulation in tropical peatlands.

4.2 Introduction

Tropical peat forests are among the world’s most carbon-rich ecosystems, vastly surpassing most other forest types in carbon density (Page and Baird, 2016). These ecosystems differ from temperate peatlands, as their peat is mainly formed by material from woody plants rather than from *Sphagnum* moss. Owing to the perennial waterlogging, which retards the decomposition process of wood, leaves, and roots, these environments have gradually amassed substantial organic deposits over millennia, which can result in the formation of peat layers of up to 20 meters thick (Anderson, 1983). Globally tropical peat forests contain an estimated 105 Gt of carbon—about 30% of the carbon stock of tropical rainforests globally—despite occupying only about 0.25% of the earth’s land surface (Page et al., 2011). As crucial carbon repositories, these peatlands significantly influence the global carbon balance (Ribeiro et al., 2021). However, Southeast Asia, which contains approximately half of these tropical peatlands, has experienced dramatic peatland forest reduction due to deforestation, drainage, and burning over recent decades. Presently, less than 30% of the region’s peat forest cover remains (Murdiyarso et al., 2010; Hooijer et al., 2012; Mishra et al., 2021), transforming these ecosystems from carbon sinks to sources of greenhouse gases.

Although tropical peat accumulation plays a critical role in global carbon sequestration (Harenda et al., 2018), the mechanisms driving this accumulation, specifically the influence of their waterlogged conditions and low nutrient status on the decomposition of plant litter, remain poorly understood. Both waterlogged and nutrient-poor conditions impede litter decomposition; anoxia in saturated soils restricts the activity and diversity of aerobic decomposers, while nutrient limitation inhibits microbial and detritivore efficacy in breaking down organic matter (Swift et al., 1979; Laiho, 2006; Baldrian, 2017). This impairment of decomposition has the potential to lead to the formation of deep peat layers in the tropical peat swamp environment (Mishra et al., 2021). The ‘home-field advantage’ (HFA) hypothesis is relevant to understanding decomposition processes in the peat forest environment. It predicts that leaf litter decomposes more rapidly in the environment it originates from (‘home’) compared to other environments (‘away’), because soil microbes adapt to are specializing in the decomposition of leaf litter from the plants in their own environment (Hunt et al., 1988; Gholz et al., 2000; Austin et al., 2014). Several studies have tested for HFA using field-based reciprocal litter transplant experiments. Although there is much variation among these studies (St John et al., 2011; Veen et al., 2015a; Fanin et al., 2021), a review of data from studies conducted in temperate and tropical forests in North America, South America, Europe, and Hawaii show that HFA is common in forests and that litter decomposes, on average, 8% faster at home than away (Ayres et al., 2009).

Home-field advantage in waterlogged forests, such as tropical peat swamp and freshwater swamp forests, is not well-explored or understood. However, in a peat swamp in Malaysia, a sclerophyllous species in the family Euphorbiaceae was found to decompose at similar rates in waterlogged areas and dry areas of the same habitat (Yule and Gomez, 2009). Meanwhile, in a natural (non-peat) freshwater swamp forest in Singapore, leaf litter decomposition was found to be driven by physical traits which varied by species (Rahman et al., 2023), was impaired was waterlogged conditions, and was largely unimpacted by HFA (Lam et al., 2021). No direct comparisons of decomposition or HFA in tropical peat swamp forests with that in adjacent ecosystems have been performed to date, but such studies are necessary to enhance our mechanistic understanding of peat accumulation processes in tropical peat forests.

Forests in Brunei cover 75% of the total land area, with 17% being peat forest that remains relatively undisturbed compared to other peat forests in Southeast Asia (Islam et al., 2018). Brunei peat forests typically form a mosaic with ‘kerangas’ forests. The term ‘kerangas’, which originates from the local Iban language, describes the sandy-soiled heath forests of Borneo that are unsuitable for rice farming due to their infertility (Brunig, 1974). Peat forests in Brunei grow on water-saturated organic deposits, often measuring between 8 m to 15 m in thickness (Kobayashi et al., 2016) Conversely, kerangas forests thrive on well-draining, nutrient poor, white sands topped with a humus layer of up to 0.7 meters (Brunig, 1974; Katagiri et al., 1991; MacKinnon et al., 2013; Din et al., 2015). The soils of both peat and kerangas forests are generally nutrient depleted (Din et al., 2015; Kobayashi, 2016; Ikbal et al., 2023). However, as I have shown in Chapter 3, peat forest soils have higher concentrations of total carbon (C), nitrogen (N), and phosphorus (P) than do kerangas forest soils, but lower amounts of labile forms of these elements such as ammonium (NH_4^+), total dissolved nitrogen (TN) and total dissolved organic carbon (TOC).

Table 4.1: Family tree abundance (number/ha) and stand basal area (m^2/ha) in peat and kerangas paired plots in Badas and Labi Forest Reserves, Brunei Darussalam. Means are shown ± SE. Values in boldface indicate statistically significantly different means at ($P < 0.05$) determined by paired t-tests.

	Tree Abundance (number/ha)			**Stand basal area (m^2/ha)**		
Family	Peat	Kerangas	t(*P*)	Peat	Kerangas	t(*P*)
Euphorbiaceae	150.0 ± 31.2	247.2 ± 83.5	1.1 (0.288)	1.3 ± 0.4	8.7 ± 4.3	1.7 (0.125)
Fabaceae	225.0 ± 85.6	183.3 ± 23.6	0.5 (0.607)	27.7 ± 19.1	6.8 ± 2.5	1.1 (0.300)
Lauraceae	100.0 ± 22.4	116.7 ± 23.6	0.4 (0.703)	0.6 ± 0.3	1.4 ± 0.4	1.4 (0.191)
Dipterocarpaceae	**163.89 ± 56.1**	**450.0 ± 98.6**	**3.1 (0.015)**	109.3 ± 31.2	88.2 ± 41	0.4 (0.679)
Myrtaceae	388.9 ± 108.3	475 ± 94.9	1.4 (0.200)	**18.5 ± 12.5**	**55.4 ± 15.2**	**2.4 (0.045)**

Notes: *P* = *P*-value. t = t-value. This table is derived from Table 3.3.

Further, as shown in Chapter 3, there are few differences between the two forest types in forest structural attributes, with significant differences in the relative abundance of Dipterocarpaceae and the stand basal area of Myrtaceae, while other common plant families, such as Fabaceae, Lauraceae, Euphorbiaceae, and Sapotaceae, do not differ significantly in either abundance or stand basal area (Table 4.1). This study system in Brunei offers a valuable opportunity to investigate decomposition and HFA in a tropical context, where climate conditions and vegetation structure are relatively constant, but hydrological conditions and soil nutrients vary greatly.

In this study system, we set up a reciprocal leaf litter transplantation decomposition experiment between adjacent paired plots of peat and kerangas forest. This involved reciprocal transplantation of leaf litter from plants of each of five families that occur in all plots. The main aim of our research was to compare plant litter decomposition rates in peat and kerangas environments, and assess how it was affected by litter quality, home-field advantage, and soil nutrient status. We tested two hypotheses to accomplish this aim:

> (H1) Decomposition and nutrient release will overall be faster for litter placed in kerangas because soil biological activity will be impaired less by waterlogging and nutrient limitation. Further, litter from kerangas vegetation will decompose and release nutrients faster regardless of where it is placed.
>
> (H2) Home field advantage will mean that litter from both peat and kerangas vegetation will decompose more rapidly than expected in the environment that it was collected (i.e., in peat and kerangas environments respectively). However, this advantage will be stronger in peat and for plant taxa that produce poorer quality litter because the microbes in the peat are better adapted for

decomposing more recalcitrant litter.

To further understand the factors that may drive HFA, we also collected measurements on litter traits for each litter type we used, and used soil nutrient data for each plot that the litter was sourced from and transplanted to, and then attempted to use these variables to predict the magnitude of litter decomposition and home-field effects. In performing our study our ultimate goal was to contribute to a better understanding of how plant litter decomposition contributes to peat accumulating in tropical forest soils.

4.3 Methods

4.3.1 Experimental design

In this chapter, we utilized the same experimental plots as described in Chapter 3. The study was conducted in the Badas and Labi Hills Forest Reserves, Belait District, Brunei Darussalam which provided an ideal system for direct comparison of two forest types (peat and kerangas). We established nine pairs of circular plots (each 11.3 m radius) in September 2021, with each pair consisting of a plot in kerangas forest and one in peat forest, resulting in a total of 18 plots. The distance between peat and kerangas plots within each pair averaged 100 m, and the minimum distance between pairs was always 300 m. A total of 12 plots were established in the Badas Forest Reserve, while six plots were established in the Labi Forest Reserve. The selection of forest patches was guided by advice from the Brunei Forestry Department. Further details of the plots and plot selection are given in Chapter 3. For the background data for each plot, we used the data provided in Chapter 3 for soil nutrient variables (i.e., total carbon, nitrogen, phosphorus, nitrate, and ammonia) and plant community properties (i.e., family composition, tree abundance, and stand basal area) provided in Chapter 3.

4.3.2 Litterbags

Vegetation measurements for each plot were made in September and October 2021. For each plot, the diameter at breast height (DBH) of each stem with a DBH greater than five cm was measured and identified to at least the family level. Within each plot we also set up a circular subplot, each with a radius of 5.65 meters for a total of 100 m^2 and for each subplot, each stem with a DBH greater than one cm was measured and identified to at least the family level. The stem diameter and frequency data were used to determine tree abundance and stand basal area, as presented in detail in Chapter 3. We conducted analyses at the family level, as species-level characterization is not feasible due to the immense biodiversity in these tropical forests. Five tree families (Euphorbiaceae, Fabaceae, Lauraceae, Dipterocarpaceae, and Myrtaceae) were selected for this experiment as they were recorded in every peat and kerangas plot.

Litter from plants of each of the five families was collected in December 2021 from all 18 plots. The collection of tree litter was facilitated by gently shaking tree stems, there by prompting abscission. From each plot, two grams of oven-dried litter from each family was placed individually into heat-sealed polypropylene (PPE) mesh bags (15 x 15 cm, 1-mm mesh). Four litterbags were prepared for each of the five families in each of the 18 plots for a total of 360 bags. Two bags for each family in each plot were placed in its “home” plot while two bags for each family in each plot were placed in its paired “away” plot. Litterbags were strung along a steel cable and pegged to the surface of each plot directly on top of the litter layer. To standardise micro-topographic conditions among plots, litterbags were always placed in transitional areas between hummocks (drier, higher ground) and hollows (waterlogged depressions). While the litterbags were not submerged at the time of placement, they experience anoxic conditions during the year due to fluctuations in the water table influenced by seasonal rainfall patterns. In November 2022, after 11 months of decomposition, all litter bags were collected, cleaned, oven-dried at $60^{o}C$ for 72 hours, and then weighed. Percent mass loss was calculated as:

% Mass Loss = 100 × ((Initial Dry Weight - Final Dry Weight) / Initial Dry Weight))

For each family in each plot, the total P, total N, total C concentrations of both the litter prior to setting up the decomposition experiment and litter after decomposition were measured using an oven-dried subsample of each soil composite. Total P was determined using the molybdenum blue method with ascorbic acid (Murphy and Riley, 1962). This involved sample ignition (550°C for 1 h) and extraction in 1 M H_2SO_4 (1:50 soil/solution ratio, 16 h), with PO_4 detection by automated molybdate colorimetry using a Tecan Spark Multimode Microplate Reader (Tecan Group, Switzerland). Total N and total C concentrations were measured using the Dumas method determined by CHNS elemental analyzer (Elementar, Germany, model Vario El Cube). Litter C to N, C to P, and N to P ratios were determined from these values. Percent release for N and P due to litter decomposition was calculated as:

% Release = 100 X ((CB* Initial Dry Weight) - (CA* Final Dry Weight))/
(CB* Initial Dry Weight))

where CB is the concentration of N or P in litter prior to setting up the decomposition experiment and CA is the concentration of N of P in litter after decomposition.

4.3.3 Data analysis

Family tree abundance and stand basal area were analysed using paired t-tests with each plot pair as a replicate block to test for differences between peat and kerangas forest. To test how habitat type and family affected litter nutrient content prior to setting up the decomposition experiment, we used linear mixed models (LMM) with habitat type, family, and their interaction as fixed factors. Plot nested within block was included as a random factor, with N = 18 plots and N = 9 blocks to control for non-independence of the five observations within each plot, as well as the non-independence of observations within each block of paired plots. When significant differences were found at $P = 0.05$, Tukey's post hoc test was conducted to compare means differences. To test the influence of plot where the litter was sourced from ('litter source'), plot where the litter was placed ('litter placed'), family, and their interactions on litter percent mass loss, nitrogen release, and phosphorus release, we used LMMs with source litter, litter placed, family, and their interactions as fixed factors. Plot nested within block was included as a random factor, with N = 18 plots and N = 9 blocks. Post hoc pairwise comparisons were conducted using Tukey's test to compare mean differences.

To investigate the drivers of HFA, we employed a similar approach to that described by Veen et al. (2015b). We assessed the strength and direction of home-field effects on litter mass loss, nitrogen release, and phosphorus release using the concept of additional decomposition at home (ADH), adapted from Ayres et al. (2009). Additional decomposition at home was calculated based on the following set of four equations,

$$(1)\ \mathrm{ADH_i} = \mathrm{HDD_i} - \mathrm{ADD_i} - \mathrm{H},$$

$$(2)\ \mathrm{HDD_i} = \ (\mathrm{D_{iI}}\text{-}\mathrm{D_{jI}}),$$

$$(3)\ \mathrm{ADD_i} = \ (\mathrm{D_{iJ}}\text{-}\mathrm{D_{jJ}}),$$

$$(4)\ H = \mathrm{HDD_i}/(n\text{-}1)$$

Here, $\mathrm{ADH_i}$ represents the additional mass loss, nitrogen release, or phosphorus release experienced by litter type i when decomposing in its home environment (I) compared to when it decomposes in an away environment (J). It measures how much more efficient decomposition is in the home environment, which indicates whether there is a home-field advantage (HFA) for that litter type. A positive value of ADHi indicates a home-field advantage, while a negative or zero value indicates no advantage or a disadvantage. HDD_i corresponds to the difference between the mass loss, nitrogen release, or phosphorus release (D) of litter type i in its home environment (I) and that of foreign litter, type j, from environment J, decomposing in the same home environment (I). ADD_i represents the difference between the mass loss, nitrogen release, or phosphorus release (D) of litter i in environment J and the mass loss, nitrogen release, or phosphorus release of litter type j in environment J. D_{iI} denotes the mass loss, nitrogen release, or phosphorus release of litter type i in environment I, D_{jI} refers to the mass loss, nitrogen release, or phosphorus release of litter type j in environment I, D_{iJ} represents the mass loss of litter type i in environment J, and D_{jJ} corresponds to the mass loss, nitrogen release, or phosphorus release of litter type J in environment J. *H* represents the sum of all HDD_i values across all litter types, divided by n-1 (where n represents the total number of litter types). This provides an overall measure of home-field advantage across the study.

To test the influence of habitat, family, and their interaction on the ADH percent litter mass loss, ADH percent nitrogen release, and ADH percent phosphorus release, we used LMM with habitat, family, and their interaction as fixed factors. Plot nested within block was included as a random factor, with N = 18 plots and N = 9 blocks to control for non-independence of the five observations within each plot, as well as the non-independence of observations within each block of paired plots. Post hoc pairwise comparisons were conducted using Tukey’s test to compare mean differences. To further understand the factors that may drive litter decomposition HFA, we used Pearson’s correlation coefficient (r; N = 18) to examine the relationships of percent litter mass loss, nitrogen release, and phosphorus release, and of ADH for percent litter mass loss, nitrogen release, and phosphorus release, with initial litter nutrient and soil (plot level) nutrient variables. Statistical analyses were performed in ‘R’ (R Core Team, 2021) using the lme4 package for mixed models (Bates and Maechler, 2009) and emmeans package for mean comparison (Lenth et al., 2022).

4.4 Results

4.4.1 Senescent litterfall

Overall, there were no differences in litter nutrient properties between peat and kerangas for any of the five families, and there were no interactive effects between forest type and family (Table 4.2). However, there were often differences among families. Specifically, litter N and P concentration differed significantly among the 5 plant families in both peat and kerangas habitats while C:N differed among families only in kerangas, while C concentration, C:P and N:P were invariant among families (Tables 4.2, 4.3). Overall, the lowest litter N and P concentration occurred for Myrtaceae. In peat, Myrtaceae has at least 25% lower N and 20% lower P concentrations than the other families, while in kerangas, Myrtaceae has at least 27% lower N, 20% lower P concentrations, and 16.8% higher C:N than all the other families. In peat the highest litter N and P was found for Fabaceae and Euphorbiaceae respectively. Meanwhile in kerangas the highest senescent litter N concentration occurred for Fabaceae and Lauraceae, while the highest P concentration occurred for Euphorbiaceae.

Table 4.2: The influence of peat versus kerangas (‘habitat’), family, and their interaction on senescent litterfall tested in linear mixed models while accounting for random variations within the Block and Plot levels. Values in boldface indicate significant effects with $P < 0.05$.

Response Variables	**Habitat**			**Family**			**Habitat * Family**		
	F	**d.f.**	***P***	***F***	**d.f.**	***P***	***F***	**d.f.**	***P***
%N	1.8	1	0.213	**6.5**	**4**	**<0.001**	1.5	4	0.220
%P	1.1	1	0.315	**9.9**	**4**	**<0.001**	0.1	4	0.972
% C	4.2	1	0.075	0.6	4	0.640	0.5	4	0.759
C:N	3.7	1	0.089	2.3	4	0.072	0.8	4	0.547
C:P	2.5	1	0.152	**7.5**	**4**	**<0.001**	0.6	4	0.648
N:P	2.6	1	0.143	1.7	4	0.155	1.1	4	0.378

For habitat, family and their interaction, the denominator degrees of freedoms are 8, 64, and 64 respectively (Kenward-Roger method).

Table 4.3: Senescent litterfall nutrient content for each family. Values are means averaged across all plots ± SE (N = 18). Different letters among families and values in boldface indicate statistically significantly different means at $P < 0.05$ (Tukey's post hoc test).

Response Variable	Euphorbiaceae	Fabaceae	Lauraceae	Dipterocarpaceae	Myrtaceae
Peat					
% N Initial	**1.00 ± 0.07^{ab}**	**1.25 ± 0.08^{a}**	**1.13 ± 0.1^{ab}**	**1.21 ± 0.17^{ab}**	**0.80 ± 0.04^{b}**
% P Initial	**0.084 ± 0.008^{a}**	**0.080 ± 0.003^{a}**	**0.075 ± 0.003^{ab}**	**0.072 ± 0.003^{ab}**	**0.060 ± 0.003^{b}**
% C Initial	45.3 ± 2.7	47.7 ± 3.2	51.5 ± 0.9	49.7 ± 2.6	44.6 ± 4.1
C:N	46.7 ± 3.6	39.2 ± 3.5	51.5 ± 9.0	45.8 ± 4.6	57.7 ± 6.8
C:P	557.6 ± 42.2	599.0 ± 39.0	696.4 ± 44.3	690.3 ± 40.0	736.4 ± 54.8
N:P	12.3 ± 1.1	15.7 ± 0.8	15.3 ± 1.4	16.9 ± 2.5	13.7 ± 1.2
Kerangas					
% N Initial	**1.10 ± 0.13^{a}**	**1.11 ± 0.12^{a}**	**1.11 ± 0.04^{a}**	**0.89 ± 0.06^{ab}**	**0.70 ± 0.09^{b}**
% P Initial	**0.087 ± 0.005^{a}**	**0.086 ± 0.006^{a}**	**0.079 ± 0.006^{ab}**	**0.073 ± 0.004^{ab}**	**0.062 ± 0.002^{b}**
% C Initial	53.9 ± 3.1	53.1 ± 4.6	54.5 ± 3.7	52.7 ± 4.7	53.0 ± 2.3
C:N	68.7 ± 23.4	55.0 ± 10.3	50.1 ± 4.3	62.2 ± 7.1	87.8 ± 12.7
C:P	**639.6 ± 55.4^{ab}**	**628.9 ± 63.0^{b}**	**711.9 ± 57.4^{ab}**	**719.0 ± 53.0^{ab}**	**864.1 ± 41.1^{a}**
N:P	12.7 ± 1.6	12.9 ± 1.2	14.6 ± 1.0	12.6 ± 1.2	11.4 ± 1.4

For habitat and family, the denominator degrees of freedoms are 8 and 64, respectively(Kenward-Roger method).

Table 4.4: The influence of source litter, where littered is placed, family, andtheir interactions on litter percent mass loss, nitrogen release, and phosphorusrelease in linear mixed models. Values in boldface indicate significant effectswith $P < 0.05$.

	% Mass Loss		**% N Release**		**% P Release**		
	F	*P*	*F*	*P*	*F*	*P*	d.f.
Source Litter	1.6	0.238	3.2	0.112	0.1	0.768	1
Litter Place	2.2	0.144	0.8	0.368	0.2	0.634	1
Family	**13.1**	**<0.001**	**6.5**	**<0.001**	**14.6**	**<0.001**	**4**
Source Litter * Litter Placed	0.9	0.349	0.2	0.648	0.0	0.947	1
Source Litter * Family	0.7	0.605	1.6	0.181	1.0	0.403	4
Litter Placed * Family	2.3	0.057	1.2	0.332	**2.5**	**0.047**	**4**
Source Litter * Litter Placed * Family	0.7	0.609	0.1	0.988	0.6	0.680	4

For litter placed and family, the denominator degrees of freedoms are 144 while for source litterthe degrees of the denominator degrees of freedoms are eight.

4.4.2 Decomposition and home-field advantage

Litter mass loss was significantly affected by where litter was sourced and plant family (Table 4.4). Generally, mass loss was higher for litter sourced from kerangas plots than that from peat plots and the highest litter mass loss occurred for Euphorbiaceae while the lowest mass loss was for Myrtaceae (Figure 4.1A). For the five plant families examined, no significant differences between peat and kerangas were observed for nitrogen release (N%) and phosphorus release (%P) (Table 4.4, Figure 4.1B-C). However, nitrogen release and phosphorus release were significantly affected by plant family. Overall, the highest litter nitrogen release occurred for Euphorbiaceae while the lowest nitrogen release was for Myrtaceae. Similarly, the highest litter phosphorus release occurred for Euphorbiaceae and Fabaceae while the lowest phosphorus release was for Myrtaceae.

There were no significant interactions between source litter and litter placed, indicating that there were no interactions between the origin of the litter and the away environment and therefore no HFA effects (Table 4.4). Additional decomposition at home (ADH) for percent litter mass loss, nitrogen release, and phosphorus release was not affected by habitat, plant family, and their interaction (Table 4.5) and was not significantly different from zero as follows: for mass loss (t = 1.7, d.f. = 89, P = 0.088), for nitrogen release (t = 1.2, d.f. = 89, P = 0.247), and for phosphorus release (t = -1.0, d.f. = 89, P = 0.335).

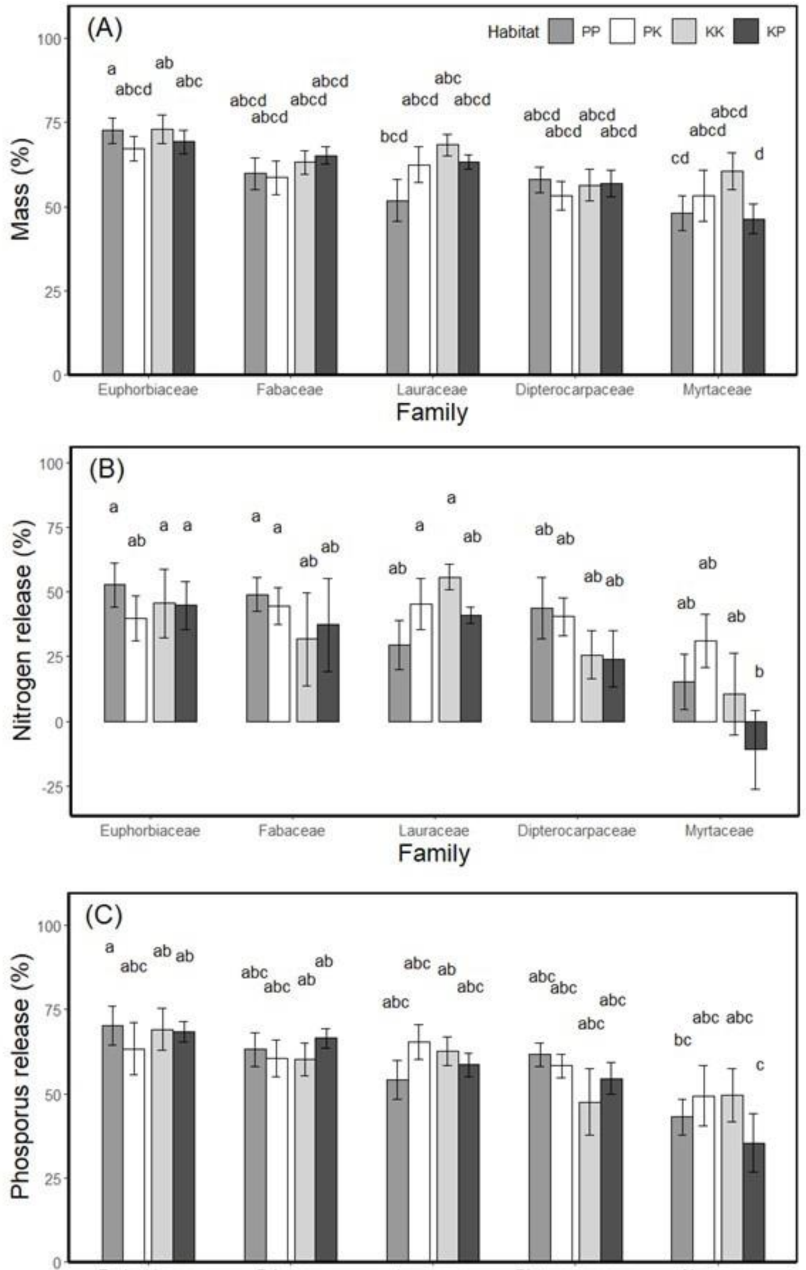

Figure 4.1: Mean litter **(A)** mass loss (%), **(B)** nitrogen release (%), and (C) phosphorus release (%) ± SE from litter for each of five families sourced and placed in either peat or kerangas plots after 11 months of decomposition (N=18). PP is litter sourced from peat and placed in peat. PK is litter sourced from peat and placed in kerangas. KK is litter sourced from kerangas and placed in kerangas. KP is litter sourced from kerangas and placed in peat. Bars topped by the same letter are not significantly different at $P < 0.05$ (Tukey's post hoc test).

Table 4.5: The influence of peat versus kerangas (‘habitat’), family, and theirinteraction on the additional decomposition at home (ADH) for percent litter mass loss, nitrogen release, and phosphorus release test in linear mixed models. Values in boldface indicate significant effects with $P < 0.05$.

	F	d.f.	*P*
% Mass loss			
Habitat	0.7	1	0.436
Family	2.4	4	0.059
Habitat* Family	0.1	4	0.983
% Nitrogen Release			
Habitat	0.9	1	0.364
Family	0.5	4	0.740
Habitat * Family	1.7	4	0.172
% Phosphorus Release			
Habitat	1.2	1	0.307
Family	0.4	4	0.797
Habitat * Family	0.7	4	0.591

Notes: F = *F*-value, d.f. = degrees of freedom, *P* = value. For habitat, family and their interaction, the denominator degrees of freedoms are 8, 64, and 64 respectively (Kenward-Roger method).

4.4.3 Relationship with litter and soil nutrients

Litter mass loss increased with increasing litter P, soil N:P, and soil NH_4^+ while it decreased with increasing litter C:P, soil C, and soil C:P (Table 4.6). In contrast, ADH for mass loss was negatively related to litter P but was unrelated to any other litter or soil nutrient variables (Table 4.7). Litter nitrogen release increased with increasing litter N, P, C:P, and N:P and decreased with litter C:N, but was unrelated to any soil nutrient variables (Table 4.6). Meanwhile ADH for nitrogen release increased with increasing litter C:N and decreased with increasing litter N, but was unrelated to any other litter or soil nutrient variables (Table 4.7). Litter phosphorus release increased with increasing litter N, P, C, and soil N, while it decreased with increasing litter C:P and N:P ratios (Table 4.6). In contrast, ADH for phosphorus release increased with increasing soil C:N and decreased with increasing soil N but was otherwise unrelated to any litter or soil nutrient variables (Table 4.7).

4.5 Discussion

We found no difference in decomposition rates and nutrient release between litter placed in kerangas forest and that placed in peat forest. We also found that litter sourced from kerangas vegetation did not decompose or release nutrients faster than that from peat vegetation regardless of where it is placed. Furthermore, we found no home field advantage in either forest type. Despite this, we did find that litter nutrient concentrations were strong predictors of litter mass loss and nutrient release across litter types. These findings are now discussed to enhance our understanding of how plant litter decomposition may contribute to peat accumulation in tropical forest soils.

4.5.1 Decomposition in peat and kerangas forests

Contrary to our first hypothesis, we found that mass loss and nutrient release rates were comparable for litter placed in kerangas forest and in peat forest. This occurred despite peat representing a much more waterlogged and anoxic environment, suggesting that the peat environment supports specialized anaerobic microbes that efficiently break down the leaf litter in those conditions (Andersen et al., 2013). Our findings are consistent with Moore and Basiliko (2006) which showed that decomposition rates are not always faster in well-drained habitats than in waterlogged habitats that experience a similar climate. In contrast to our hypothesis, we also found that litter sourced from kerangas vegetation did not decompose and release nutrients faster than that from peat vegetation in either forest type. In a global data analysis, Veen (2015a) found dissimilarity in litter quality between ‘home’ and ‘away’ sites as a key factor influencing the differing decomposition rates across habitats, and our lack of differences in decomposition between kerangas and peat litter is reflective of the lack of difference in litter quality between the two habitats. Conversely, decomposition varied significantly across plant families in both habitat types, with Euphorbiaceae decomposing fastest and Myrtaceae decomposing slowest, in line with their high and low litter N and P contents, respectively (Figure 4.1A and Table 4.3). This means that most of the variability in litter decomposition in our study system is driven by variation in traits among taxa within forest types (Cornwell et al. 2008, Richardson et al. 2008) rather than by variation among habitats.

While the 1 mm mesh litterbags in our study may have altered redox potential by restricting oxygen exchange in both peat and kerangas forests, it is important to acknowledge that the two environments present inherently different conditions. In peat forests, where litterbags were at times fully submerged, the redox potential would be

Table 4.6: Pearson's correlation coefficient (r; N = 18) of percent litter massloss, nitrogen release, and phosphorus release versus initial litter nutrient and soil nutrient variables: nitrogen content (N) , phosphorus content (P), carbon content (C), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P),and nitrogen to phosphorus ratio (N:P). Values in boldface indicate significant effects with $P < 0.05$.

	% Mass Loss r (*P*)	% N Release r (*P*)	% P Release r (*P*)
Litter			
N	0.078 (0.296)	**0.629 (<0.001)**	**0.151 (0.043)**
P	**0.294 (<0.001)**	**0.276 (<0.001)**	**0.475 (<0.001)**
C	0.007 (0.922)	0.035 (0.641)	**0.267 (<0.001)**
C:N	0.105 (0.3230	**-0.538 (<0.001)**	0.056 (0.453)
C:P	**-0.178 (0.093)**	**0.191 (0.010)**	**-0.156 (0.036)**
N:P	-0.138 (0.194)	**0.487 (<0.001)**	**-0.151 (0.043)**
Soil			
N	0.047 (0.536)	-0.045 (0.548)	**0.157 (0.035)**
P	-0.083 (0.270)	-0.089 (0.233)	0.095 (0.204)
C	**-0.156 (0.037)**	0.083 (0.271)	0.058 (0.440)
C:N	**-0.179 (0.016)**	0.108 (0.150)	-0.044 (0.558)
C:P	-0.019 (0.797)	0.146 (0.051)	-0.109 (0.144)
N:P	**0.156 (0.037)**	-0.100 (0.179)	0.046 (0.542)
NO_3^-	-0.107 (0.153)	0.024 (0.748)	0.033 (0.664)
NH_4^+	**0.153 (0.040)**	-0.087 (0.248)	0.009 (0.904)

Notes: r = correlation coefficient, *P* = *P*-value.

significantly lower due to anoxic conditions. This could have led to a greater degree of organic matter preservation compared to kerangas forests, where litterbags were placed in well-drained soils with intermittent oxygen availability. Even if the kerangas litterbags had restricted air movement and thus slightly reduced redox potential, the environmental context is vastly different from the fully submerged, oxygen-deprived conditions of peat soils.

4.5.2 Home-field advantage (HFA) in litter decomposition

In contrast to our second hypothesis, we observed no evidence for HFA in either peat or kerangas forest, and therefore no evidence to support our hypothesis that HFA will be stronger in peat or for plant taxa that produce poorer quality litter. This is likely due to high tree diversity in both environments which could prevent decomposer communities from specializing on particular litter types, thus limiting HFA (Lam et al., 2021). This is in contrast with an analogous study in a forest with lower tree diversity which found individual tree species to create a home-field advantage for their own litter through their effects on soil properties (Vivanco and Austin, 2008). Our findings are also inconsistent with a reciprocal litter transplant litterbag study that observed a positive HFA effect in a tropical peat forest dominated by a single species of palm in Panama (Hoyos-Santillan et al., 2018), suggesting that HFA may only occur in peat forest ecosystems with a lower number of (co)dominant species than occurred in our study sites. Our findings are however in line with studies that found no consistent HFA effects in freshwater swamp forests in Singapore (Lam et al., 2021), and a neotropical heath forest in northern Brazil (de Alencar et al., 2022), both of which are species rich systems. Despite the challenging anoxic conditions in peat, which typically slow or halt decomposition, microbes in peat forests are specialized for functioning in waterlogged conditions and maintaining similar decomposition rates to microbes in kerangas forests. The presence of these microbes in peat forests is further supported by a previous study, which measured an average soil respiration rate of 359 mg CO_2 m^{-2} hr^{-1} on the same peat dome (Lupascu et al., 2020b). Although this rate does not differentiate between plant (root) and microbial respiration (Hanson et al., 2000; Kuzyakov, 2006), it suggests that significant microbial activity is occurring even under the waterlogged conditions of the peat forest.

4.5.3 Role of litter traits and soil nutrient status in driving HFA

We found that litter nutrients (and to a lesser extent soil nutrients) served as predictors of litter mass loss, nitrogen release, and phosphorus release, in part because those families that decomposed fastest had higher litter N and P than those that decomposed slowest. Despite this, litter and soil nutrient properties were generally unable to predict HFA. This limited predictive power is likely due to the low level of dissimilarity in plant community composition at least at the family level (Table 4.1) and in soil properties (Chapter 3, Table 3.1) between 'home' and 'away' sites, given that dissimilarity in these types of attributes across sites are the most important drivers of home field-effects (Veen et al., 2015a; Oliva et al., 2023). Our results therefore contrast recent findings that HFA effects vary across some ecosystems as a result of changes in soil litter quality and the efficiency of decomposers within soil communities (Wang et al., 2020) but agree with another study showing that home-field effects are generally independent of variation in climate conditions and soil properties (Veen et al., 2015b).

The finding that family-level influences on leaf traits are stronger than site-specific effects suggests that these traits are deeply phylogenetically conserved. Traits like LMA, LDMC, and phosphorus resorption appear to be genetically controlled, showing limited plasticity and making them less adaptable to variations in environmental conditions (Wright et al., 2004; Donovan et al., 2011). These low-plasticity traits may have evolved within plant families to be well-suited to a narrow range of aboveground environmental conditions, which leads to consistency in trait expression across sites.

Aboveground, both forest types are comparable in characteristics such as tree abundance, stand basal area, ground cover, and diversity, despite significant differences in soil conditions between the waterlogged peat and well-draining kerangas sites. This similarity aboveground likely reduces the selective pressure for leaf trait adjustments between sites, thereby further supporting the consistency of family-level traits. These findings highlight how evolutionary history has shaped functional traits within lineages to remain stable across varying conditions (Ackerly, 2003), suggesting that aboveground habitat uniformity can reinforce trait conservation even amid differing soils.

Table 4.7: Pearson's correlation coefficient (r; N = 18) of additional decomposition at home (ADH) for percent litter mass loss, nitrogen release, and phosphorus release versus initial litter nutrient content and soil nutrient variables: nitrogen content (N), phosphorus content (P), carbon content (C), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P), and nitrogen to phosphorus ratio (N:P). Values in boldface indicate significant effects with $P < 0.05$.

	ADH % Mass Loss r (*P*)	ADH % N Release r (*P*)	ADH % P Release r (*P*)
Litter			
N	-0.153 (0.150)	**-0.214 (0.043)**	-0.051 (0.636)
P	**-0.217 (0.040)**	-0.090 (0.401)	-0.094 (0.380)
C	-0.083 (0.435)	0.101 (0.342)	0.065 (0.543)
C:N	0.079 (0.460)	**0.316 (0.002)**	-0.012 (0.911)
C:P	0.102 (0.339)	0.142 (0.182)	0.100 (0.347)
N:P	-0.005 (0.964)	-0.169 (0.112)	0.021 (0.847)
Soil			
N	-0.105 (0.327)	-0.032 (0.768)	-0.173 (0.103)
P	0.079 (0.461)	0.108 (0.310)	0.031 (0.769)
C	0.080 (0.455)	-0.080 (0.455)	0.193 (0.068)
C:N	0.131 (0.220)	-0.071 (0.508)	**0.269 (0.010)**
C:P	-0.051 (0.634)	-0.192 (0.069)	0.025 (0.814)
N:P	-0.173 (0.102)	0.014 (0.892)	**-0.314 (0.003)**
NO_3^-	-0.131 (0.217)	-0.191 (0.071)	0.011 (0.919)
NH_4^+	-0.147 (0.166)	0.043 (0.686)	-0.165 (0.119)

Notes: r = correlation coefficient, *P* = *P*-value.

4.5.4 Carbon accumulation in peat forests

Our study explored the decomposition processes that could potentially underpin peat accumulation in tropical forests, by highlighting that rates of plant litter decomposition and nutrient release are similar in both waterlogged peat and well-drained kerangas forest, and that peat accumulation is therefore unlikely to be driven by differences in the rates of decomposition of freshly fallen litter between the two environments. Additionally, the lack of HFA in both peat and kerangas forests suggests that peat accumulation is not affected by differences in HFA and therefore the pre-adaption of the decomposer communities between the two environments. Overall, our findings show that initial leaf litter decomposition processes, and the traits that underpin these processes, do not contribute to organic matter accumulation in peat forests, despite a widespread view that these are important determinants of soil carbon sequestration (Berg and Meenteneyer, 2002; Wardle et al., 2004).

What causes organic matter to accumulate in peat forests but not in kerangas forests, given their similar leaf litter decomposition rates and leaf litter qualities, and the absence of HFA? One possibility is that the activity of larger soil fauna such as termites, which are important drivers of decomposition in tropical forests (Seibold et al., 2001; Zanne et al., 2022) could be impeded by anoxic conditions and waterlogging in peat forests (Coyle et al., 2017; Mishra et al., 2021). The effects of these fauna were excluded in this experiment due to the use of 1 mm mesh litterbags (Bradford et al., 2002).

A second possibility is that while this study focused on leaf litter, a substantive proportion of litter in these ecosystems consists of wood and roots (Andriesse, 1988; Ong et al., 2015), whose quantity and quality could potentially vary between peat and kerangas forests. Recent studies suggest that the more recalcitrant nature of wood and roots, particularly in waterlogged peat soils, leads to slower decomposition rates, contributing to long-term soil organic matter (SOM) accumulation (Crowther et al., 2019; Lavallee et al., 2020).

A third possibility is that the litter initially accumulates on the ground surface (which is where our litter bags were placed) and in peat forest this surface is less consistently waterlogged than deeper in the soil profile. It could be that litter material that remains undecomposed after the first year or two subsequently integrates into the deeper soil layers where it encounters more consistently waterlogged and anoxic conditions which impedes further breakdown (Frolking et al., 2010). This is supported by findings that SOM accumulation in tropical peatlands is less a function of fresh litter decomposition and more dependent on the long-term preservation of organic materials in anaerobic conditions (Hoyt et al., 2021).

Additionally, soil processes such as physicochemical stabilization, where organic matter binds with minerals or is incorporated into soil aggregates, can further slow decomposition and enhance carbon sequestration in peat soils (Lehmann and Kleber, 2015). Thus, while leaf litter decomposition rates may be similar between peat and kerangas forests, the stabilization of SOM in waterlogged peat environments, due to both biological factors (e.g., faunal exclusion) and physicochemical processes, plays a crucial role in the observed carbon accumulation (Kuzyakov et al., 2020).

4.6 Conclusions

Our results highlight that despite waterlogged and anoxic conditions in peat forest, there is little difference between peat and kerangas environments in leaf litter quality or the decomposition processes that we studied. Despite their similarities, peat forests, which are rich in biodiversity and dense in carbon, are severely threatened ecosystems. This necessitates the maintenance and restoration of their hydrology to preserve their ecosystem functions and carbon storage potential, particularly in the face of land use changes that impact on groundwater levels (Holden et al., 2004, Li et al., 2007). Ultimately these forests are critical carbon sinks, but contrary to studies pointing to leaf litter quality and initial decomposition of leaf litter driving C storage in many ecosystems (García-Palacios et al., 2003; Wieder et al., 2009), we find little evidence that this contributes to the enormous accumulation of organic matter in peatlands. As such, there is a need to explore other drivers to better understand processes that lead to this accumulation.

Chapter 5

Peatland degradation: examining impacts on soil, plant diversity, forest structure, and biomass

5.1 Abstract

Tropical peatlands, which are a critical global sink storage, are increasingly being threatened by deforestation, drainage, and fires. Despite their importance and the threats that they face, the influence of tropical peat forest degradation on belowground and aboveground forest characteristics is not well understood. This study examined the effects of fire and drainage on tropical peat forests in the Badas Forest Reserve in Brunei Darussalam, with focus on how these factors impact forest biodiversity, structure, and carbon storage. We established five replicated transects of 1,800 meters length each across a large peat dome; each of these transects represented a degradation gradient from pristine to severely degraded peat forest. Belowground, our study revealed that total phosphorus and dissolved organic nitrogen and carbon to be least on the most degraded sites while ammonium was invariant across the degradation gradient. Total phosphorus was 45.4% lower, dissolved organic nitrogen 32.9% lower, and dissolved organic carbon 34.4% lower compared to pristine sites. Aboveground, we found that fire and drainage significantly reduced tree abundance, diversity, and biomass, and that early in the degradation process there was a loss of large dipterocarp trees that led to a significant decline of aboveground carbon storage, totaling

approximately 620 kt across 1,980 hectares of the peat dome. These insights underscore the importance of early intervention in forest degradation for effective conservation strategies and emphasizes the need for comprehensive management approaches to maintain these critical carbon and biodiversity reservoirs.

5.2 Introduction

Tropical peatlands are mostly forested ecosystems with deep layers of peat formed from partially decomposed woody vegetation, often extending up to 20 m in depth (Anderson, 1983), and as such they are distinct from temperate peatlands that originate primarily from low-statured vegetation such as *Sphagnum* moss, sedges, pines or black spruce trees (Rydin and Jeglum, 2013). Despite occupying only around 3% of the global land area, peatland ecosystems are critical carbon sinks, which collectively sequester an estimated 500-700 Gt of carbon (Page et al., 2011; Page and Hooijer, 2016; Leifeld et al., 2019). Tropical peatlands occupy an area of nearly 500,000 km^2, and they store about 105 Gt of carbon in both forest biomass and subterranean peat deposits (Crezee et al., 2022; Hastie et al., 2022). Despite their critical role in the global carbon cycle and as reservoirs of biodiversity, tropical peatlands face rapid depletion from deforestation, drainage, and burning. Currently in Southeast Asia less than 30% of peat forest cover remains (Murdiyarso et al., 2010; Hooijer et al., 2012; Mishra et al., 2021) and if current degradation rates continue, 98% of these peatlands could disappear by 2100 (Page et al., 2011; Leifeld et al., 2019).

Despite their importance and the threats that they face, the influence of tropical peat forest degradation on aboveground and below ground community and ecosystem properties are not well understood. Fires in tropical peat forests not only impact the aboveground vegetation but also burn the underlying peat, resulting in the emission of significantly more CO_2 compared to forest fires on mineral-rich soils (Page et al., 2002; Ballhorn et al., 2009; Cochrane et al., 2009). Peat forest fires also affect forest structure and diversity by greatly decreasing the abundance of many plant, animal, and microbial taxa (Agus et al., 2019; Mishra et al., 2021). Fire impacts soil properties by initially releasing mineral nutrients and increasing pH through peat breakdown and ash accumulation, but also causing longer-term reductions in soil fertility as a result of loss of total nutrient capital from the system (Agus et al., 2019). Further, drainage of peatlands and the resultant lowering of the water table leads to increased soil subsidence, greenhouse gas release, and susceptibility to fires (Mishra et al., 2021; Somers et al., 2023). Studies that have analysed peat forest characteristics typically focus on either pristine sites or degraded sites. As a result, there is a lack of studies that have directly analysed how peat forest characteristics change along degradation gradients. In addition, few studies characterize the dual effects of both fire and drainage degradation on peatlands even though these effects frequently occur in tandem.

Located in northwest Borneo, Brunei contains 4,018 km^2 of forest, of which 79% is relatively intact, 15% is degraded, and 6% is severely degraded (Bryan et al., 2013). Approximately 909 km^2 or 23% of the total forested area of Brunei is under peat forest (Kobayashi, 2016). In the Belait District, the Badas Forest Reserve contains the Badas peat dome which is 15.5 km wide and across it there is a strong degradation gradient of peat forest ranging from pristine to severely degraded (Becek et al., 2022). Specifically, a 1-2.5 m deep drainage canal of approximately 7 km length was dug across part of the Badas peat dome along the Jalan Badas road by the early 1950s, which resulted in significant drainage and peat subsidence (Suhip et al., 2020). Further, over the past few decades, fires have repeatedly occurred across the affected area with a major fire occurring in early 2016 (Addly et al., 2022). While a few studies have characterized tree diversity and community structure of the Badas peat dome (Anderson, 1963; Hassan et al., 2016; Nafiah et al., 2022), there is a scarcity of research specifically addressing the impacts of fire and drainage degradation of tropical forested peat domes (Cobb et al., 2020; Addly et al., 2022; Somers et al., 2023). As a result, we still have a limited understanding as to the extent of the impact of fire and drainage on below ground and above ground characteristics in tropical peat forests. Thus, the degradation gradients across the Badas peat dome in Brunei presents a crucial opportunity to examine the consequences of fire and drainage on tropical peat forests.

In this study system, we set up transects across the Badas peat dome to assess the gradient from pristine forest to forest that has been highly degraded by drainage and fire. The main aim of our research was to analyse the effect of fire and water drainage on aboveground and belowground characteristics across these transects. We tested the following hypotheses to accomplish this aim:

> (H1) available nutrients will be highest in heavy degraded and most degraded plots due to lower water table levels which allows for increased mineralization.
>
> (H2) plant diversity and community structure will shift significantly along the degradation gradient, with lower diversity and greater domination by resource-acquisitive plant taxa in the intermediate to most degraded areas (due to the increased mineralization and canopy openness) as compared to higher diversity and domination by resource-conservative plant families in lightly degraded and pristine areas.

> (H3) as forest degradation intensifies, tree abundance, stand basal area, canopy height and emergent layer height will decrease due to the loss of mature trees and the consequent reduction in canopy complexity. Meanwhile ground cover will increase due to increased light and nutrient availability favouring fast-growing plant species.

In addition to addressing these hypotheses, we attempted to quantify how much biomass and carbon was lost due to peatland degradation (drainage and fire) in the vicinity of the Jalan Badas road. By addressing these hypotheses in combination, we aim to better understand how fire and drainage degradation affects peat forest in order to better inform peatland restoration.

5.3 Methods

5.3.1 Experimental design

The study was conducted in the Badas Forest Reserve, Belait District, Brunei Darussalam. We established five transects in November 2022, with each transect consisting of five plots resulting in a total of 25 plots (Figure 5.1). The start of each transect was established near an extensive peatland drainage canal alongside the Jalan Badas road (Figure 5.1). A degradation gradient, influenced by both fire and drainage, was observed, with greater disturbance occurring with increasing proximity to the canal (Addly et al., 2022). Along this gradient, the forest near the canal is gone due to drainage and repeated fires, leaving the most degraded and heavily degraded areas in the open. The intermediate degraded areas are closer to the forest edge, while lightly degraded and pristine areas are further into the forest (Figure 1.3). Canals have been shown to lower the water table by up to 0.50 m near the canal compared to 1000 m away (Ritzema et al., 2008), leading to increased peat oxidation, subsidence, and fire risk (Sinclair et al., 2020). A previous study, which included two transects from this research, found that fire occurrence was highest (~4 fires) near the canal and decreased toward the forest edge (~1 fire), (Addly et al., 2022). These factors create a clear degradation gradient, which was used to define the stages of degradation. The minimum distance between adjacent transects was 500 m. Along each transect, we categorized five plot types based on their proximity to the drainage canal and degradation intensity: ‘pristine’ plots (1.8 km from the canal, no fire occurrences, minimal impact from drainage), ‘lightly degraded’ (800 m from the canal, no fire occurrences, some impact from drainage), ‘intermediate degraded’ (200 m from the canal, some fire occurrences, moderate impact from drainage), ‘heavily degraded’ (60 m from the canal, moderate fire occurrences, heavy impact from drainage), and ‘most degraded' (25 m from the canal, most fire occurrences, largest impact from drainage). At leach plot location we set up a 20 m x 20 m plot with poles and flagged all trees of at least five cm diameter at breast height (DBH). Within each plot we set up a10 m x 10 m subplot and flagged all trees of at least one cm diameter at breast height (DBH). To better represent the sparser large-DBH trees in the 'Pristine' and 'Lightly degraded' plots, we set up a larger 40 m x 40 m plot centred on the 20 m x 20 m plot, and flagged all trees with a diameter at breast height (DBH) of at least 10 cm. Plots were set up in November 2022, and all measurements and sampling were performed over the following month.

Within each peat plot one composite soil sample was collected to 15 cm depth. Each composite sample was collected by selecting eight points (two in each quadrant of the plot) and sampling soil at each point. All eight soil samples within each plot were collected using a Russian peat corer, bulked, and homogenised manually by thorough mixing in a sealed plastic bag. All samples were packaged in the field in double zip-lock bags and kept cool until analyses were performed. Samples were weighed to measure wet weight, oven dried at 60°C for three days, then weighed again to record dry weight. Bulk density was determined using the oven dry weights and known volume of each sample. Potassium chloride (KCl) extraction (Øien and Selmer-Olsen, 1980; Gianello and Bremner, 1986) was performed on fresh subsamples of each composite sample (10 g with 50 ml 1M solution KCl) for subsequent analysis of mineral nutrients. All samples were sent by courier to Singapore for nutrient analysis.

5.3.2 Soil properties

Soil chemical properties were measured in the same way as in Chapter 3. A subsample of the fresh composite soil from each plot was measured for available nutrients. KCl extractions were used to measure nitrate (NO_3^-) and ammonium (NH_4^+) using a SEAL AutoAnalyzer (SEAL Analytical, USA, model AA500). Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in the KCl extracts using a Total Organic Carbon analyzer (Shimadzu Scientific Instruments, Japan, model TOC-LCPH).

An oven-dried subsample of each soil composite was measured for total nutrients. Total N and total C concentrations were measured using the Dumas method determined by CHNS elemental analyzer (Elementar, Germany, model Vario El Cube). Total P was determined using the molybdenum blue method with ascorbic acid (Murphy and Riley, 1962). This involved sample ignition (550°C for 1 h) and extraction in 1 M H_2SO_4

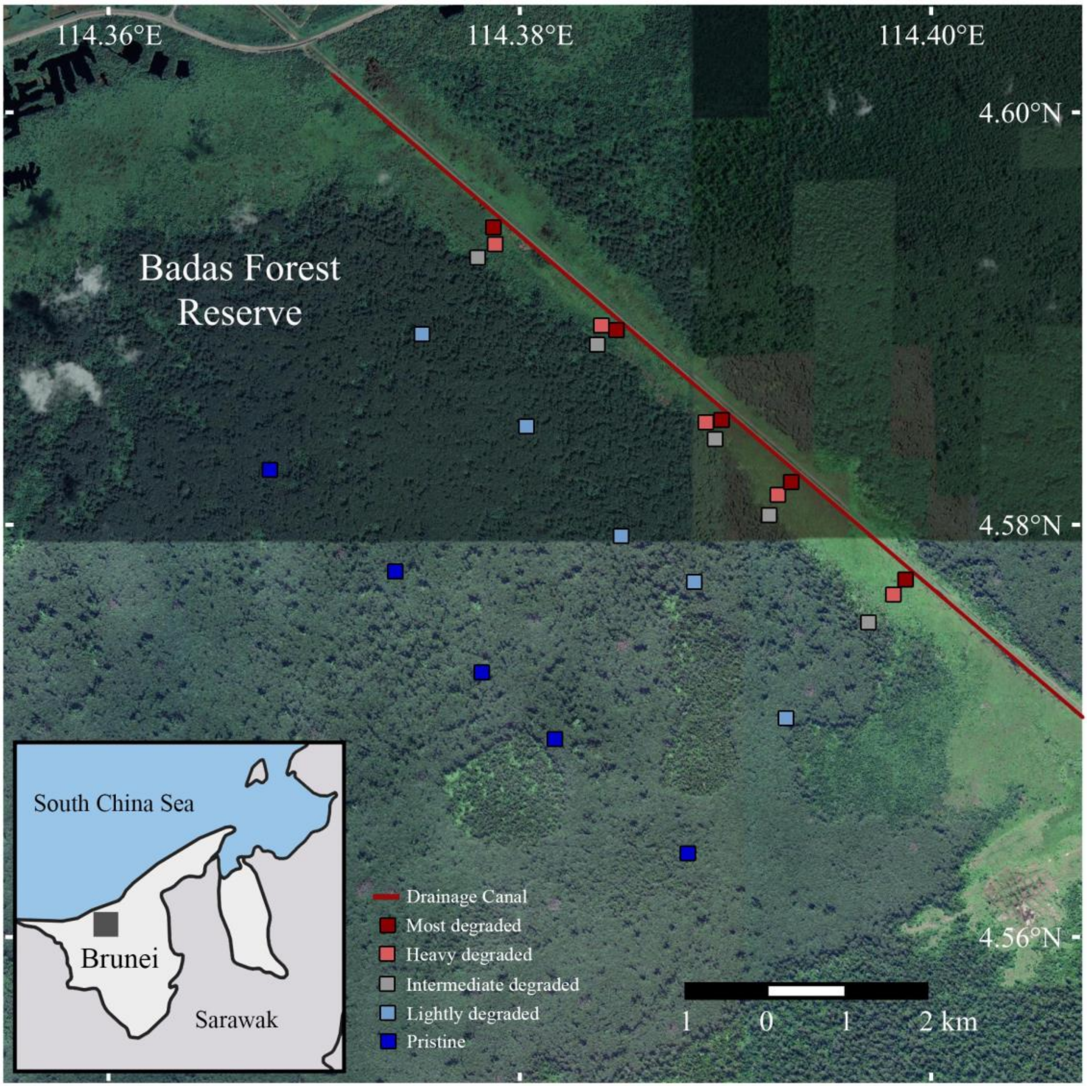

Figure 5.1: Location of the study sites in the Badas Forest Reserve, Belait District, Brunei Darussalam. Twenty-five 400 m^2 plots were established along five fire and drainage degradation transects. The red line is the drainage canal. Dark blue squares are pristine plots, light blue are lightly degraded, gray are intermediate degraded, light red are heavy degraded, and dark red squares are the most degraded plots. The location of the forest reserve within Brunei Darussalam is shown in the inset.

(1:50 soil/solution ratio, 16 h), with PO_4 detection by automated molybdate colorimetry using a Tecan Spark Multimode Microplate Reader (Tecan Group, Switzerland). Soil C to N, C to P, and N to P ratios were determined from these values.

5.3.3 Floristic measurements and biomass estimation

For each plot, the diameter at breast height (DBH) of each stem with a DBH greater than five cm was measured and identified to at least the family level. For each subplot, each stem with a DBH greater than one cm was measured and identified to at least the family level. For each extended (40 m x 40 m) plot, each stem with a DBH greater than 10 cm was measured. The stem diameter and frequency data were used to determine tree abundance and stand basal area, as well as the Shannon-Weiner diversity index (family level), Simpson's diversity index (family level) and total family richness. We conducted analyses at the family level, as species-level characterization was not feasible due to the substantive biodiversity in these tropical forests. Plant families in this study were classified as 'acquisitive' or 'conservative' based on a review of the literature, which assessed traits related to the rate of foliar investment recovery and turnover of matter and energy. 'Acquisitive' species were identified by rapid resource utilization traits, while 'conservative' species exhibited slower resource use efficiency and investment return (Gorné et al., 2022). For each plot, emergent tree height and canopy tree height were estimated for multiple trees using a range finder while canopy openness was measured at the center of each plot using a spherical densiometer. Further, for each subplot, the height and percentage of ground cover of all plants occupying space on the forest floor were visually estimated and identified to at least the family level.

For each plot, aboveground biomass (ABG) of all trees over five cm DBH was determined. We applied the allometric equation presented by Chave et al. (2005) for moist tropical forests which was developed from an extensive database spanning multiple dipterocarp forests in Southeast Asia, to estimate AGB from our field measurements. AGB (kg) was estimated as:

$$\mathrm{AGB} = \rho \times e^{-1.499+2.148\times\ln(\mathrm{DBH})+0.207\times(\ln(\mathrm{DBH}))^{2}-0.0281\times(\ln(\mathrm{DBH}))^{3}}$$

where is wood density (g/cm^3) and DBH is diameter at breast height (cm). A wood density of 0.443 g/cm^3 was used for *Shorea albida* (Alan Bunga), (Monda et al., 2015) and 0.6 g/cm^3 was applied for all other species (Osunkoya et al., 2007). For each plot, the aboveground carbon of all trees over five cm DBH was determined. To do this, the biomass of each tree as described above was converted to carbon using a coefficient of 0.5 (Baccini et al., 2012).

For the peatland that we studied, aboveground carbon (AGC) loss of all heavily and mostly degraded areas was determined. We utilized QGIS (QGIS Development Team 2023), a widely used open-source GIS software, to calculate the area of the red polygon in Figure 5.2, which was identified as the most degraded areas due to their lack of tree canopy cover. AGC (kg) was estimated as:

$$\mathrm{AGC} = (\mathrm{CP} - \mathrm{CD}) \times \mathrm{TA}$$

where CP is average aboveground carbon of pristine plots (kg/ha), CD is average above ground carbon of heavily and mostly degraded plots (kg/ha), and TA is total area (ha) of the most degraded areas.

5.3.4 Data analysis

All soil variables were analysed using one-way ANOVA to test for differences among the five distinct plot types established in our study. When significant differences were found at $P = 0.05$, Tukey's post hoc test was conducted for pairwise comparisons. Data were log-transformed if needed, based on assessments of normality (using visual inspection of Q-Q plots or Shapiro-Wilk tests) and homoscedasticity (using Levene's test), to conform to the assumptions of normality and homoscedasticity for ANOVA and t-tests. Further, differences in soil variables among the five distinct plot types established in our study were assessed using principal component analysis (PCA).

All forest stand variables including community structure, forest structure, diversity, and above ground biomass were analysed using the Kruskal-Wallis test because unequal variances among means prevented us from satisfying the assumptions of ANOVA. When significant differences were found at $P = 0.05$, Bonferroni post hoc test was conducted for pairwise comparisons. To assess potential spatial autocorrelation among the plots and transects, Moran's I tests on both belowground soil properties and aboveground forest structure characteristics. Statistical analyses were performed in 'R' (R Core Team, 2021) using the FactoMineR package for PCA (Lê et al., 2008) and PMCMRplus package for non-parametric pairwise comparisons (Pohlert and Pohlert, 2018).

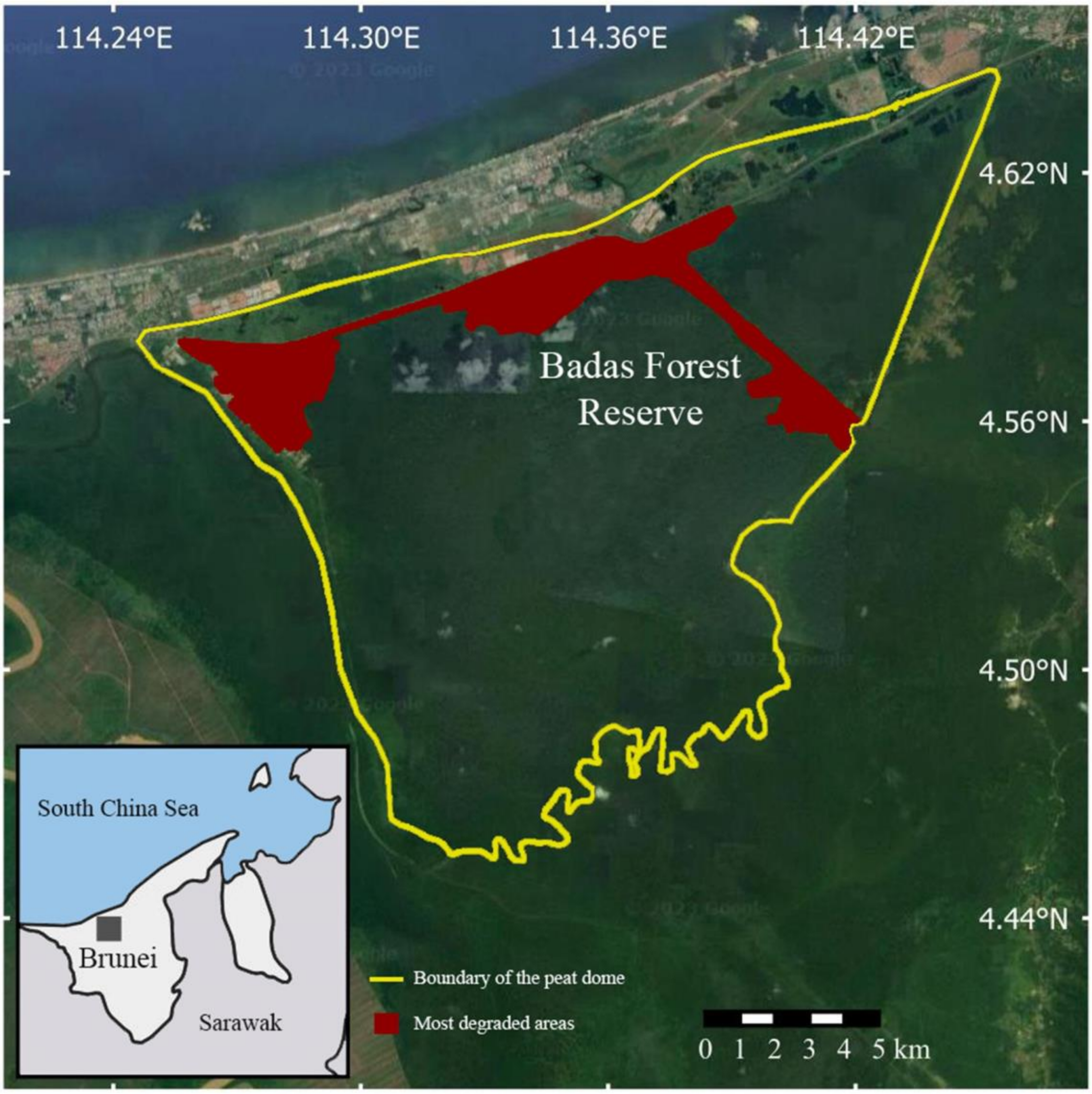

Figure 5.2: Location of the peatland and the Badas Forest Reserve, Belait District, Brunei Darussalam. The red polygon represents the most degraded areas that lack tree canopy cover. The location of peat dome and the forest reserve within Brunei Darussalam are shown in the inset.

Table 5.1: Soil nutrient relations and bulk density of five peat forest degradation stages along five fire and drainage degradation transects in Belait District, Brunei Darussalam. Values are means ± SE (N=25). Different letters among families and values in boldface indicate statistically significantly different means at $P < 0.05$ (Tukey's post hoc test).

Soil Variables	Pristine	Lightly degraded	Intermediate degraded	Heavy degraded	Most degraded	$F_{4,19}$ (P)
C (%)	47.73 ± 0.29	49.32 ± 0.85	47.93 ± 0.72	47.62 ± 0.89	43.55 ± 3.12	1.8 (0.174)
N (%)	1.51 ± 0.05	1.55 ± 0.05	1.45 ± 0.06	1.3 ± 0.05	1.2 ± 0.15	3.2 (0.038)
P (%)	**0.108 ± 0.007^a**	**0.116 ± 0.01^a**	**0.08 ± 0.008^b**	**0.07 ± 0.004^b**	**0.059 ± 0.005^b**	**14.4 (<0.001)**
C:N	31.69 ± 0.91	31.93 ± 0.53	33.14 ± 0.83	36.92 ± 1.13	37.45 ± 2.38	4.2 (0.014)
C:P	**447.69 ± 26.04^b**	**439.01 ± 37.51^b**	**624.18 ± 71.85^a**	**691.32 ± 49.67^a**	**744.07 ± 43.11^a**	**11.5 (<0.001)**
N:P	**14.08 ± 0.43^b**	**13.76 ± 1.14^b**	**18.82 ± 2.08^{ab}**	**18.81 ± 1.56^{ab}**	**20.13 ± 1.42^a**	**5.3 (0.005)**
NH_4^+ (mg/L)	2.5 ± 0.17	2.4 ± 0.19	2.8 ± 0.26	2.01 ± 0.26	2.27 ± 0.25	2.0 (0.142)
TN (µg g^{-1})	**9.04 ± 0.89^a**	**9.51 ± 0.8^a**	**9.02 ± 0.95^a**	**5.58 ± 0.49^b**	**6.07 ± 0.8^b**	**10.3 (<0.001)**
TOC (µg g^{-1})	**42.35 ± 3.58^a**	**45.72 ± 3.38^a**	**43.88 ± 3.97^a**	**25.69 ± 1.27^b**	**27.79 ± 1.6^b**	**11.2 (<0.001)**
Bulk density (g/cm^3)	**0.087 ± 0.01^{ab}**	**0.085 ± 0.008^{ab}**	**0.103 ± 0.007^a**	**0.056 ± 0.007^b**	**0.0774 ± 0.0139^{ab}**	**3.5 (0.025)**

Notes: Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in KCl extracts.

5.4 Results

5.4.1 Differences in soil variables

Soil variables differed significantly among the five peat forest degradation stages (Table 5.1). Pristine and lightly degraded plots had significantly higher concentrations of total P compared to the three other plots. Conversely, the heavy degraded and most degraded stages had significantly higher ratios of C:P and N:P compared to the three other stages. Total dissolved N and TOC concentrations were higher in the pristine, lightly degraded and intermediate stages than in the heavy degraded and most degraded stages. Moreover, the bulk density of the intermediate degraded stage was significantly (and 1.8 times) greater than that of the heavily degraded stage.

Together, the first two axes of the PCA of the accounted for 84.9% of the total variation in soil nutrients (Figure 5.3). The primary ordination axis (PC1) explained 61.0% of the variation and represented increasing values of all soil variables (NH_4+, TN, TOC, total N, total C, and total P) concentrations while the secondary ordination axis (PC2) accounted for 23.9% of the variation and represented a gradient of increasing NH_4+, TN, and TOC, along with decreasing total C, total N, and total P. There was only a modest separation of the means of the five degradation stages by the PCA, but the five stages did vary in how the individual plots were spread out. The intermediate degraded, lightly degraded, and pristine stages were represented by medium sized clusters and were associated with all measured total and available nutrients. The most degraded and

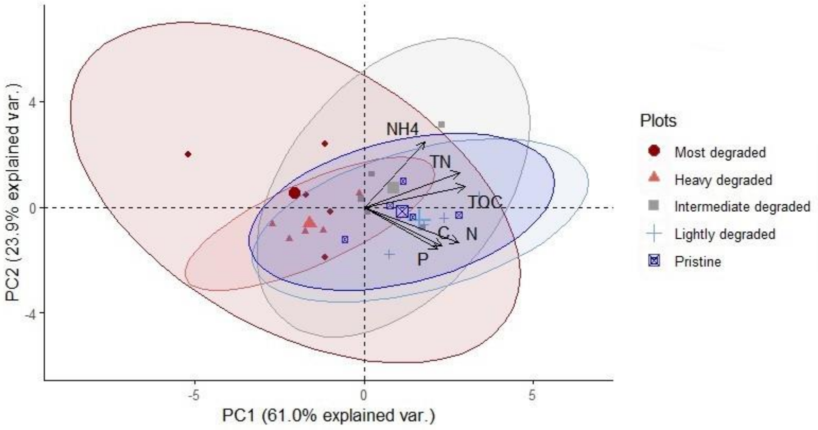

Figure 5.3: Principal component analysis of concentration of total and available nutrients of 15 cm soil cores of five peat forest degradation stages along five fire and drainage degradation transects in the Badas Forest Reserve, Brunei Darussalam. Small symbols represent individual plots while large open symbols represent overall means. Ellipses represent the 95% confidence region for each degradation stage. N, C, and P are total nitrogen, total carbon, and total phosphorus concentrations respectively. NH_4^+ is ammonium. Total dissolved nitrogen (TN) and total dissolved organic carbon (TOC) were measured in KCl extracts.

heavy degraded were represented by the largest and smallest clusters respectively and were separated from the other three soil types along PC1.

Of the ten soil variables analysed for spatial autocorrelations, only those related to phosphorus (e.g., P, CP, NP) exhibited weak but statistically significant spatial autocorrelation. In contrast, none of the six aboveground forest structure characteristics showed significant spatial autocorrelation. Given these findings, spatial autocorrelation is generally low across the dataset, with only mild effects observed in a subset of the soil properties. This suggests that overall spatial dependency is not a major factor in the data.

5.4.2 Differences in community composition

Significant differences among peat forest degradation stages were found for 10 of the 12 families when stand basal area and tree abundance were considered (Tables 5.2-3). For those 10 families, stand basal area and tree abundance was higher in pristine, lightly degraded, and intermediate degraded stages compared to the other two stages from which trees were largely absent. Some families differed also in how they varied among pristine, lightly degraded, and intermediate degraded stages. Stand basal area of Dipterocarpaceae was 1.2 times higher in pristine forest than in lightly degraded and 11.8 times higher in pristine than in intermediate degraded forest while tree abundance of dipterocarps was 1.6 times higher in pristine forest than in lightly degraded and 4.7 times higher in pristine than in intermediate degraded forest. Conversely, stand basal area of Fagaceae was 51.3 times higher in intermediate degraded than pristine forest and 13.7 times higher in intermediate degraded than in lightly degraded forest while tree abundance of Fagaceae was 3.9 times higher in intermediate degraded than pristine forest and 3.0 times higher in intermediate degraded than in lightly degraded forest.

Ground cover percentage did not differ significantly between heavily degraded and pristine plots. However, heavily degraded areas were dominated by herbaceous vegetation, particularly ferns and sedges. In most and heavily degraded plots, species such as *Stenochlaena palustris*, *Blechnum indicum*, and *Scleria purpurascens* often accounted for more than 90% of the ground cover. In intermediate and lightly degraded plots, herbaceous cover decreased as small tree regeneration increased. Pristine areas were characterized by small tree regeneration, *Pandanus*, and *Nepenthes* (pitcher plants).

Table 5.2: Tree family resource use strategies and stand basal area (m^2/ha) in five peat forest degradation stages along five fire and drainagedegradation transects in Badas Forest Reserve, Brunei Darussalam. Values are means averaged across all plots **±** SE (N=25). Significantdifferences among families were determined using the Kruskal-Wallis test ($P < 0.05$), with different letters among families and values in boldface indicating significant differences (Bonferroni post hoc test).

		Stand basal area (m^2/ha)					
Family	Resource use Strategy	Pristine	Lightly degraded	Intermediate degraded	Heavy degraded	Most degraded	χ^2 (P)
Annonaceae	CON	2.8 ± 1.8	0.01 ± 0.01	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	7.8 (0.098)
Aquifoliaceae	CON	**0.5 ± 0.3**^{a}	**1.0 ± 0.3**^{a}	**0.4 ± 0.2**^{a}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**18.2 (0.001)**
Dipterocarpaceae	CON	**142.0 ± 21.0**^{a}	**119.7 ± 32.6**^{a}	**12.0 ± 7.7**^{b}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**21.0 (<0.001)**
Euphorbiaceae	ACQ	**0.4 ± 0.3**^{ab}	**4.3 ± 2.7**^{a}	**9.0 ± 8.2**^{a}	**0.0 ± 0.0**^{b}	**0.001 ± 0.001**^{b}	**14.6 (0.006)**
Fagaceae	CON	**0.4 ± 0.2**^{b}	**1.5 ± 0.5**^{b}	**20.5 ± 4.2**^{a}	**0.0 ± 0.0**^{c}	**0.0 ± 0.0**^{c}	**20.1 (<0.001)**
Lauraceae	CON	**1.6 ± 1.1**^{a}	**0.9 ± 0.8**^{a}	**21.1 ± 20.8**^{a}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**16.7 (0.002)**
Myrtaceae	CON	**1.5 ± 1.3**^{ab}	**7.0 ± 4.8**^{a}	**18.2 ± 9.3**^{a}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**15.9 (0.003)**
Phyllanthaceae	ACQ	1.0 ± 0.7	0.07 ± 0.04	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	8.9 (0.064)
Rubiaceae	ACQ	**18.9 ± 13.3**^{a}	**4.8 ± 3.2**^{a}	**8.3 ± 4.6**^{a}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**19.1 (<0.001)**
Sapotaceae	CON	**15.9 ± 11.0**^{a}	**34.9 ± 14.5**^{a}	**16.7 ± 15.6**^{ab}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**16.7 (0.002)**
Ebenaceae	CON	**0.4 ± 0.2**^{a}	**0.3 ± 0.1**^{ab}	**4.3 ± 4.3**^{ab}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**12.0 (0.018)**
Crypteroniaceae	CON	**0.8 ± 0.7**^{ab}	**19.0 ± 16.2**^{a}	**0.7 ± 0.5**^{ab}	**0.0 ± 0.0**^{b}	**0.0 ± 0.0**^{b}	**11.2 (0.025)**

Notes: CON = resource-conservative, ACQ = resource-acquisitive, P = P-value. χ^2 = chi-square value.

Table 5.3: Tree family resource use strategies and tree abundance (number/ha) in five peat forest degradation stages along five fire and drainage degradation transects in Badas Forest Reserve, Brunei Darussalam. Values are means averaged across all plots ± SE (N = 25). Significantdifferences among families were determined using the Kruskal-Wallis test ($P < 0.05$), with different letters among families and values in boldface indicating significant differences (Bonferroni post hoc test).

		Tree Abundance (number/ha)					
Family	Resource use Strategy	Pristine	Lightly degraded	Intermediate degraded	Heavy degraded	Most degraded	χ^2 (P)
Annonaceae	CON	150. ± 63.2	10.0 ± 6.1	40.0 ± 34.1	0.0 ± 0.0	0.0 ± 0.0	7.9 (0.097)
Aquifoliaceae	CON	**115.0 ± 35.9^{b}**	**295.0 ± 45.0^{a}**	**75.0 ± 35.4^{b}**	**0.0 ± 0.0^{c}**	**0.0 ± 0.0^{c}**	**20.6 (<0.001)**
Dipterocarpaceae	CON	**140.0 ± 20.3^{a}**	**90.0 ± 20.3^{a}**	**30.0 ± 14.6^{b}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**20.2 (<0.001)**
Euphorbiaceae	ACQ	**55.0 ± 24.2^{ab}**	**175.0 ± 61.7^{a}**	**250.0 ± 165.3^{a}**	**0.0 ± 0.0^{b}**	**5.0 ± 5.0^{b}**	**14.7 (0.005)**
Fagaceae	CON	**75.0 ± 41.1^{b}**	**100.0 ± 30.6^{b}**	**295.0 ± 25.5^{a}**	**0.0 ± 0.0^{c}**	**0.0 ± 0.0^{c}**	**19.5 (<0.001)**
Lauraceae	CON	**100.0 ± 69.4^{a}**	**70.0 ± 18.4^{a}**	**85.0 ± 37.6^{a}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**17.1 (0.002)**
Myrtaceae	CON	**210.0 ± 128.6^{a}**	**200.0 ± 80.2^{a}**	**470.0 ± 139.5^{a}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**15.3 (0.004)**
Phyllanthaceae	ACQ	115.0 ± 70.5	55.0 ± 27.8	55.0 ± 25.5	0.0 ± 0.0	0.0 ± 0.0	8.8 (0.066)
Rubiaceae	ACQ	**465.0 ± 168.8^{a}**	**350.0 ± 107.5^{a}**	**535.0 ± 198.4^{a}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**18.8 (<0.001)**
Sapotaceae	CON	**100.0 ± 19.4^{a}**	**235.0 ± 73.1^{a}**	**130.0 ± 58.3^{a}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**16.1 (0.003)**
Ebenaceae	CON	**40.0 ± 12.7^{a}**	**35.0 ± 17.0^{ab}**	**45.0 ± 27.8^{ab}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**11.7 (0.020)**
Crypteroniaceae	CON	**20.0 ± 9.4^{ab}**	**60.0 ± 17.0^{a}**	**25.0 ± 15.8^{ab}**	**0.0 ± 0.0^{b}**	**0.0 ± 0.0^{b}**	**11.4 (0.023)**

Notes: CON = resource-conservative, ACQ = resource-acquisitive, P = P-value. χ^2 = chi-square value.

5.4.3 Variation in forest stand characteristics

Significant differences among peat forest degradation stages were found for all measured forest structure characteristics (Figure 5.4A-F). Pristine, lightly degraded, and intermediate degraded plots consistently displayed significantly higher values of tree abundance, stand basal area, emergent tree height, and canopy tree height compared to heavy degraded and most degraded plots. Additionally, the emergent tree height in the lightly degraded stage plots was significantly (and 2.4 times) greater than that in intermediate plots. Further, the heavy degraded and most degraded plots had a significantly higher canopy openness and ground cover percentage compared to lightly degraded and intermediate degraded plots. While ground cover percentage did not differ between heavy degraded and pristine plots, ground cover in heavy degraded areas were dominated by ferns and sedges whereas ground cover in pristine areas were dominated by *Pandanus* plants.

Significant differences among forest degradation stages were found for all measures of diversity (family, Simpson, Shannon) (Figure 5.5A-C). Pristine, lightly degraded, and intermediate degraded stages consistently showed significantly higher values for all diversity measures compared to heavy degraded and most degraded stages. Additionally, family richness was significantly higher in lightly degraded than in pristine plots, while Shannon's index was significantly higher in lightly degraded than in intermediate degraded plots.

Above ground tree biomass (ABG) also differed significantly among forest degradation stages (Figure 5.6). The heavy degraded and most degraded stages had minimal biomass. Further, above ground biomass of pristine and lightly degraded plots was both significantly (3.7 and 4.1 times, respectively) higher than in intermediate degraded plots.

The total area of the most degraded areas that lacked a tree canopy cover (the red polygon in Figure 5.2) was 1,980 ha. The average aboveground carbon of pristine plots was 315 tonnes/ha while the average aboveground carbon of heavily and mostly degraded plots zero tonnes/ha. For the peat dome that we studied, aboveground carbon (AGC) loss of the most degraded areas was estimated to 620 kt.

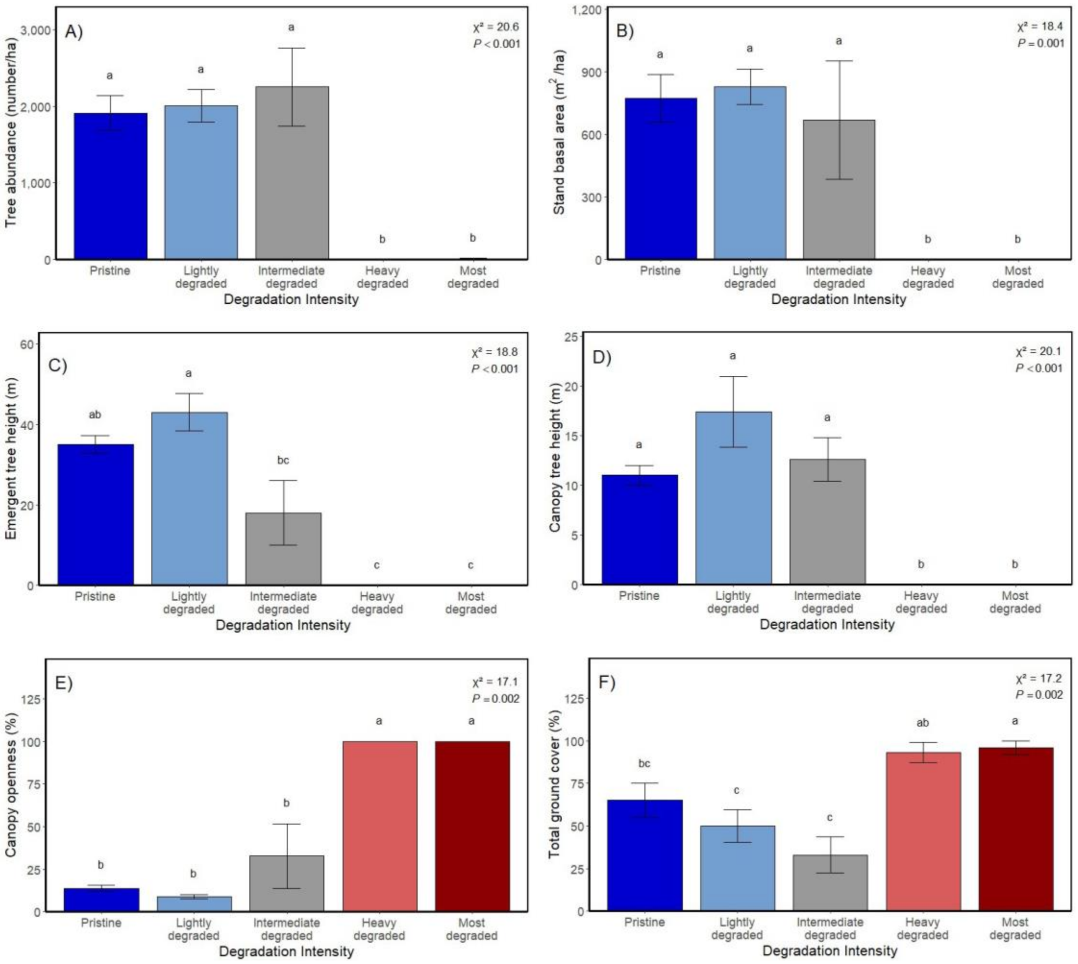

Figure 5.4: Forest structure characteristics in Badas Forest Reserve, Brunei Darussalam. Mean values and standard errors (SE) for **A)** Tree abundance, **B)** Stand basal area, **C)** Emergent tree height, **D)** Canopy tree height, **E)** Canopy openness, and **F)** Total ground cover (%) were derived from plots sampled along fire and drainage degradation transects. Significant differences among means were determined using the Kruskal-Wallis test ($P < 0.05$). Bars topped by the same letter are not significantly different at $P < 0.05$ (Bonferroni post hoc test).

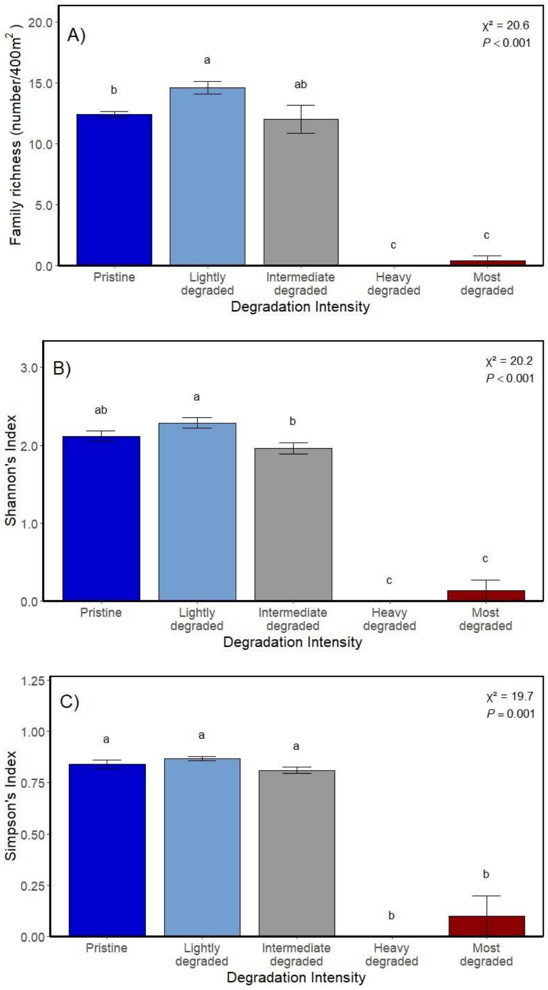

Figure 5.5: Tree diversity characteristics in Badas Forest Reserve, Brunei Darussalam. Mean values and standard errors (SE) for **A)** Family richness (number/400 m^2), **B)** Shannon's Index, and **C)** Simpson's Index were derived from plots sampled along fire and drainage degradation transects. Shannon's and Simpson's indices were computed using plant families. Significant differences among means were determined using the Kruskal-Wallis test ($P < 0.05$). Bars topped by the same letter are not significantly different at $P < 0.05$ (Bonferroni post hoc test).

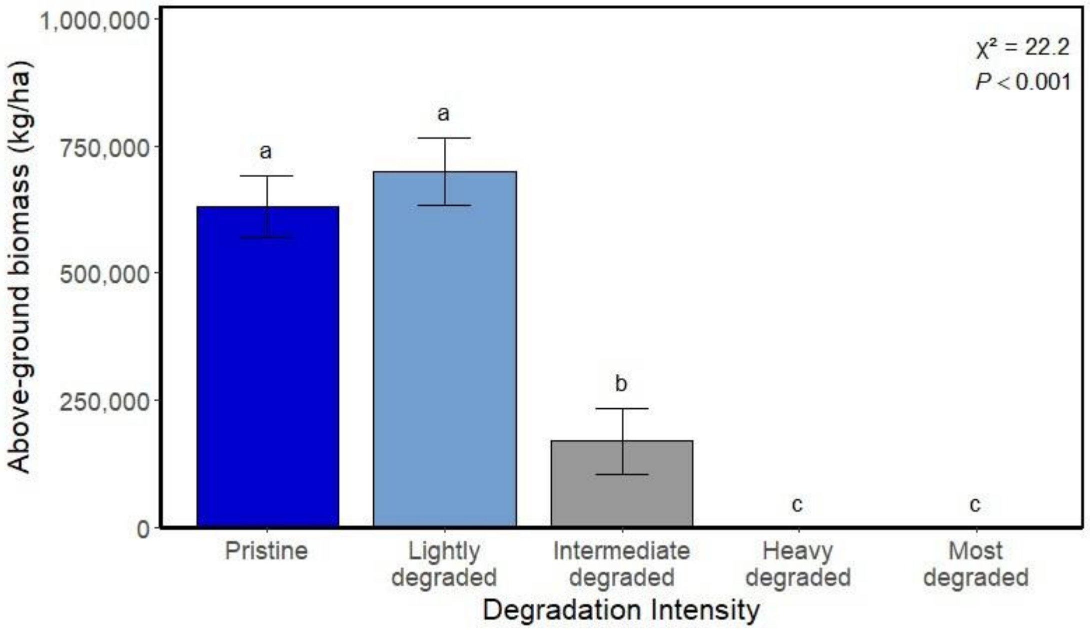

Figure 5.6: Mean above ground biomass estimates of trees (kg/ha) ± SE from plots along fire and drainage degradation transects in the Badas Forest Reserve, Brunei Darussalam. Significant differences among means were determined using the Kruskal-Wallis test ($P < 0.05$). Bars topped by the same letter are not significantly different at $P < 0.05$ (Bonferroni post hoc test).

5.5 Discussion

We found total phosphorus and dissolved organic N and C to be least on the most degraded sites. Furthermore, the most degraded plots had the lowest tree abundance, diversity, and canopy height, and greatest canopy openness and ground vegetation cover. In addition, we found that aboveground biomass decreased as degradation intensified and we quantified aboveground carbon lost due to fire and degradation associated with drainage. These findings are now discussed in the context of the structural and functional difference across degradation gradients in peat forest.

5.5.1 Soil nutrient differences

Contrary to our first hypothesis, we did not find available nutrients to be greater in the most degraded sites; instead, we found that NH_4^+ was invariant across the degradation gradient while dissolved organic N declined. Further, total P was least in the most degraded sites. This decline in nutrients with degradation is likely a consequence of aerobic conditions caused by drainage in the most degraded plots (Hoyos-Santillan et al., 2019) supporting greater microbial activity, thus initially speeding up the decomposition process and increasing nutrient mineralization, but leading to a subsequent net loss of nutrients from the system from leaching (Jauhiainen et al., 2005; Addly et al., 2022). As degradation progresses, phosphorus shifts from organic to more labile forms, which are easily lost through runoff and leaching, depleting the nutrient pool (Jauhiainen et al., 2005). In lightly degraded sites, phosphorus may still be retained in organic matter, but as degradation continues, labile phosphorus becomes dominant. In heavily degraded sites, both fire and drainage accelerate phosphorus loss through leaching and runoff, leading to phosphorus depletion, as seen in our findings. Our findings align with those of Leng et al. (2019) and Mishra et al. (2021) in emphasizing the key influence of oxygen availability and hydrological factors in impacting soil nutrient availability, dynamics, and losses in tropical peatlands.

Another possible driver of loss of available nutrients in the most degraded sites involves loss of nutrient capital associated with fire causing the burning and loss of peat and its associated nutrients (Malmer, 2004; Mishra et al., 2021). This impact is known to be especially pronounced in repeatedly burned dipterocarp forests, where most of the belowground nutrient capital is stored in the leaf litter layer which is susceptible to being consumed by fires (Wanthongchai et al 2008). Reduced plant cover and soil organic matter further disrupt the phosphorus cycle, leading to less nutrient uptake and increased phosphorus losses through runoff and percolation (Leng et al., 2019; Mishra et al., 2021). Over time, this phosphorus depletion hinders vegetation recovery and reduces ecosystem productivity (Malmer, 2004). Meanwhile the very low concentrations of NH_4^+ and its invariance across the degradation gradient, points to a very low residence time of NH_4^+ in the soil post-mineralization, suggesting either rapid plant uptake, or in the case of the most degraded plots, losses from leaching and burning (Agus et al., 2020).

Soil nutrient concentrations in peatlands can fluctuate significantly between wet and dry seasons due to shifts in waterlogging and oxygen availability (Macrae et al., 2013). Given that we sampled only once during the year, our study may have missed seasonal variations in nutrient dynamics. Future studies should aim to sample during multiple periods across the year to capture seasonal dynamics, providing a more comprehensive view of nutrient cycling in this ecosystem.

5.5.2 Forest stand characteristics

In agreement with our second hypothesis, we observed reduced plant diversity in our most degraded plots. However, we observed no decline in plant diversity in intermediate degraded plots relative to lightly degraded or pristine plots, despite some vegetation compositional changes and reduced concentrations of soil P. The intermediate plots are in the forest edge, a transitional zone between peat forest (lightly degraded or pristine forest) and relatively open fern-dominated areas (heavily degraded plots), and while they show early stages of degradation, they still provide suitable habitat for a wide range of tree species (Murcia, 1995). Intermediate degradation in these plots was primarily caused by fire, which destroyed many trees and allowed ferns and sedges to occupy roughly half of each plot. There is no evidence that the largest trees were felled by humans (Addly et al., 2022). Degradation was further compounded by drainage from the nearby canal, likely altering hydrological conditions, hindering seedling recruitment, and exacerbating forest decline. The intermediate plots now show a mixture of early-successional species (ferns and sedges), new tree growth, and a partial canopy, indicating the early stages of forest recovery. While these conditions are unfavourable for certain resource conservative plant species, they simultaneously support resource-acquisitive taxa, meaning that they maintain a plant diversity that is comparable to the pristine forest stands, despite the area's degradation.

Also, in agreement with our second hypothesis, we observed greater domination by resource-acquisitive plant taxa (i.e. ferns and sedges) in the most heavily degraded plots and domination by resource-conservative tree families in lightly degraded and pristine areas. Notably, we observed a substantially greater stand basal area and tree abundance of the resource-conservative family, Dipterocarpaceae, in lightly degraded and pristine plots compared to the intermediate or more degraded plots. This could be due to the adaptation of Dipterocarpaceae species to the lower light and higher soil P conditions found in lightly degraded and pristine peat forests (Paoli et al., 2006; Dent et al., 2016). However, in contrast to our hypothesis, we observed an increase in stand basal area and tree abundance of the resource-conservative family, Fagaceae, in intermediate plots compared to lightly degraded and pristine plots. This is likely due to the phenotypic plasticity of Fagaceae species, which allows them to adapt to changes in hydrology and soil phosphorus (Kawai et al., 2020) that occur during the early stages of degradation in intermediate plots. Fagaceae may also benefit from reduced competition with dipterocarps at this stage, as both families are ectomycorrhizal (Brearley, 2012; Wu et al., 2018) and likely utilize similar resources.

In agreement with our third hypothesis, we observed a decrease in tree abundance, stand basal area, canopy height, and emergent layer height, along with an increase in canopy openness and total ground cover in the most degraded plots. This is due to the loss of mature trees (including most large emergent trees in Dipterocarpaceae) and the consequent reduction in canopy complexity. The resulting increase in light availability, combined with increased aerobic soil conditions and likely greater nutrient mineralization associated with heavy degradation, provides improved growing conditions for resource-acquisitive ferns and sedges, predominantly *Stenochlaena palustris*, *Blechnum indicum*, and *Scleria purpurascens* (Henneron et al., 2017). However, we did not observe any resource-conservative taxa, such as *Dactylocladus stenostachys* and *Ilex cymosa*, or resource-acquisitive tree taxa, such as *Timonius flavescens*, in the most degraded areas, likely due to the formation of dense fern-dominated thickets, which are known to reduce seedling survival and retard forest regeneration (Ssali et al., 2017).

5.5.3 Biomass and carbon loss

We found that above ground biomass decreased as degradation intensified, with the heavy degraded and most degraded plots having almost no above ground woody biomass. Despite finding no significant differences in tree abundance, stand basal area, emergent tree height, canopy height and diversity between intermediate degraded plots and lightly degraded or pristine areas, we found a very large reduction in woody biomass in the intermediate plots. This is most likely due to the loss of large dipterocarp trees, particularly *Shorea albida* (Table 5.2). This, along with field observations of dead standing trees, suggests that large dipterocarps are especially vulnerable to the initial stages of degradation occurring in intermediate plots, likely because of the disproportionate sensitivity of large trees to water stress due to hydraulic limitations (Slik et al., 2013). The loss of these large trees not only reflects the current state of degradation but also signals the potential for further decline in forest health, underscoring the need for management actions to protect existing large trees (Lindenmayer and Laurance, 2017). This study demonstrates that while diversity and structure measures provide insights to forest degradation, quantifying aboveground biomass is needed to provide a more complete insight to forest health.

We calculated that approximately 1,980 hectares throughout the peat dome that we studied were heavily to mostly degraded, resulting in 0.62 Mt in above ground carbon loss due to loss of trees resulting from changed hydrological conditions and repeated fires. While many studies have focused on quantifying peat carbon stocks and carbon loss from the peat itself (Jaenicke et al., 2008; Page et al., 2011; Setiawan et al., 2015; Cobb et al., 2020), this study shows that a substantive amount of carbon is also lost above ground during peatland degradation. This type of loss also needs to be acknowledged in carbon assessments and policies focused on tropical peatland restoration.

5.6 Conclusions

This study enhances understanding of the effects of fire and drainage degradation on tropical peat forests by showing that pristine, lightly degraded, and intermediate degraded peatlands have some similarities in forest stand and belowground characteristics, despite differences in their degree of degradation. However, the variation in biomass and aboveground carbon storage across these three stages underscores the need to quantify biomass for a more comprehensive understanding of forest health and highlights the significant carbon loss resulting from changes in forest structure due to the loss of large dipterocarps in the early stages of degradation. Further research is needed to determine if these findings apply to other tropical peat forests, particularly for those degraded by both fire and drainage, to advance our understanding of the process of peat forest degradation and inform restoration strategies. Tropical peat forest holds globally significant carbon stores and our findings indicate that the initial degradation of aboveground peat forests (such as is occurring in our intermediate stage) leads to large declines in aboveground carbon storage even before other conventional measurements of forest characteristics (i.e. diversity, tree abundance, stand basal area) begin to change. There is therefore a clear research need to focus on the process of peat forest degradation starting from the early stages of the process to more reliably account for carbon sequestration and carbon losses of these forests.

Chapter 6

Discussion

6.1 Main findings

This aim of this dissertation is to examine the ecological dynamics of Panama's lowland forests and Brunei's waterlogged peat and kerangas forests, focusing on aboveground and belowground properties. Field transplant experiments were utilized to study seedling performance in Panama while paired plot experiments and measurements across degradation gradients were employed to study soil nutrient dynamics, tree diversity, forest structure, and decomposition rates in Brunei. First, we found, for a lowland tropical forest in Panama, that soil nutrients and water availability influence seedling growth and survival of understory palm species. Then we found, that for a comparison of peat forest and kerangas forest, that despite differences in soil conditions, tree diversity and structural characteristics were invariant across the two forest types, suggesting that belowground carbon accumulation in peat forests is likely instead driven by processes operating in the belowground environment. Then we found that waterlogged conditions affect soil nutrient availability but do not slow down decomposition rates of leaf litter in peat forest. Finally, we found that the loss of large trees such as *Shorea albida* in early degradation stages affects aboveground carbon storage in peat forest. These findings are now discussed in the context of soil nutrients, soil water content, and species-specific responses in tropical forests.

6.1.1 Soil nutrients

In our study of tropical forests, we explored the variability of soil nutrients, focusing on both total and available nutrients in diverse environments. We found that both total and available nutrients varied along a rainfall gradient in lowland tropical forests in Panama. We extended our research to examine the influence of soil water content on soil nutrient availability in peat forests in Brunei. We hypothesized that waterlogged soils, typically found in pristine to lightly degraded areas of peat forests, would exhibit higher total nutrient concentrations and lower available nutrient concentrations compared to less saturated soils (kerangas-sand, peat from heavily degraded peat forest). In partial alignment with our hypothesis, we found higher total phosphorus in waterlogged peat soils. This is most likely a consequence of anoxic conditions of the pristine peat (Hoyos-Santillan et al., 2019) limiting microbial activity, thus slowing down the decomposition process and impairing nutrient mineralization (Jauhiainen et al., 2005). Our findings are consistent with Leng et al. (2019) and Mishra et al. (2021), which underscores the critical role of oxygen availability and hydrological factors in soil nutrient dynamics in tropical peatlands. Our research indicates a clear link between soil nutrient concentrations and soil moisture content across lowland forests, waterlogged peat forests along a drainage degradation gradient, and well-draining kerangas forests. In particular it emphasizes the influence of water in shaping soil nutrient dynamics and, by extension, the ecological characteristics of tropical forests.

6.1.2 Soil water content

Our research indicates that soil water content influences tropical forest plants at various stages of growth, from seedlings to established large trees. In controlled and field experiments in Panama, we observed that seedling mortality was predominantly influenced by dry season water availability rather than soil nutrient levels. This finding suggests that seedling survival, and consequently species distribution within lowland tropical ecosystems, is significantly constrained by water availability during dry periods. Additionally, our research indicates that peat forest in Brunei in the early stages of drainage and fire degradation leads to a substantial reduction in woody biomass, mainly due to the loss of large dipterocarp trees such as *Shorea albida*. Field observations of dead, free-standing *Shorea albida* trees, coupled with the known disproportionate sensitivity of large trees to water stress due to hydraulic limitations, highlight their vulnerability to changes in soil water content. This pattern aligns with findings from Slik et al. (2013) which emphasizes the impact of water stress on *Shorea albida*. Many trees in peat forests possess adaptations for growth and survival in waterlogged conditions, such as buttresses for stability and knee roots and pneumatophores for gaseous exchange (Yule, 2010), and our research suggests that in tropical forests, it is in fact the lack of water that significantly impacts plant survival. Our research collectively indicates that soil water content exerts a significant influence on plant life in tropical forests, affecting plants at various stages of growth and impacting the key ecosystem processes that they drive such as carbon sequestration.

Contrary to expectations, our research found that waterlogged soils in tropical peat forests do not impede ecosystem processes such as leaf litter decomposition relative to in kerangas forest, at least in the first year after litter fall. This result challenges the prevailing view that waterlogged soils in peat forests slow down the decomposition process. As such, leaf litter decomposition processes do not appear to contribute to organic matter accumulation in peat forests, despite their widely recognized role in soil carbon sequestration in other ecosystems (Berg and Meenteneyer, 2002; Wardle et al., 2004). More generally, our research underscores the influence of soil moisture on several aspects of ecosystem dynamics in lowland tropical forests. It highlights how soil moisture affects plant growth and survival, with species-specific responses that can impact processes like carbon sequestration. Additionally, our findings reveal that the role of soil moisture in broader ecosystem processes, such as belowground carbon storage and the contribution of leaf litter decomposition to it, is more complex than previously understood. Introducing an additional experimental condition to compare submerged versus non-submerged litter could provide valuable insights and further our understanding of decomposition in peat swamp forests in future studies.

6.1.3 Species-specific responses

We found that plants have species-specific responses to both soil nutrient availability and soil water content. For example, in lowland forests in Panama, we found that for seedlings of various understory species, factors such as biomass allocation, relative growth rate (RGR), and survival are strongly influenced by soil nutrient availability and water availability during the dry season. These species-specific and tree family-specific responses in Brunei, do not however manifest as changes in overall forest diversity or structure, but rather in community composition. Despite the waterlogged and nutrient-poor conditions of the Brunei peat forests, we observed no significant differences in tree diversity, abundance, or stand basal area compared to kerangas forests. However, we observed family-specific responses to these soil conditions, and notably for Dipterocarpaceae which had larger diameter but fewer trees in peat compared to kerangas forests. Furthermore, along a drainage and fire degradation gradient in peat forest, we found that there were no significant differences in overall diversity and forest structure between intermediate degraded areas and pristine or lightly degraded areas despite large variations in soil nutrient availability and water content. However, despite this there were distinct compositional changes, in that in intermediate degraded areas, Dipterocarpaceae were less abundant and smaller in diameter compared to those in pristine and lightly degraded areas.

Intermediate degradation in these plots was primarily caused by fire, which destroyed many trees and allowed ferns and sedges to occupy roughly half of each plot. There is no evidence that the largest trees were felled by humans (Addly et al., 2022). Degradation was further compounded by drainage from the nearby canal, likely altering hydrological conditions, hindering seedling recruitment, and exacerbating forest decline. The intermediate plots now show a mixture of early-successional species (ferns and sedges), new tree growth, and a partial canopy, indicating the early stages of forest recovery.

As new trees mature, they may eventually form a full canopy, potentially suppressing the growth of ferns and sedges and allowing for further successional progress toward a more forested state. Seedling recruitment remains inconsistent: in some sections, ferns and sedges inhibit seedling establishment, while in others, recruitment is occurring. Resource-conservative *Shorea albida* is notably absent from regeneration in these plots. However, resource-conservative Fagaceae, including *Lithocarpus* species, exhibited significantly higher stand basal area in intermediate degraded forests compared to pristine plots which is consistent with findings by Okuda et al. (2002). This increase in stand basal area may be attributed to water table height at intermediate degraded plots, as *Lithocarpus* species have shown high seedling growth rates in degraded peat environments (Lampela et al., 2017). However, extreme fluctuations in water table height and high temperatures limit their growth (Lampela et al., 2017).

These findings emphasize that while soil nutrient availability and water content may not necessarily manifest in obvious differences in tree diversity or forest structure, they do induce species-specific responses that lead to shifts in community composition. Alterations in the abundance or biomass of key species like *Shorea albida* in peat forest can have significant impacts on ecosystem processes, such as a forest's aboveground carbon storage capacity. Therefore, it is necessary to recognize and understand species-specific responses to environmental changes as they play a key role in the functioning of tropical forest ecosystems.

6.2 Contributions to tropical forest ecology

This dissertation has contributed to our understanding of tropical forest ecology, particularly in terms of the interactions between aboveground and belowground ecosystem properties and processes. It has helped to bridge gaps in our understanding of how soil nutrient and moisture availability impact the survival, growth, and functional traits of understory plant seedlings in lowland rainforests in Panama, and thus shed light on understory dynamics. Further, through the use of paired plots for characterizing peat and kerangas forests in Brunei, this research has not only highlighted the distinct differences between these two forest types but also lays a foundation for subsequent studies to explore more nuanced aspects of these diverse ecosystems. The investigation of decomposition processes revealed a lack of home-field advantage in both peat and kerangas forests and therefore challenges the expectation of faster decomposition (and thus less carbon sequestration due to leaf litter) in less waterlogged environments. Furthermore, this research has bridged gaps in understanding the dual effects of fire and drainage degradation on the forest characteristics of tropical peatlands, and it underscores the importance of *Shorea albida* in driving carbon storage and forest health. This research in total has provided valuable insights into the interplay of various factors that affect peat forests (Figure 6.1) and contributes to a deeper understanding of the resilience and vulnerability of these ecosystems to external perturbations and underscores the need for management actions to protect existing large *Shorea albida* trees.

6.3 Broader implications: role in climate change mitigation

The collective findings from this dissertation provide crucial insights into the complex dynamics of carbon sequestration in tropical forests, particularly in Southeast Asian peatlands. They highlight the interplay between various ecological processes and their influence on carbon storage, exploring factors that affect carbon sequestration of an ecosystem that is an important sink of carbon. Our studies reveal that leaf litter quality or initial decomposition of leaf litter is not an important driver of carbon storage and peat accumulation in tropical peat forests. Instead, they suggest that there are other drivers of peat accumulation in these forests such as the low densities of larger soil decomposer fauna (e.g., termites) and inputs of large amounts of low quality of wood and root litter. This research also underscores how changes in environmental conditions, such as soil nutrient alterations and moisture availability, along with forest degradation,

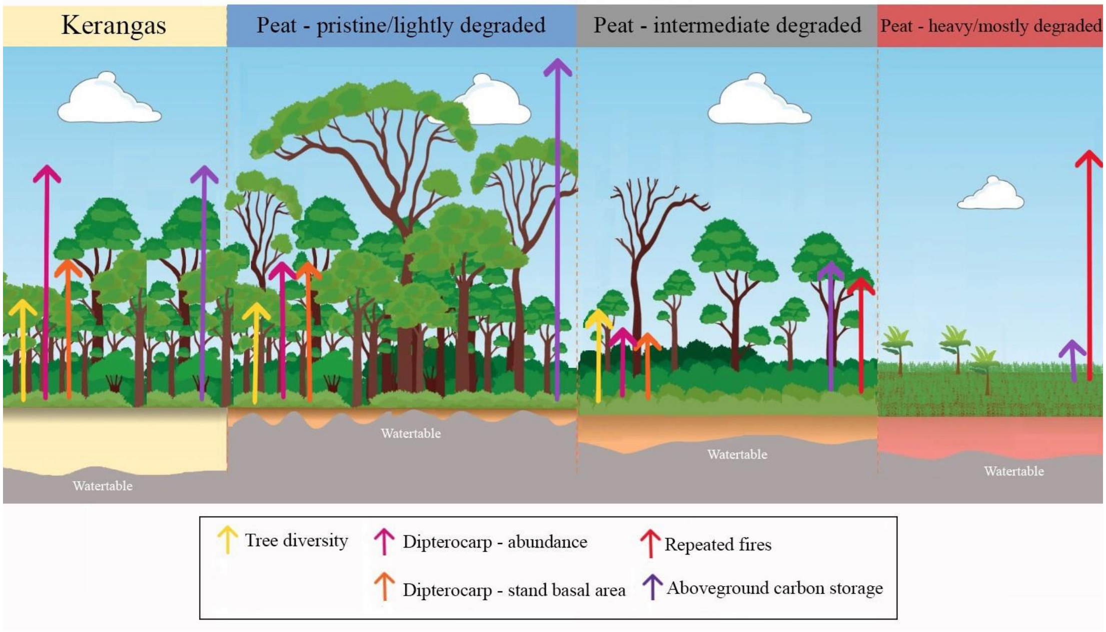

Figure 6.1: Aboveground forest characteristics of kerangas forest and peat forest along a drainage and fire degradation gradient in the Badas Forest Reserve, Belait District, Brunei Darussalam. The length of the arrows indicates the relative magnitude or quantity of each characteristic. Figure has been modified from Page et al. (2022).

can significantly affect plant growth, forest structure, and ultimately aboveground carbon storage. The loss of key species such as dipterocarps in the early stages of peat forest degradation indicates that even the early stage of degradation has profound implications for carbon dynamics. In total this integrated study enriches our understanding of the factors that determine the role of tropical forests as a globally important carbon sink that is essential in the fight against climate change.

6.4 Future research

6.4.1 Investigation of other decomposition processes

Future research aimed at understanding why organic matter accumulates in peat forests, despite this dissertation revealing their similarities to kerangas forests in terms of plant communities, leaf and litter traits, and decomposition rates, should prioritize three areas. First, there is a need to investigate how variations in soil nutrient availability and water content influence the wood characteristics of dominant plant species in peat forest. For example, the wood density of *Shorea albida* is known to vary in response to forest characteristics (Monda et al., 2015). Differences in the quantity, quality and decomposability of wood and root litter between peat and kerangas forests, may contribute to differences in organic matter accumulation between these habitats, and the accumulation of peat in peat forest. Second, emphasis should be placed on examining the role of soil fauna, such as termites, in decomposition, with a specific focus on how these organisms adapt their activity to the anoxic conditions in peat forests and how they interact with woods of varying density (Seibold et al., 2001; Coyle et al., 2017). As such it may be that the conditions of peat forests are unfavourable for termite activity, and that this might impede decomposition and contribute to peat accumulation. Third, longitudinal studies which track how litter progresses from the surface to the deeper, consistently waterlogged layers within peat forests are needed, as its decomposition might be impeded only deeper in the peat profile. These focused areas of research are key to elucidating the distinct ecological mechanisms that drive organic matter accumulation in peat forests.

6.4.2 Investigation of early degradation impact

Future research focusing on the initial stages of forest degradation is crucial for a comprehensive understanding of the process of tropical peat forest degradation. There is a need for studies that aim to identify and analyse the early changes in forest structure, biodiversity, and carbon dynamics that occur during the onset of degradation. These include shifts in soil nutrients and soil water content, and how these alterations affect the recruitment, growth rate, and distribution of key plant species such as dipterocarps, which play a vital role aboveground carbon storage and are particularly sensitive to water stress (Slik et al., 2013). Furthermore, our findings from Panama, demonstrate that soil nutrient and moisture content influence the growth and distribution of understory palm species and suggest an indirect impact on tree seedling recruitment and forest regeneration. Investigating these dynamics in the understory palms of Brunei’s peat forests is essential to determine if similar influences affect the recruitment of key species like *Shorea albida*. Quantifying changes in biomass and aboveground carbon storage during these initial stages is essential, as it can provide insights into the substantial carbon loss linked to the structural changes in the forest and the loss of large dipterocarp trees. To develop effective conservation and restoration strategies, it is imperative to understand how these early-stage changes, often triggered by factors such as fire and drainage, affect the overall health of peat forests. Testing various restoration approaches in these degraded environments will be key to mitigating the impacts of their degradation and enhancing their carbon sequestration and role as carbon sinks. Such studies not only contribute to the ecological understanding of peat forest degradation but also guide practical actions for their restoration and preservation.

6.5 Conclusions

Our research across various tropical forests in both Panama and Brunei reveals that both soil nutrient availability and water content have profound, species-specific impacts on plant life, from seedlings to mature trees. While these factors significantly influence plant growth and adaptations, they do not uniformly alter overall forest diversity or structure. However, they do lead to notable changes in community composition, which can have substantial effects on ecosystem functions like carbon storage. These insights collectively enhance our understanding of how belowground conditions shape the ecological dynamics and carbon sequestration capabilities of tropical forests.

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Appendix

Supporting Information for Chapter 2

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Palm Species Traits Determine Soil Nutrient Effects on Seedling Performance