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# Ecological responses of a Bornean heath forest (*kerangas*) to experimental lime and nitrogen addition

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**Abstract**:

Heath forests are a rare but widespread forest type found across the tropics that have low productivity and relatively low plant species diversity but with high endemism. These forests develop on strongly weathered spodosols that are acidic soils with low nutrients, which is generally believed to explain heath forest distribution. In this study, I tested whether tropical heath forest productivity is limited by low soil nitrogen (N) availability, soil acidity or an interaction between the two, with a factorial N and $CaCO_3$ addition experiment in a Bornean heath forest. I also assessed the susceptibility of this forest type to the predicted increases of N deposition in tropical areas. I recorded the highest wet inorganic N deposition rate measured in Malaysia (7.45 kg N $ha^{-1}$ $yr^{-1}$) that was dominated by $NH_4^+$-N and most likely derived from agro-industrial fertilization. Prior to the experimental treatments of my plots, I correlated edaphic and topographical differences among plots with species diversity, distribution and stand structure. Soil acidity had the greatest influence on species distribution and forest structure but the subsequent experimental liming did not affect tree performance, only soil acidity and the decomposer community. On the other hand, N addition increased tree relative growth rates, and foliar N concentration after only two years of treatment, but no effect of N addition was detectable on litterfall mass during one year of fertilisation. Overall, both the correlational study on habitat filtering and N addition found most effect on trees 5-10 cm DBH but both acquisitive and conservative species reacted equally to N addition. My results show that heath forest productivity is N limited; moreover, increased N deposition is likely to further acidify this forests' soil – as seen in soil leachate after one year of N fertilization - possibly increasing the amount of undecomposed organic matter and reducing the availability of soil nutrients to forest trees. Our results from litterfall, fresh leaves and soil leachate also present further hypotheses to be tested suggesting that soil phosphorus (P) and iron (Fe) could be limiting in this forest typology. In conclusion, I show that tropical heath forest are sensitive to N availability. To conserve this unique forest type, local governments should develop policies to limit atmospheric N input.

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# 1 General introduction.

## 1.1 The tropical rain forest nutrient limitation paradigm:

Tropical rain forests host ~50 % of all tree species (Groombridge and Jenkins 2003) and provide fundamental ecosystem services such as water cycling (Devaraju et al. 2015), as well as acting as major carbon (C) stocks (Malhi and Grace 2000). Often growing on highly weathered soils, tropical rain forest productivity is often limited by nutrient availability, such as nitrogen (N) and phosphorus (P), thus the capacity of rain forests to assimilate and store C is regulated by soil nutrient availability (Fernandez-Martina et al. 2014). Models investigating ecosystem responses to global changes only partially account for the influence of soil nutrient limitation on terrestrial ecosystems, for example, C storage (Achat et al. 2016). This is due to the lack of experiments investigating the C-N-P coupled stoichiometry, in particular at tropical latitudes (Wright et al. 2018). Soil nutrients also play a major role also in explaining plant species diversity and distribution at tropical latitudes (Duivenvoorden 1994; Phillips et al. 2003; Slik et al. 2009).

In the last few decades, a general paradigm of soil nutrient limitation has been developed for temperate (Vitousek and Howarth 1991), lowland and montane tropical forests (Tanner et al. 1998; Vitousek 1984). Before the industrial revolution, the only input to soil N was biological N fixation by symbionts and lightning (Fowler et al. 2013) with biological N fixation higher in the tropics than temperate regions (Cleveland et al. 1999). Phosphorus, on the other hand, enters ecosystems mainly through the erosion and weathering of rocks. As a consequence, zones with active tectonic uplift (e.g. mountains) and recovering from recent glaciations (e.g. temperate soils) have P-rich soils (Porder et al. 2007). Older soils, instead, underwent climatic and chemical weathering through time, which leached P out of soil horizons. In these soils P becomes limiting, especially in highly weathered lowland tropical rain forests. These processes, along with support provided by studies analysing leaf (Aerts and Chapin 2000; Hedin 2004), litterfall (Vitousek 1982; Vitousek 1984) and soil nutrient chemistry (Turner and Condron 2013; Walker and Syers 1976), allowed the development of the forest nutrient limitation paradigm suggesting that tropical lowland rain forests are limited by soil P, whereas tropical montane and temperate forest are limited by soil N. However, generalisations have to be made carefully, especially in the tropics. The surprising species diversity of tropical forests with widely nutrient depleted systems leads to high degrees of specialisation with multiple nutrient limitations likely (Kaspari and Powers 2016). The interaction of many shaping forces, such as climate, soil, light availability and water availability contribute to create a mosaic pattern of forest types, with high soil and species diversity (Richards 1959). If we exclude sub-alpine, high mountain and cloud forests and consider only the lowland tropical forest, at the lowest end of the forest productivity scale, we find a peculiar forest formation, namely tropical heath forests (HF).

## 1.2 Heath forest:

This stunted forest is ubiquitous across the tropics, growing in scattered “islands” among the dominant Lowland Evergreen Rain Forest (LERF). The greatest extent of HFs are located in the South American upper Rio Negro and Rio Orinoco basins, where they spread among seven countries (Anderson 1981; Luizao 1996) and are more commonly known as white sand forest (Fine and Bruna 2016). In Asia, HFs are best developed on the island of Borneo (Brünig 1974) occupying, for example, around 11 % the total area of Kalimantan (MacKinnon et al. 1996). However, they are also present in Papua, peninsular Malaysia (Whitmore 1984), and in the islands between west Borneo and Sumatra (Kartawinata 1980). Few surveys have been undertaken in Africa, but coastal HFs have been identified in Cameroon (McKey et al. 1978), Gabon and Ivory Coast (Whitmore 1990).

### 1.2.1 Heath Forest Vegetation:

Heath forests are easily recognizable by their vegetation physiognomy. Trees have a shorter stature and smaller average diameter than in LERFs, resulting in a lower basal area and aboveground net primary production defined as the sum of wood mass growth increment rate, and litterfall production (Miyamoto et al. 1997; Proctor et al. 1983b). Tree crowns are small in heath forest, leading to high light availability at ground level, which fosters the growth of a thick understorey, as well as epiphytic and bryophytic communities (Frahm and Gradstein 1991; Richards 1936). Kenzo et al. (2014), for example, found that for a given area the number of trees >10 cm DBH was similar between a HF and a LERF in Sarawak, whereas the number of trees 1 to 10 cm DBH was almost double in the HF with respect to the LERF. Heath Forest tree species are generally characterised by being long-lived (Miyamoto et al. 1997), with small and thick leaves (Becker et al. 1999; Peace and Macdonald 1981; Turner 1994) with low nitrogen and phosphorus concentrations (Aoyagi and Kitayama 2016; Luizao 1994; Turner et al. 2000), high phenolic concentration (Dent et al. 2006; Janzen 1974; Whitmore 1990) and low wood nutrient concentrations (Aoyagi and Kitayama 2016). HFs notably lack buttressed trees (Proctor et al. 1983a) and often have a dense superficial root layer with a high proportion of fine roots embedded in the soil surface litter layer when compared to other forest formations (Klinge and Herrera 1978; Luizao et al. 2007). Heath Forest plant communities are less species rich than the neighbouring LERFs (Anderson 1981; Nilus 2003; Proctor et al. 1983a) but contain a high number of plant (Anderson 1981; Fine et al. 2010; Newbery 1991) as well as animal (Borges et al. 2016; Woxvold and Noske 2011) specialist species. Garcia (2016), for example, found that 23 % of tree species from western Amazonian HFs were HF specialists. Furthermore, the specialists and endemic species of HFs have been identified as important for medicinal (e.g. ant plants in South-east Asian HFs. Low et al. 2016; Ong et al. 1998; Kartawinata 1980) and ornamental properties (e.g. orchids endemic to South-east Asian HFs; Wood 1984; Ong et al. 1998) as well as for evolutionary research (e.g. Guyana Shield HFs may be ancestral seats of Neotropical diversity. Frasier et al. 2008).

### 1.2.2 Heath Forest Soil:

Since the 19th Century, early explorers associated the peculiar tropical heath forest flora with a characteristic sandy soil (Beccari 1902; Spruce 1908). Researchers proposed HF's sandy soil to originate from four non mutually exclusive events: i) weathering of parent material (sandstone and conglomerates of mainly Tertiary age, mostly found on the island of Borneo); ii) deposition of alluvial material (namely “Pleistocenic terraces” both from rivers or sea); iii) deposition of eolian material (called paleodunes, only in South America); and iv) podzolisation of Oxisols (which leaches organic matter and clay constituents leaving only sand (Adeney et al. 2016; Anderson 1981; Andriesse 1968). These four events often converge in the formation of a “hardpan”, which is an indurated layer composed of humic colloids and quartz particulates that accumulate at a given soil depth because of a transition in soil texture. The sandy soil is subjected to heavy tropical rainfall that settles the smaller soil particles in the deepest horizon of the soil resulting in a coarse-textured sandy horizon overlaying a deeper finer-textured horizon. The humic colloids and quartz flour produced in a later stage of soil and vegetation development will thus be deposited at the transition zone of these two horizons (Andriesse 1968). The intense leaching displaces also iron (Fe) and aluminium (Al; Andriesse 1968, 1970).

The lack of clay in the upper horizons reduces the cation retention capacity of the mineral soils, leading to an abundance of protons ($H^+$) that strongly acidify the soil (Tanaka et al. 2013). Heath forest spodosols are generally the most acidic of all spodosols (e.g. pH between 3 [Andriesse 1968] and 4.75 [Wahyudi 2012]). Such an acidity hampers organic matter decomposition, resulting in a thick undecomposed organic layer above the mineral sand (Proctor et al. 1983a). Also, organic matter is slowly eluviated to the lower soil horizons increasing the soil C:N ratio (Kartawinata 1980; Luizao 1994; Luizao et al. 2007; Wood and Beckett 1961). The downward movement of organic matter can create notable belowground C storage. Montes et al. (2011) estimated that, across all Amazonian spodosols, there is an overall soil C storage of 13.6 ± 1.1 PgC, which is five times higher than the whole tropics’ annual C emission from deforestation (Pan et al. 2011). So, despite tropical heath forests’ low aboveground carbon stocks and productivity, it appears that HFs’ soil might be an important location for C storage.

### 1.2.3 Hypotheses proposed for processes leading to HF formation:

Until now, the most supported hypotheses explaining HF trees stunted features and low productivity are: low soil N availability (Brearley et al. 2011; Luizao 1994; Moran et al. 2000; Proctor et al. 1983a; Proctor 1999; Vitousek and Matson 1988), low soil pH (Luizao et al. 2007; Proctor 1999; Vernimmen et al. 2013), or an interaction of the two (Luizao 1996). With regard to nitrogen, several authors found low N concentration and high nutrient-use efficiency in HF litterfall, and suggested these signs to be indicative of nitrogen limitation (Coomes 1997; Dent et al. 2006; Moran et al. 2000; Peace and Macdonald 1981). Luizao (1996) found soil total nitrogen to be higher in the upper layer of HF rather than LERF in Brazil. Amounts of soil total nitrogen similar to that of Vernimmen et al. (2006) and Dent et al. (2006) have also been recorded by Andriesse (1968), Katagiri et al. (1991), Wahyudi (2012) and Oktavia et al. (2015) in different HFs around Borneo. This is reasonable taking into account the low heath forests' soil decomposition rate, which results in a soil with a high amount of undecomposed organic matter. Nonetheless, Vernimmen et al. (2013) and Dent et al. (2006) found soil soluble N (dissolved organic nitrogen plus $NH_4^+$, $NO_3^-$ and $NO_2^-$) to be similar among HF and LERF in Barito Ulu and in Kabili-Sepilok, respectively. This suggests that the amount of available soil nitrogen would not change much among HFs and LERFs and thus it would not limit HF productivity. Proctor (1999), on the other hand, suggested that HF trees minimize N uptake by roots because it requires co-transport of $H^+$, which is abundant in HF soil and extremely toxic to plants (Foy et al. 1984). This minimisation in nutrient uptake might explain the low nutrient content found in HF leaves. Janzen (1974) and Turner (1994) propose that the low availability of soil nutrients makes leaves extremely expensive to plants and they suggest that HF leaf sclerophylly has evolved to defend these leaves from insect herbivory.

Low soil pH inhibits bacterial growth, and thus litter decomposition, but not fungal growth (Brady and Weil 2002). The differential response of bacteria and fungi to soil pH might explain the high N immobilization seen by Luizao et al. (2007) during a laboratory-based nitrogen addition experiment on Amazonian HF soil. On the other hand, Singer (1984) proposed that Amazonian HFs low decomposition rate was due to a strong inhibition of decomposer micro-organisms by mycorrhizal fungi that appeared to be abundant in Neotropical heath forests (Roy et al. 2016). Corroborating this hypothesis, Moyersoen et al. (2001) found a higher arbuscular mycorrhizal abundance in a Bornean HF in comparison with LERF. In conclusion, it is clear that an overarching understanding on the importance of nutrient limitation for heath forests is still lacking (Miyamoto et al. 2016).

## 1.3 Nitrogen deposition:

Since the 1960's, fossil fuel and biomass burning, as well as fertilizer use, have been increasing the concentration of atmospheric reactive nitrogen (N) with a consequent increase in N deposition to ecosystems (Bauters et al. 2018; Galloway et al. 2003, 2004; Kanakidou et al. 2016; Matson et al. 1999; Reay et al. 2008; Ponette-González et al. 2016; Tilman et al. 2002). Dentener et al. (2006), for instance, proposed that more than 11 % of non-agricultural vegetated land is subjected to N deposition exceeding the critical load of 10 kg N ha$^{-1}$ yr$^{-1}$. At temperate latitudes, the effects of N deposition have been well studied thanks to several fertilization experiments (e.g. Magill et al. 2000; Matson et al. 2002; McNulty et al. 2017). The most pervasive responses to artificial N addition are soil acidification and base cation losses (Matson et al. 2002). The N-limited nature of temperate ecosystems also means that N deposition drives increased tree growth as well as microbial and plant community composition shifts (Anderson-Texeira et al. 2015; Bobbink et al. 2010; Lu et al. 2014; Stevens et al. 2004; Zhang et al. 2018). On the other hand, due to the high amount of N they already cycle, tropical rain forests have long been considered prone to N saturation, and consequently to soil acidification, and increased $N_2O$ emissions as well as river eutrophication (Bouwman et al. 2002; Brookshire et al. 2012). Despite the importance of tropical rain forests for global climate mitigation (Watson et al. 2018), only 14 fertilisation experiments have been undertaken in species-rich LERF (Wright et al. 2018). Furthermore, recent tropical studies (Townsend et al. 2011; Kaspari and Powers 2016; Wright et al. 2018) cast doubts on the paradigm of lowland rain forest nutrient limitation, underscoring the pervasive multiple nutrient limitation in rainforests. This increases the uncertainty of the possible responses of tropical rain forests to increased N availability from N deposition. A further incentive to focus on the effects of N deposition on tropical ecosystems is the increasing rate of use of N fertilisers in tropical countries that are currently consuming 70 % of N fertilisers globally (Albanito et al. 2017). Equatorial South-east Asia has been rapidly converted to one of the most extensive tropical agro-industrial landscape worldwide. In the state of Sabah, for instance, oil palm is cultivated on ~1.5 million ha (21 % of the total land surface area; MPOB, 2016). Hewitt et al. (2009) estimated oil palm plantation nitrous oxides ($NO_x$) emissions to be ~2.5 times greater than native rain forest – although this study did not analyse $NH_x$ emissions, which are produced abundantly after crop fertilization (Bobbink et al. 2010). Malaysia has the highest net $N_2O$-N emissions among 12 tropical countries examined, largely due to palm oil cultivation (Albanito et al. 2017).

Focusing on the biogeochemistry of tropical forests under N deposition, Lu et al. (2014) found experimental N deposition enhanced soil acidification, through a liberation of $H^+$ ions, decreased base saturation and increased cation exchange capacity (CEC). This seems paradoxical, as CEC would normally decrease with soil acidity (Gillman 1991) but they showed that the soil CEC increase was due to the coupled increase of soil organic carbon due to slower decomposition rates. In temperate forests, an increase in soil acidity would lead to $Al^+$ mobilisation that would buffer the toxicity of $H^+$ ions but increase $Al^+$ toxicity (Gillman 1991). Nonetheless, Lu et al. (2014) showed that this does not happen in $Al^+$ poor tropical soils. Aluminium was already leached from their experimental site so that it could not be mobilized to alleviate $H^+$ toxicity. Such soils are called “acid-sensitive” and have very limited buffering capacity so small variations in soil chemistry can have clear implications for soil fertility, with consequent feedback on species distribution, forest productivity, aboveground and belowground C stocks.

### 1.4 Aim of this study:

Tropical heath forests are rich in endemic species, contain large amounts of soil C and, possibly, are highly sensitive to nitrogen deposition due to their nutrient-poor soil. The primary aim of this study was to discover if tropical heath forests are limited by low soil N, soil acidity or a combination of the two and to obtain insight on how heath forest might react to increased N deposition. We addressed this question by performing a factorial N (in the form of urea) and $CaCO_3$ (lime) addition in the Kabili-Sepilok Forest Reserve, Sabah, Malaysian Borneo. We studied the effects of nutrient manipulation and liming on tree diameter growth rates, foliar nutrients, litterfall mass and nutrient content, soil nutrients and organic matter decomposition.

### 1.4.1 Overview of each chapter:

*In the second chapter* we estimated the extent of wet inorganic nitrogen deposition occurring in an open field station nearby our study site. We collected and analysed rainfall throughout one year and tested whether the detected N deposition was linked to the biomass burning that seasonally affects southern Borneo. To this aim, we compared our N deposition dataset with backward projections of wind trajectories arriving at our study site together with satellite-derived fire maps for the island of Borneo and Philippines.

*In the third chapter* we describe the floristic and edaphic features of our study plots before the treatments were applied. We investigated how soil chemistry and topography influence species distribution, α- and β-diversity as well as forest structure (i.e. stem density and basal area) in relation to tree size in our forest plots. This gave us insights into the possible edaphic limitations that this particular site might have before starting the experiment, as well as which tree sizes might be most affected by the treatments.

*In the fourth chapter* we assessed whether the productivity in this tropical heath forest was limited by low nitrogen availability, pH or an interaction of the two. To this end, we performed a factorial N (urea) and $CaCO_3$ (lime) addition experiment and studied the influence that the treatments had on tree diameter growth rates, litterfall mass, nutrient concentrations and herbivory, as well as soil nutrient dynamics. We also assessed if the changes in tree stem diameter growth among treatments was different among size classes (as suggested from results in chapter two) and depended upon species functional identity. This allowed us to consider which species might be the most responsive to changes in nutrient availability over the longer term.

*In the fifth chapter* we studied if the stoichiometry of fresh leaves collected from the ten most common species in our plots showed any change after two years of experimental treatments. Here we also assessed the status and changes in N:P ratio, given its potential role as a proxy for nutrient limitation. We also screened for changes in other leaf elements because, in such a nutrient poor soil, N might not be the only limiting nutrient. Furthermore, we addressed whether the functional strategy of our ten focal species showed any correlation with changes in leaf elemental concentrations to predict the reactions of different functional strategies to increased availability of nutrients.

*In the sixth chapter* we tested whether the change in N availability, soil pH or an interaction of the two had any effect on the decomposition rate of organic matter (i.e. leaf litter and wood), fungal abundance and mesofaunal activity. These organisms and ecological processes cycle nutrients and thus a limitation on their activity will likely impact other compartments of the ecosystem (e.g. the vegetation).

*In the seventh chapter* we present a synthesis of the work and summarize further hypotheses that it would be useful to test to improve our understanding of heath forest nutrient-cycling processes and the effects of N deposition on this environment.

### 1.5 Study site:

Our experimental site is in the Kabili-Sepilok Forest Reserve, situated around 5° 51' N and 117° 56' E in the state of Sabah, Malaysian Borneo (Figure 1.1a). The climate is perhumid equatorial (Köppen classification: Af; Peel et al. 2002) and has a mean annual precipitation of 2975 mm (Dent et al. 2006). Nearly half of the annual precipitation falls between November and February; all months have more than 100 mm precipitation except for a short dry season in April with an average of 55 mm (Fox 1973). The reserve soils originate from three bedrock types i.e. mudstone, sandstone and some siltstone whose age is upper Miocene or younger.

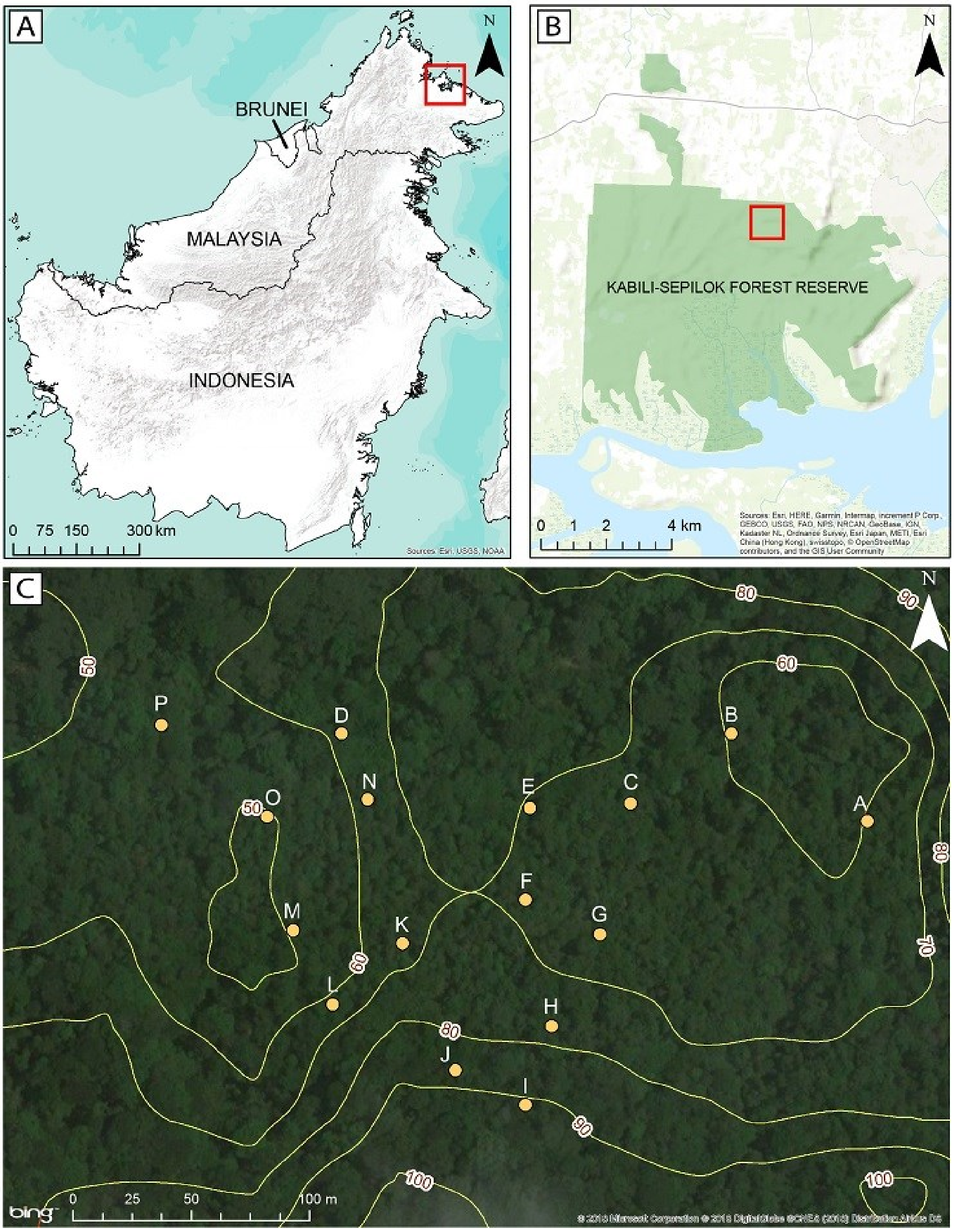


*Figure 1.1 Location of the study site. A) The island of Borneo with the approximate position of the Kabili-Sepilok Forest Reserve (Sabah, Malaysia) highlighted in red. B) The Kabili-Sepilok Forest reserve with the approximate location of the study plots highlighted and C) the study plots position on the field*

Sandstone rises up to ~170 m a.s.l. forming the prominent scarps and ridges that characterise the reserve whereas mudstone generally gives rise to smaller hills. Siltstone is found over a smaller area, intermixed with the former two bedrocks. The gentle slopes on the side of the hills host the Maliau soil association that is composed of Haplic Acrisols (Ultisols in the USDA soil taxonomy) with some podzolised areas characterised by the presence of bleached sand, often with an indurated hardpan. This soil formation gives rise to the “kerangas” or Heath forest (Fox 1973; Nilus 2003). Beyond the heath forest, another two soil-forest associations are present in the reserve (i.e. alluvial forest and sandstone forest). In 2016, we installed our experimental forest plots (Figure 1.1c) outside the permanent monitoring forest research plots established by Nilus (2003). Further description of our study site is given in Chapter 2 and 3.

# 2 Assessment of wet inorganic nitrogen deposition in an oil palm estate-forest matrix environment.

**Abstract:** Nitrogen (N) emissions and consequent deposition have increased in the last decades and significantly affect forest dynamics, carbon stocks and biodiversity in temperate latitudes. Nonetheless, in tropical latitudes there is a dearth of reactive N deposition assessments. In this chapter, we measured the amount of precipitation, rainwater pH and inorganic N concentration throughout one year at the boundary of a forest reserve in Malaysian Borneo. We then correlated our monthly cumulative wet N deposition with the cumulative number of fires that wind trajectories arriving at our study site passed over before rainfall sampling. We found that wet deposition comprised 90.4 % $NH_4^+$ and 9.6 %. $NO_3^-$ and that our study site had the highest annual wet inorganic N deposition recorded for a Malaysian forest environment (7.45 kg N $ha^{-1}$ $yr^{-1}$). We suspect that this value might increase if also accounting for organic and dry N deposition. The fires maps highlighted a fire season in Kalimantan and Sarawak around September and one in the south-west Philippines around April. Despite this, there was no correlation among fire occurrences and changes in N deposition, N concentration in rainfall or rainfall pH. So, we conclude that haze from fires does not influence N deposition at our study site. We suggest that changes in rainfall $NH_4^+$ concentration at our study site are due to $NH_4^+$ derived from agro-industrial fertilisation. Nonetheless, we advise for an isotopic approach to identify the source of N deposition in this Malaysian forest.

## 2.1 Introduction:

The tropics are composed of a matrix of forests types. Whilst the widespread lowland evergreen rainforest is thought to be phosphorus (P) limited, other tropical forest types, such as heath and montane tropical forests, are considered N poor (Benner et al. 2011; Moran et al. 2000; Tanner et al. 1992) and thus may respond differently than lowland evergreen rain forests to increases in N inputs. The use of fertilizers, fossil fuel and biomass burning have been increasing the concentration of atmospheric reactive N since the 1960s with a consequent increase of N deposition

(Galloway et al. 2003, 2004). The global dataset of Vet et al. (2014) presents a useful set of annual wet inorganic N measurements that allows a comparison of worldwide N deposition rates ranging from 0.17 kg N $ha^{-1}$ $yr^{-1}$ in Alaska to 27.07 kg N $ha^{-1}$ $yr^{-1}$ in parts of China $^{-1}$. Dentener et al. (2006) proposed that, globally, more than 11 % of non-agricultural vegetated land was subjected to an amount of wet and dry inorganic N deposition exceeding a critical load of 10 kg N $ha^{-1}$ $yr^{-1}$, above which a negative effect on vegetation is expected. Critical loads change according to abiotic and biotic conditions. Acidic European coniferous forests, for example, have a N critical load of 10 - 20 kg N $ha^{-1}$ $yr^{-1}$ (Bobbink and Roelofs 1995) whereas Chinese subtropical evergreen forests have a N critical load of 20 - 70 kg N $ha^{-1}$ $yr^{-1}$ (Liu et al. 2011). In the tropics, when N deposition exceeds N critical loads, soil pH drops due to increased $H^+$, which becomes dominant in the soil cation pool (Lu et al. 2014), and plant biodiversity decreases (Lu et al. 2010; Midolo et al. 2018). Although the rate of N deposition is predicted to increase in tropical areas (Phoenix et al. 2006), few monitoring stations and studies exist in these zones (Vet et al. 2014).

South-east Asia seasonally undergoes a burning season, usually around September-October (Jones 2006), where land is cleared and burned to establish plantations (Barber and Schweithelm 2000). The highest fire density is recorded in Kalimantan and Sumatra, Indonesia (Lohman et al. 2007) and, to a lesser extent, in Malaysian Borneo and Brunei (Aiken 2004). Biomass burning in tropical regions produces a haze that has been recognised as an important source of atmospheric N input (Andreae et al. 1988; Crutzen and Andreae 1990; Lobert et al. 1990). Furthermore, agro-industrial crops such as oil palm (Carrasco et al. 2014) and rubber (Warren-Thomas et al. 2015) plantations drive the need of tropical countries for N fertilizers. Tropical countries alone consume ca. 70 % of the N fertilizers produced globally (Albanito et al. 2017). Nonetheless, few accounts of N deposition exist for Malaysian Borneo, where rain forests are enclosed in a mosaic of oil palm estates (Abram et al. 2014) and are likely to undergo seasonal haze pollution from fires. In this study, we assessed, for the first time, the amount of wet $NH_4^+$ and $NO_3^-$ deposition deposited near the boundary of the pristine Kabili-Sepilok Forest Reserve, Sabah, Malaysia and hypothesise the potential sources of this N deposition.

## 2.2 Methods:

### 2.2.1 Study area:

Our collection site was located at Sabah Forestry Department's Forest Research Centre (FRC) in Sepilok, Sabah, Malaysia (Figure 2.1). The FRC building is surrounded by a matrix of residential dwellings, fruit orchards and oil palm estates with an urban centre (Sandakan) about 10 km to the east. Further south (c. 1 km) and west (c. 0.5 km) extends a 44 $km^2$ primary forest, the Kabili-Sepilok Forest Reserve. The climate is equatorial with a mean temperature of c. $26^0$C and an annual rainfall of c. 3000 mm (Fox 1974; Nilus 2003). Most of the rain falls between November and February due to the influence of the north-east monsoon, which brings winds from the Philippines. The driest month is usually April, when frequently the rainfall can be less than 100 mm $month^{-1}$ (Nilus 2003). From June to August the south-west monsoon brings air masses from the Indonesian state of Kalimantan, southern Borneo (Fox 1974).

### 2.2.2 Sampling and analysis:

We collected rainwater with a wet-only sampler placed on the tallest point of the FRC building. Sampling was carried out two times per week over a period of 12 months from September 2016 to August 2017. We recorded rainwater volume using a rain gauge, sub-samples of which were filtered with a 0.2 µm filter. We recorded rainwater pH with a Corning 240 pH meter, then acidified the samples to pH ~2 with a $H_2SO_4$ solution at 50 % and stored them in a -$20^0$ C refrigerator until $NH_4^+$ and $NO_3^-$ analyses on a segmented flow analyser (Astoria-Pacific A2, Clackamas, OR, USA) in the facilities of the Kabili-Sepilok FRC. We did not measure total dissolved N, so our results refer to inorganic N only. We calculated monthly deposition of N derived from $NH_4^+$ and $NO_3^-$ (referred as $NH_4^+$-N and $NO_3^-$-N) as well as the monthly volume-weighted concentration of $NH_4^+$ and $NO_3^-$. Volume-weighted concentration is a routine measure that express the average concentration of ions in the total volume of precipitation that fell within a certain time period. Volume weighted concentration was calculated as $C_i = \Sigma_j P_j C_{ij} / \Sigma_j P_j$ where $P_j$ is the amount of precipitation in sampling j (mm) and $C_{ij}$ is the concentration of constituent i for sampling j (µmol $l^{-1}$) (EPA, 1994).

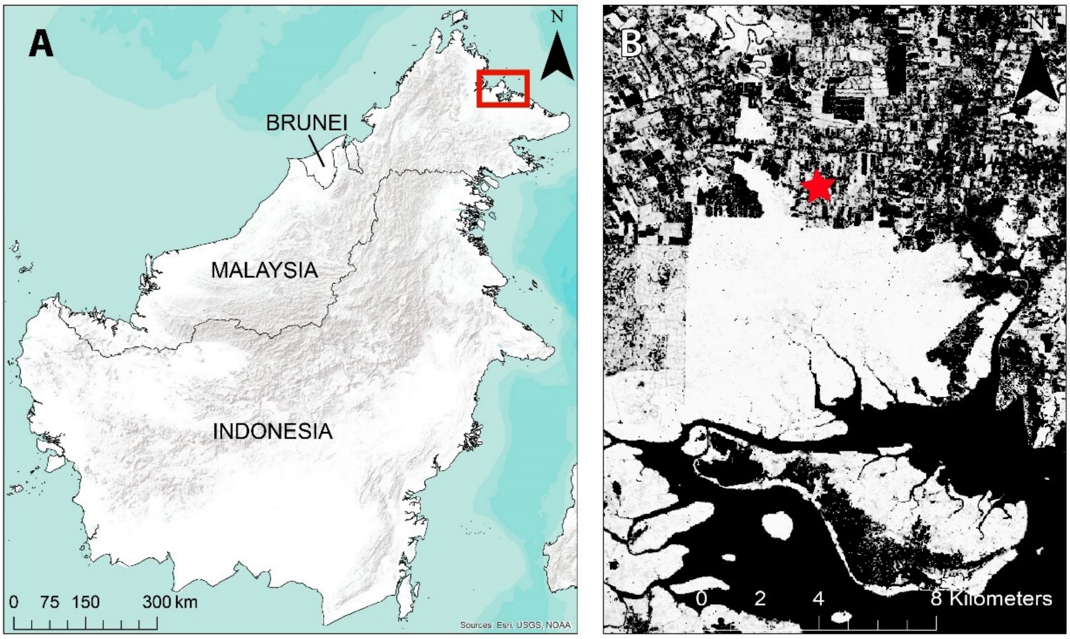


*Figure 2.1 Location of the study site. A) The island of Borneo with the approximate position of the Kabili-Sepilok Forest Reserve (Sabah, Malaysia) highlighted in red. B) The Kabili-Sepilok Forest Reserve with the location of the Forest Research Centre (red star) highlighted. Panel B shows forested areas in white and non-forest areas in black (data from Hansen et al. 2013).*

### 2.2.3 Wind trajectories, fires, and the correlation with N deposition:

To investigate whether the changes in wet N deposition were due to active fires, we back-crossed wind trajectories with fire maps for the study area generated using the HYSPLIT model provided by NOAA (www.ready.noaa.gov; Draxler and Rholph 2015) with ESRI ArcMap (version 10.3.1). Through the study period (September 2016 to August 2017), we generated twelve wind trajectories (width of 12 km) every two weeks at three different altitudes (40 m, 100 m and 1000 m) each running for 315 hrs. We obtained the fire maps from NASA's FIRMS system, which offers observations of active fires detected by VRIIS and MODIS C6 satellites (https://earthdata.nasa.gov/earth-observation-data/near-real-time/firms Accessed:

3-12-2018). Then we counted how many fires the winds arriving at our study site passed over every two weeks. We finally calculated the cumulative monthly fire count (MFC) to correlate changes in monthly cumulative wet N deposition and concentration in rainfall with the potential air pollution derived from fires. Given the normal distribution of our variables (Shapiro-Wilk's test), we examined the correlations among MFC, monthly rainfall, rainwater pH, $NH_4^+$-N and $NO_3^-$-N total monthly deposition, and $NH_4^+$ and $NO_3^-$ concentration in rainfall with Pearson correlation tests. All the statistical analyses were performed with R version 3.5.1 (R Development Core Team 2009).

## 2.3 Results:

During the 12 months of rainfall monitoring, we recorded 4637 mm total rainfall which was higher than the mean of 3000 mm $yr^{-1}$ for this location (Fox, 1973; www.ncdc.noaa.gov/cdo-web/) During this time the driest month was, unexpectedly, February with 175 mm rainfall which followed January, the wettest month (653 mm; Figure 2.2). The monthly mean volume- weighted concentration of $NH_4^+$ in rainfall was lowest in October 2016 (3.5 µmol $l^{-1}$; Table 2.1) and peaked in June 2017 (21.6 µmol $l^{-1}$), declining again in the following two months. The volume- weighted concentration of $NO_3^-$ remained constant through the year (1.1 µmol $l^{-1}$ ± 0.09 SE; Figure 2.2). June 2017 also had the highest total amount of wet $NH_4^+$-N deposition (1.28 kg N $ha^{-1}$), whereas the lowest amount of $NH_4^+$-N deposition was in October 2016 (0.21 kg N $ha^{-1.}$ ). In total, we calculated a deposition rate of wet inorganic N of 7.45 kg N $ha^{-1}$ $yr^{-1}$ which was dominated by $NH_4^+$ (90.4 %) with $NO_3^-$ making up the remainder (9.6 %). Rainfall had an annual mean pH of 5.38 ± 0.02 SE with the most acidic rain event being in October 2016 (pH 4.71) and the least acidic in August 2017 (pH 5.82).

The winds coming from Philippines are characteristic of the north-east monsoon (usually from November to February), although these winds were still active until April 2017 (Figure 2.3). The south-west monsoon usually appears around June and July but, from our simulation, these months seem to have quite weak winds; strong south-west monsoon winds arrived only in August. Throughout our study period, two major fire periods were visible. The first was between September and October 2016 with high concentrations of fires in Kalimantan and Sarawak. The second was between March and May 2017 in the western part of Philippines (i.e. Palawan, Western Visayas and Negros Island as well as Zamboanga peninsula; Figure 2.3).

The winds arriving at our study site in August 2017 passed over the highest number of fires (184 fires), whereas the wind arriving in June 2016 had the lowest MFC (11 fires). Winds from September and October 2016 intercepted fires from both Sarawak and Kalimantan, whereas the last two months of the north-east monsoon (March and April) intercepted the fires in the south-west Philippines.

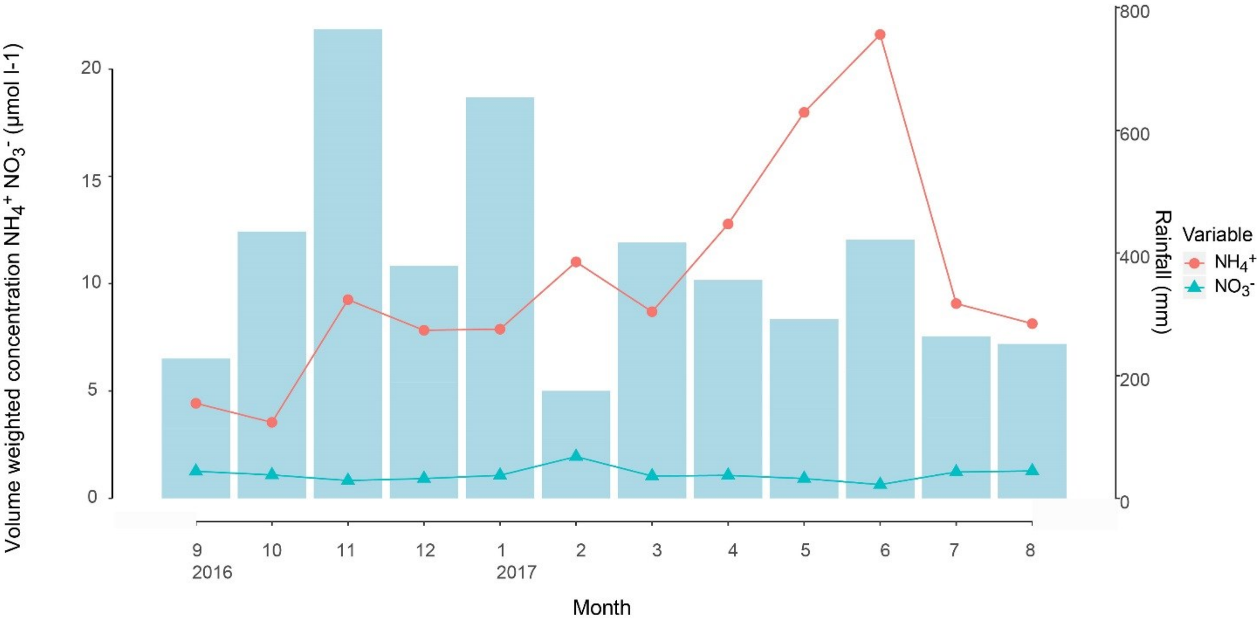


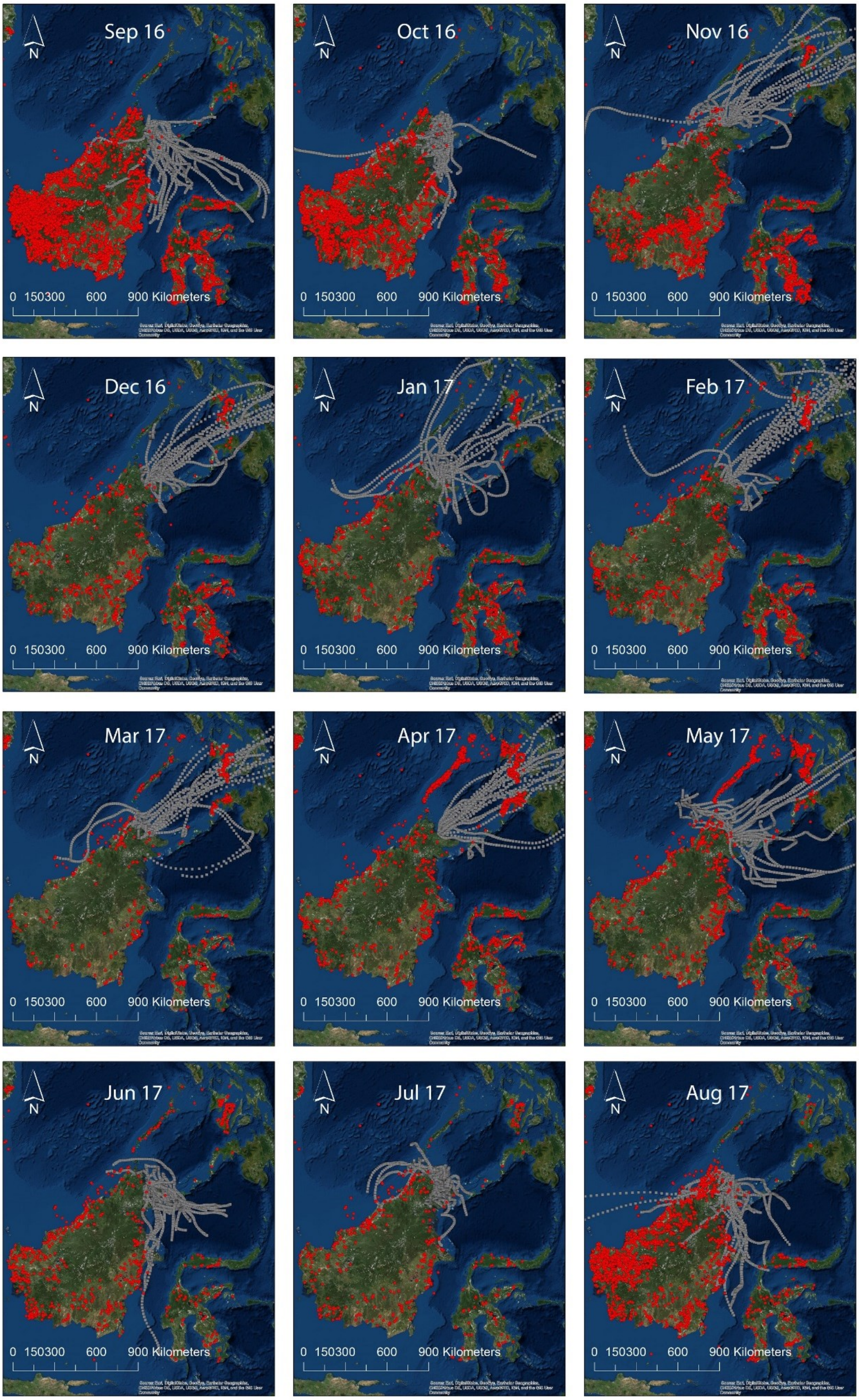
*Figure 2.2 Cumulative monthly rainfall in our study site in Sepilok, Sabah, Malaysia (blue bars) and volume- weighted mean concentration of $NH_4^+$ and $NO_3^-$.*

The Pearson analysis showed the total amount of $NH_4^+$-N deposition was positively correlated with $NH_4^+$ ($r$= 0.73, $p$<0.01; Table 2.2) and negatively with $NO_3^-$ ($r$= 0.70, $p$<0.05) concentration in rainwater, whereas the total amount of $NO_3^-$-N deposition was positively correlated with monthly rainfall (*r*=0.69, *p*<0.05). Neither was correlated with MFC (*p*>0.05).

*Table 2.1 Monthly mean pH and the cumulative amount of wet $NH_4^+$-N and $NO_3^-$-N (kg $ha^{-1}$) in rainfall collected in our study site in Sepilok, Sabah, Malaysia.*

| Date | | pH | $NH_4^+$-N | $NO_3^-$-N |
|---|---|---|---|---|
| 2016 | Sep | 5.37 | 0.35 | 0.08 |
| | Oct | 5.17 | 0.21 | 0.07 |
| | Nov | 5.38 | 0.99 | 0.09 |
| | Dec | 5.30 | 0.41 | 0.05 |
| 2017 | Jan | 5.44 | 0.72 | 0.09 |
| | Feb | 5.45 | 0.27 | 0.05 |
| | Mar | 5.34 | 0.51 | 0.06 |
| | Apr | 5.44 | 0.64 | 0.05 |
| | May | 5.46 | 0.73 | 0.04 |
| | Jun | 5.39 | 1.28 | 0.04 |
| | Jul | 5.32 | 0.33 | 0.04 |
| | Aug | 5.47 | 0.29 | 0.04 |
| Total | | - | 6.74 | 0.71 |

*Figure 2.3 (Next page) Intersection of the fire map obtained for Borneo and surrounding regions (MODIS C6 and VRIIS satellites) with the backward wind trajectories (grey dotted lines) generated with the HYSPLIT model provided by NOAA. Backward wind trajectories were generated every two weeks at three different altitudes (40 m, 100 m and 1000 m) each running for 315 hrs. The backward wind trajectories end at our samples collection site in Sepilok, Sabah, Malaysia.*


Sep 16
Oct 16
Nov 16
Dec 16
Jan 17
Feb 17
Mar 17
Apr 17
May 17
Jun 17
Jul 17
Aug 17
N
0 150300 600 900 Kilometers

## 2.4 Discussion:

Nitrogen deposition can have major effects on N-limited ecosystems (Anderson-Teixeira et al. 2015; Bobbink et al. 2010). Here, we assessed the amount of N deposition for a single location in Sabah, Malaysian Borneo, where forests are in close proximity to N-emitting sources such as fires and agro-industrial cultivation. We also assessed the relationship between N deposition and the occurrence of fires.

Our study site was subjected to the highest wet inorganic N deposition rate (7.45 kg N $ha^{-1}$ $yr^{-1}$; Table 2.3) measured for a forest environment in Malaysia, and the pattern of $NH_4^+$-N concentration in rainfall suggested seasonal wet N deposition variation. Our wet inorganic N deposition rate was higher than both lowland pristine forest from 1.09 to 2.2 kg N $ha^{-1}$ $yr^{-1}$ in Danum Valley, Sabah, Malaysia (Vet et al. 2014, Yamashita et al. 2014) or forest surrounded by oil palm and rubber cultivation with 6.2 kg N $ha^{-1}$ $yr^{-1}$ in Pasoh Forest Reserve, peninsular Malaysia (Manokaran 1980, Okuda et al. 2003) as well as montane forest with relatively low disturbance and N emission sources (3 kg N $ha^{-1}$ $yr^{-1}$ in Berembun, peninsular Malaysia; Yusop and Nik 1989 and 3.7 kg N $ha^{-1}$ $yr^{-1}$ in Tanah Rata, peninsular Malaysia; Vet et al. 2014). The values for other forest sites presented in table 2.3 (China, Germany, USA) have to be read minding that N deposition varies greatly among sites within geographical areas and that one value can not be representative of a whole geographic area.

As we measured only wet inorganic N deposition, overlooking organic N and dry deposition (which can equal or exceed wet N deposition), it is likely that the total N deposition in our study site exceeds the proposed critical load of 10 – 15 kg N $ha^{-1}$ $yr^{-1}$ proposed by Bobbink et al. (2010) as potentially damaging to temperate forests. Mean rainfall pH was high and characteristic of an environment with low emissions of oxidised N, nonetheless, pH sometimes fell below the lower threshold of 5.3 indicating acidic deposition (Vet et al. 2014). Given the low and stable oxidised N concentration recorded during our monitoring, this pH variation might be driven by fluctuations in S concentration (Charlson and Rhode 1982), which we did not measure. We acknowledge that the use of only one rain gauge collector poses a limitation to the statistical power of our study. Nonetheless, the results we collected are intriguing and might stimulate further research on N deposition in forests close-by agro-industrial plantations.

The seasonal pattern of fires we detected is typical for Borneo, with most active fires in September (Giglio et al. 2006). On the other hand, the high number of fires in south-west Philippines is concomitant with the dry season for the area (Philippine Atmospheric, Geophysical and Astronomical Services Administration. http://bagong.pagasa.dost.gov.ph/) suggesting a seasonal fire regime. Nonetheless, we did not find any correlation between the number of fires that winds coming to our study site intercepted with monthly wet inorganic N deposition, $NH_4^+$ or $NO_3^-$ concentration in rainwater. In contrast, the winds from the month with the highest rainwater $NH_4^+$ concentration (June 2017) intercepted the least number of fires. Furthermore, biomass combustion generally produces oxidised N forms (Andreae et al. 1988; Radojevic 2003), which were low in our rainfall samples in addition to being

*Table 2.2 Pearson correlation coefficients between the number of fires that winds arriving at our sampling site passed over in the month before rainfall (MFC) and different monthly rainfall characteristics (rainfall amount, mean rainwater pH, $NH_4^+$ and $NO_3^-$ mean concentration in rainfall as well as total $NH_4^+$-N and $NO_3^-$-N deposition). Rainfall samples were collected throughout one year at the Forest Research Centre, Sepilok, Sabah, Malaysia. Significance values ('***' < 0.001 '**' <0.01, '*' < 0.05) are in bold.*

| | Rainwater pH | MFC | $NH_4^+$ µmol $l^{-1}$ | $NO_3^-$ µmol $l^{-1}$ | $NH_4^+$ kg $ha^{-1}$ | $NO_3^-$ kg $ha^{-1}$ |
|---|---|---|---|---|---|---|
| Rainfall (mm) | -0.13 | -0.27 | -0.06 | -0.57 | 0.57 | **0.69**$^{**}$ |
| Rainwater pH | | 0.12 | 0.49 | 0.20 | 0.30 | -0.19 |
| MFC | | | -0.35 | 0.26 | -0.47 | -0.10 |
| $NH_4^+$ µmol $l^{-1}$ | | | | -0.36 | **0.73**$^{**}$ | -0.55 |
| $NO_3^-$ µmol $l^{-1}$ | | | | | **-0.70**$^{*}$ | -0.08 |
| $NH_4^+$kg $ha^{-1}$ | | | | | | 0.08 |

stable through the year and comprising only 9 % of the total N deposition. Therefore, we conclude that the amount and changes of wet inorganic N deposition were not influenced by the fires intercepted by winds arriving at our location. Long-range atmospheric transport of reactive N forms is considered unlikely in the tropics due to the high rainfall (Ayers et al. 2000).

*Table 2.3 Comparison of annual wet inorganic N deposition rates in some Malaysian and non-Malaysian sites.*

| Site | $NH_4^+$-N | $NO_3^-$-N | pH | Reference |
|---|---|---|---|---|
| | kg ha$^{-1}$ yr$^{-1}$ | | | |
| **Forest** | | | | |
| Sepilok (East Malaysia) | 6.7 | 0.7 | 5.4 | This study |
| Danum (East Malaysia) | 0.7 | 0.4 | 5.1 | Vet et al. 2014 |
| Pasoh (West Malaysia) | 2.3 | 3.9 | 5.8 | Manokaran 1980 |
| Berembun (West Malaysia) | 1.4 | 1.6 | 5.9 | Yusop and Nik 1989 |
| Tanah Rata (West Malaysia) | 1.4 | 2.1 | 4.9 | Vet et al. 2014 |
| Neuglobsow (Germany) | 3.2 | 2.7 | 4.8 | Vet et al. 2014 |
| Starkey forest (USA) | 0.2 | 0.3 | 5.3 | Vet et al. 2014 |
| Xi'an-Jiwozi (China) | 1.2 | 1.0 | 6.1 | Vet et al. 2014 |
| **City** | | | | |
| Singapore | 11.5 | 13.4 | - | Karthikeyan et al. 2009 |

We thus consider it unlikely that fires and haze affected N deposition at our study site. We suggest that the increased $NH_4^+$ concentration in rainwater was due to agro-industrial fertilization. Oil palms are regularly fertilised leading to high nitrous oxide ($N_2O$) emissions that can increase ~160 times from natural forest to oil palm plantation (Fowler et al. 2011). Few studies have analysed reduced N emissions (NHx), which are produced in abundance after crop fertilization (Bobbink et al. 2010; Bouwman et al. 1997). We hypothesize that the relatively still air seen throughout May and June led to an accumulation of $NH_4^+$ in the air mass that was washed out in rainwater.

## 2.5 Conclusion:

Nitrogen deposition poses hazards to N limited forest systems, which might, as result, undergo biodiversity loss and changes in forest dynamics. Here we assessed the magnitude of wet inorganic N deposition over one year at a site close to a pristine forest reserve. The study site is surrounded by oil palm cultivation and might be affected by the seasonal haze and N deposition from forest fires. We found our site to have the highest amount of wet inorganic N deposition recorded in Malaysia. The deposition was mainly composed of $NH_4^+$ that increased substantially in the months of April, May and June 2017. When we tested whether the increase in rainwater $NH_4^+$ correlated with seasonal changes in forest fires at a large scale by crossing backward wind trajectories with fires occurrence for Borneo and Philippines we did not find evidence that forest fires influence the concentration or the total deposition of inorganic N. Therefore, we hypothesized that changes in rainwater $NH_4^+$ concentration were due to $NH_4^+$ accumulation sourced from the surrounding fertilized oil palm estates. To further test this hypothesis, the isotopic signature of rainfall-derived N could be compared the isotopic N signature of fertilisers used in the area. Should this case be strengthened, then policy makers and local authorities should consider prescribing limits to the amount of fertiliser used in plantations.

# 3 Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest.

After: “Soil characteristics influence species composition and forest structure differentially among size classes in a Bornean heath forest” by Giacomo Sellan, Jill Thompson, Noreen Majalap and Francis Q. Brearley. Accepted for publication in Plant and Soil.

**Abstract:** Whilst several studies have shown that edaphic variability influences species composition in nutrient-poor tropical forests, the determinants of local species distributions and, in particular, how these change from younger to mature individuals in such forests are still under debate, and have been poorly explored in tropical heath forests that are among the least fertile tropical forest ecosystems. We investigated the influence of soil fertility and topography on a Bornean heath forest species composition, α-, β-diversity and tree size structure among size classes by recording all trees ≥ 1 cm DBH in 16 forest plots totalling 0.36 ha. Tree species distributions generally followed gradients in available Al and soil depth; α- and β-diversity were linked to soil depth, and to some extent also to pH and the H:Al ratio. In contrast, forest structural attributes (basal area and stem density) were negatively correlated with both available and total P and a wider suite of soil nutrients, although trees ≥ 10 cm DBH were positively correlated with total P. Our study shows that heath forest species distribution, richness and structure is related to both edaphic and topographic characteristics and that soil acidity might have a strong influence in shaping these forests’ features. Among size classes, small trees are less influenced by soil and topography, whereas the sensitivity to these variables increases with tree size. We thus highlight that multiple edaphic factors influence different aspects of tropical forest structure, including different tree life stages, and species composition.

### 3.1 Introduction:

Tropical forests have the highest tree species diversity in the world (Gentry 1988; Ghazoul and Sheil 2010; Whitmore 1990), but we still strive to understand how such diversity is created and maintained. Several theories have been proposed to address this question such as the Janzen–Connell hypothesis (Janzen 1970, Connell 1971), neutral theory (Hubbell 2001) and environmental filtering (Baldeck et al. 2013). Although the drivers explained by different hypotheses might operate simultaneously and might have divergent controlling factors among sites, environmental factors influence tree species distribution and community composition in a considerable number of studies (Wright 2002, Legendre et al. 2005). In particular, climatic factors are important at continental scales (ter Steege et al. 2006, Zhang et al. 2016), whereas at smaller scales, topography and soil chemistry (Clark et al. 1998, Phillips et al. 2003) have a greater influence on species distributions (Condit et al. 2013, Jucker et al. 2018).

Most broad-scale studies of tree distribution only consider trees with a stem diameter at breast height (1.3 m; DBH) greater than 5 cm or 10 cm (e.g. Slik et al. 2015), so younger trees with smaller DBH (i.e. saplings) are often overlooked. In Borneo, for example, Paoli et al. (2006) and Sukri et al. (2012) reported small DBH trees to be distributed irrespectively of soil nutrient concentrations, whereas the distributions of larger DBH individuals were significantly influenced by edaphic variables. This implies that through tree ontogeny, individuals become more susceptible to the selective pressure of soil fertility so only the species adapted to particular soil conditions survive and grow (Russo et al. 2005). It is noteworthy that many experimental studies of forest nutrient limitation focus on seedlings and saplings grown in pots with different nutrient additions (e.g. Brearley et al. 2007, Nilus et al. 2011). If selective *in situ* response to soil fertility differ among size classes, then conclusions from pot bioassays must be taken with caution. It is thus paramount to consider trees from smaller size classes when conducting *in situ* studies of soil influences on species distribution and forest structure.

Heath forests occur throughout the tropics on nutrient-poor sandy soil (spodosols), with vegetation physiognomy characterised by a generally stunted appearance, sclerophyllous leaves and short, untapered stems (Richards 1936, Janzen 1974, Peace and Macdonald 1981, Turner 1994, Becker et al. 1999, Proctor 1999, Turner et al. 2000, Kenzo et al. 2014). These forests also have a high density of understorey trees, low species diversity (Anderson 1981, Frasier et al. 2008), and a high degree of endemism (Garcia 2016). Heath forest distributions and the characteristic features of their trees have been ascribed to low soil pH (Luizao et al. 2007), deficient soil nitrogen (Luizao 1994, Proctor 1999, Proctor et al. 1983, Brearley et al. 2011) or the interaction of these two factors (Luizao 1996). A number of studies (Brünig 1974, Newbery 1991, Newbery et al. 1986) classified several typologies of Bornean heath forests (known as kerangas locally) but few have linked heath forest species distribution to either soil chemical or topographic variables. Nonetheless, these valuable studies draw some notable conclusions. At Gunung Mulu (Sarawak, Malaysia), Newbery and Proctor (1984) focussed on differences in soil chemistry and found species distribution to be associated with differences in soil organic C and CEC, whilst Miyamoto et al. (2003) found the most abundant tree species to be weakly associated with humus depth in a Central Kalimantan (Indonesia) heath forest. Din et al. (2015), instead, ascribed variation in a Bruneian heath forest community to soil N concentration but highlighted that other topographic and edaphic variables, not considered in their study, might also have an effect on species distributions.

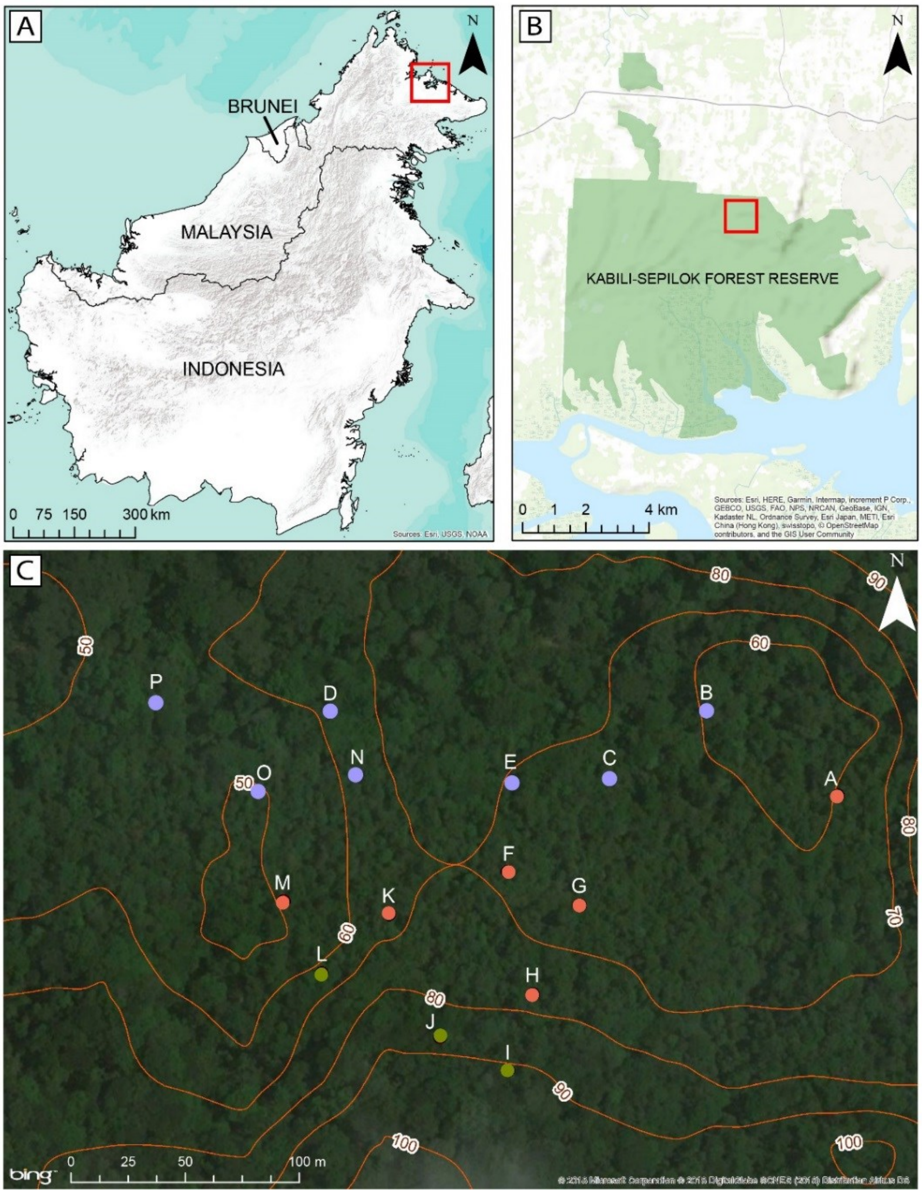
In this study, we used sixteen small plots in heath forest situated in north-east Malaysian Borneo. All plots were in close proximity to one another (within an area c. 0.05 km$^2$) to limit potential differences in bedrock and rainfall patterns and their influence on tree species distribution and forest structure. In particular, in this study we asked: (1) which soil chemical and topographic factors significantly influenced forest tree species composition and structure, and (2) how the influence of these factors varied among tree-size classes?

## 3.2 Methods:

Our experimental site is the Kabili-Sepilok Forest Reserve (KSFR), located in the Malaysian state of Sabah on the island of Borneo (5° 51' N, 117° 58' E)

Figure *3.1*a and b). Local bedrock consists of sandstone interbedded with occasional mudstone inclusions. The climate is equatorial with an annual precipitation of c. 3000 mm; only one month (April) receives less than 100 mm on average (Fox 1973, Nilus

2003). In April 2016 we installed sixteen 15 m x 15 m plots within the kerangas forest of the KSFR, all at least 30 m apart from one another (Figure 3.1c) over spodosol (USDA soil classification) soils. The plots were located on a gently sloping (c. 15 °), north-facing hillside.



Sources: Esri, USGS, NOAA

Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, © OpenStreetMap contributors, and the GIS User Community

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*Figure 3.1 Location of the study site. A) The island of Borneo with the approximate position of the Kabili-Sepilok Forest Reserve (Sabah, Malaysia) highlighted in red. B) The Kabili-Sepilok Forest reserve with the approximate location of the study plots highlighted and C) the study plots position on the forest. Colour of the name of plots reflects their grouing on the DCA ordination.*

Plot slope was determined as the mean value of four measurements of the angle from the top to the bottom of each plot using a hypsometer (Vertex IV, Haglöf, Långsele, Sweden). Plot elevation was determined with a GPS (Garmin Etrex 10, Garmin Ltd, Kansas City, KS, USA). Within all plots, trees and lianas ≥1 cm diameter at breast height (DBH; diameter measured at 1.3 m from the ground) were permanently tagged and their DBH recorded. Furthermore, we recorded the height of 25 randomly selected trees per plot spanning the tallest to the shortest tree with a hypsometer (Vertex IV, Haglöf, Långsele, Sweden) to relate the DBH to position in the canopy. Lianas were measured at 1.3 metres from their last rooting point. We then binned trees with DBH: ≥1-<2 cm, ≥2-<5 cm, ≥5-<10 cm and ≥10 cm (from now on referred as <2, 2-5, 5-10, and >10 cm DBH). Species identification was carried out by staff from Kabili-Sepilok Forest Research Centre Herbarium.

### 3.2.1 Soil sampling and soil chemical analysis:

Within every plot, a single soil pit of approximately 30 cm x 30 cm was dug to compare soil depths across the plots. Each plot was divided into four subplots (7.5 m x 7. 5 m) and a soil sample from the top 5 cm was collected in each subplot following removal of roots and coarse undecomposed leaves by digging a hole of approximately 10 cm x 10 cm using a knife; we collected 64 samples from the 16 plots in total. Each soil sample was split in two subsamples. The first subsample (approximately 2 g) was added to 30 ml of 1 M KCl and shaken for one hour in the field, allowed to equilibrate in a refrigerator for 18 hours, then filtered and analysed for $NH_4^+$ and $NO_3^-$ on a segmented flow analyser (Astoria-Pacific A2, Clackamas, OR, USA). On the second subsample, we measured moisture content, pH, available and total nutrients, C and N as well as exchangeable acidity and Al. Soil moisture content was determined gravimetrically after drying 3 g of soil to a constant weight at 105ºC. To measure pH, 5 g of fresh soil was shaken in 12.5 ml of distilled water overnight and pH recorded with a Corning 240 pH meter. We then oven dried at 50°C and ground the remaining soil for use in macro and micro-nutrient analysis. Samples (0.25 g) were microwave-digested (Mars Xpress 5, CEM Corporation, Matthews, NC, USA) for total Al and P analysis with a solution of 8 ml $HNO_3$ and 2 ml deionised $H_2O$.

Extractable soil P, Fe and Mn were extracted with a Mehlich I solution (2 g of soil shaken with 20 ml of Mehlich I solution for 5 minutes on a reciprocating shaker at 120 oscillations per minute; Wuenscher et al. 2015). For soil exchangeable Ca, Na, Mg and K, we added 2 g of soil to 20 ml of 1 M ammonium acetate and shook for two hours using a reciprocating shaker at 120 oscillations per minute (modified from Van Reeuwijk 2002). We determined exchangeable acidity ($H^+$ and Al) through titration of a 1 M KCl extraction (5 g soil and 50 ml KCl shaken for one hour) with 0.02 M NaOH and 0.01 % phenolphthalein (modified from Van Reeuwijk 2002).  We also measured exchangeable Al on the 1 M KCl extracts. Cation and metal concentrations were quantified using an iCAP Duo 6300 inductively coupled plasma optical emission spectrometer (Thermo Scientific, Waltham, MA, USA). Cation exchange capacity was calculated as sum of bases and exchangeable acidity. Total C and N concentrations were determined by combusting 0.15 g of soil in a Leco TruSpec CN analyser (St Joseph, MI, USA).

### 3.2.2 Statistical analysis:

For the ordinations, we used the package *vegan* (Oksanen 2015) in R 3.5.1 (R Development Core Team 2009). We visualised soil differences among plots by performing a redundancy analysis (RDA; significance checked with 999 permutations) of soil chemistry variables constrained by topography where all the variables were centred and scaled. We determined collinearity and selected the main variables that accounted for edaphic variation amongst plots for the canonical correspondence (CCA) analysis with a principal component analysis (PCA) following the approach of Abdi and Williams (2010). This consisted of selecting the variables that exceeded the expected average contribution to the two first principal components. Selected variables were then used as explanatory variables alongside topographical data for CCA ordination of our tree community dataset.

We calculated α-diversity with the Shannon-Wiener (*H'*) index, whereas for β-diversity we calculated a matrix of total dissimilarity between plots with Jaccard dissimilarity index (function *beta.pair()* of the R package *betapart*; Baselga and Orme 2012). A preliminary exploration of community composition across our plots was carried out using a detrended correspondence analysis (DCA). We then identified associations of selected species to soil variables following Shenbrot et al. (1991) who considered the position of the species centroids with respect to the standard error of the CCA ordination main centroid. If a species' centroid was located within the triplot main centroid's standard deviation, the species was labelled as a "generalist", whereas species that had a positive or negative position along an axis were considered a "specialist" (Table 3.5). The criterion to select species were a) their abundance among the plots using Shannon-Wiener diversity index and b) their score on the first two CCA axes. We centred and scaled the chemical, topographic variables as well as the absolute species abundances before the CCA, down-weighted the importance of rare species with the "*downweight()*" function in R package *vegan* (Oksanen 2015) and visualised the results using a CCA triplot. The significance of edaphic and topographic variables was obtained with a permutational ANOVA (999 permutations; Oksanen 2015) by terms that also report a *pseudo F* test (i.e. the ratio of constrained and unconstrained total inertia, each divided by their respective degrees of freedom). We performed a non- parametric Spearman correlation to determine correlations among α-diversity, stem density and basal area with the same chemical and topographical variables used in the CCA, whereas we performed a Mantel test (9999 permutations) to assess whether β-diversity correlated with soil or topographic variables selected with PCA. We used a Mantel test because β-diversity is presented as a dissimilarity matrix. The CCA, Spearman correlations and Mantel test were performed with all trees combined and then re-run with the four tree size classes (<2, 2-5, 5-10 and >10 cm DBH).

## 3.3 Results:

The forest plots were characterized by a typical short-statured heath forest with a canopy height of approximately 28 m. In total, we tagged 3336 living individuals ≥ 1cm DBH. The understorey was dense with a mean of 0.73 trees 1-5 cm DBH per $m^2$ and 0.19 trees ≥ 5 cm DBH per $m^2$; lianas were scarce (a mean across 16 plots of 217 individuals per ha).

*Table 3.1 Stem density and basal area of the 20 most common species in heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia.*

| Species | % of total stem density | % of total basal area |
|---|---|---|
| *Gaertnera junghuhniana* (Rubiaceae) | 12.74 | 1.48 |
| *Diospyros fusiformis* (Ebenaceae) | 7.45 | 0.65 |
| *Syzygium caudatilimbum* (Myrtaceae) | 6.07 | 1.25 |
| *Pimelodendron griffithianum* (Euphorbiaceae) | 5.63 | 10.12 |
| *Dracaena elliptica* (Asparagaceae) | 5.38 | 0.58 |
| *Cotylelobium melanoxylon* (Dipterocarpacae) | 4.78 | 12.71 |
| *Garcinia bancana* (Clusiaceae) | 3.35 | 6.84 |
| *Cleistanthus gracilis* (Phyllantaceae*)* | 3.13 | 1.78 |
| *Actinodaphne borneensis* (Lauraceae) | 3.00 | 0.97 |
| *Tristaniopsis obovata* (Myrtaceae) | 2.75 | 19.22 |
| *Chionanthus pluriflorus* (Oleaceae) | 2.63 | 0.77 |
| *Ternstroemia aneura* (Pentaphylacaceae) | 2.53 | 0.89 |
| *Shorea multiflora* (Dipterocarpaceae) | 2.44 | 3.21 |
| *Myrsine* sp. (Primulaceae) | 1.85 | 0.39 |
| *Calophyllum* sp. (Clusiaceae) | 1.75 | 1.37 |
| *Palaquium rostratum* (Sapotaceae) | 1.19 | 3.26 |
| *Eurycoma longifolia* (Simaroubaceae) | 1.00 | 0.17 |
| *Anisophyllea disticha* (Anisophylleaceae) | 0.90 | 0.04 |
| *Madhuca pallida* (Sapotaceae) | 0.84 | 2.45 |
| *Hancea griffithiana* (Euphorbiaceae) | 0.66 | 0.09 |
| Cumulative total | 67.7 | 65.1 |

Trees < 2 cm DBH had a mean height of 2.9 m (± 0.9 SD), trees 2-5 cm DBH had a mean height of 5.9 m (± 1.7), trees 5-10 cm DBH had a mean height of 11.4 m (± 2.8) and trees > 10 cm DBH had a mean height of 21.0 m (± 5.3). Throughout our plots, there was a mean of 199.7 (± 30.1) stems plot$^{-1}$ whereas basal area had a mean of 36.3 (±10.9) m$^{2}$ ha$^{-1}$. Relative basal area and stem density for the 20 most abundant species is shown in Table 3.1.

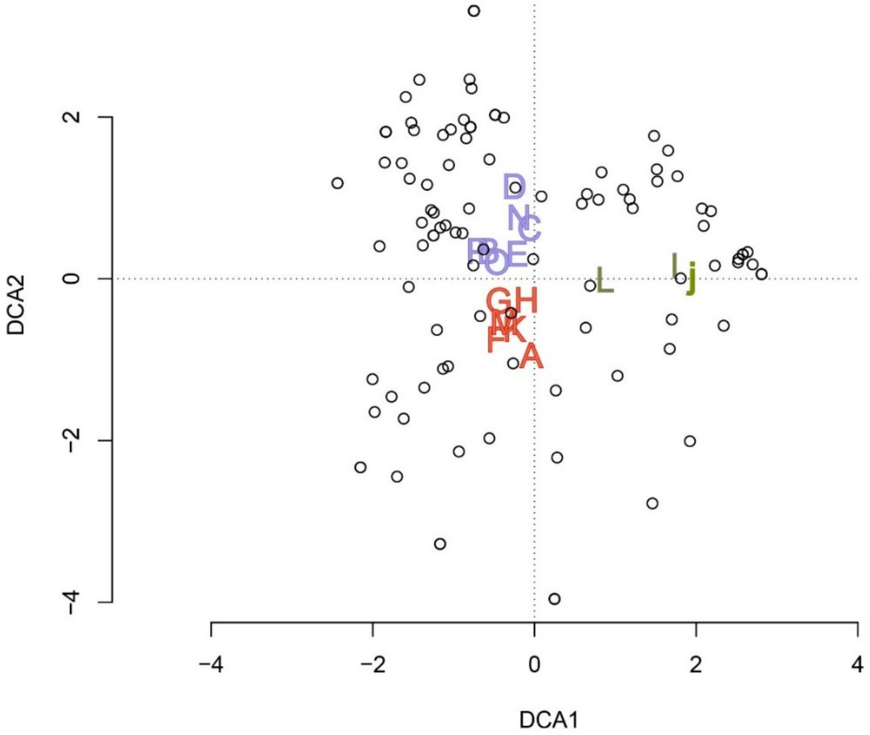

*Figure 3.2 Detrended correspondence analysis (DCA) using the absolute density of the 126 species found in 16 heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA ordination.*

### 3.3.1 Tree diversity:

In total we identified 2398 trees and shrubs to species level and 784 trees to genus, 12 to family with 142 not identified. We found 124 species within 48 families of which Myrtaceae (19 %) and Rubiaceae (14%) were most abundant. Myrtaceae had the greatest basal area (31 %), followed by Dipterocarpaceae (19 %), Clusiaceae (11 %), Euphorbiaceae (10 %) and Sapotaceae (5 %). Alpha diversity (*H'*) throughout the plots had a mean of 3.48 (±0.23 SD). The DCA (Figure 3.2) revealed three main plot groupings that reflected plot position on the hillslope, with strong floristic similarity between plot I, J and L near the ridge crest, A, F, G, H, K and M in the middle of the hill and B, C, D, E, N, O and P at the base (Figure 3.1).

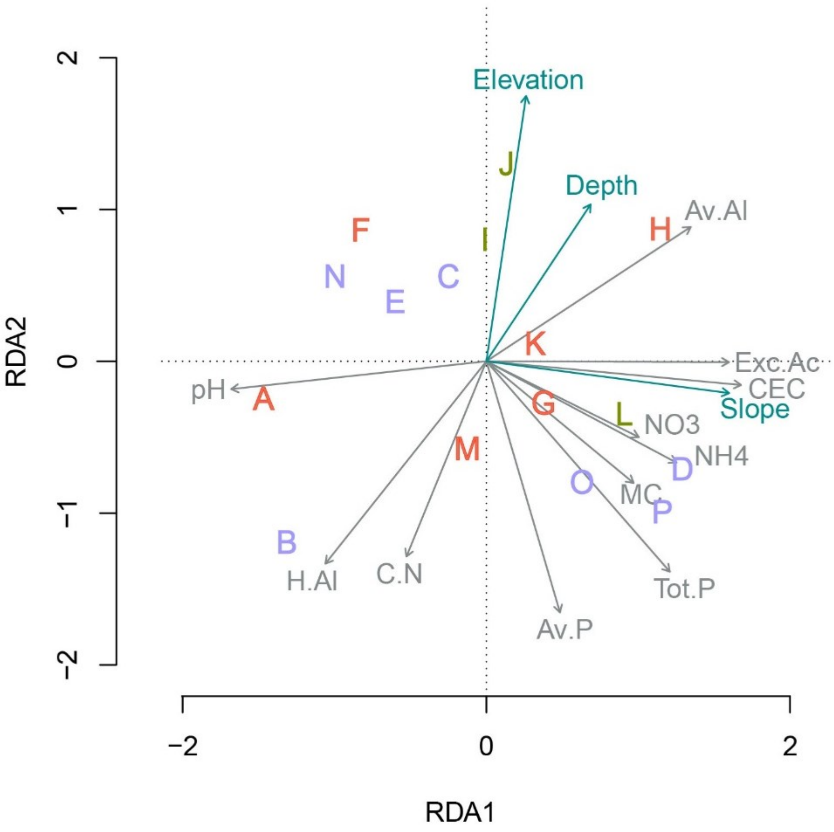

*Figure 3.3 Redundancy analysis (RDA) biplot with the main soil chemical variables (grey) constrained by plot topography (blue) in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA ordination.*

### 3.3.2 Topography, soil chemistry and PCA gradient:

The plots lay on a gently sloping hill with an elevation spanning 50 m between the highest and the lowest plot. Plots at the top of the slope had deeper (i.e. > 90 cm in plot I) podzolised soil than lower elevation plots (i.e. 24 cm in plot D). Generally, all plots were acidic (pH < 4) with a high concentration of total Al (mean 247 ± 28 SD µg $g^{-1}$) and a very low CEC (mean 3.75 ± 0.3 $cmol_c$ $kg^{-1}$), due largely to the high exchangeable acidity. Soil C:N ratio was high (mean 22.9 ± 0.7). Low soil N was reflected by low ammonium (mean 8.5 ± 1.1 μg $g^{-1}$) and nitrate (mean 0.59 ± 0.1 μg $g^{-1}$) concentrations (

Table 3.2).

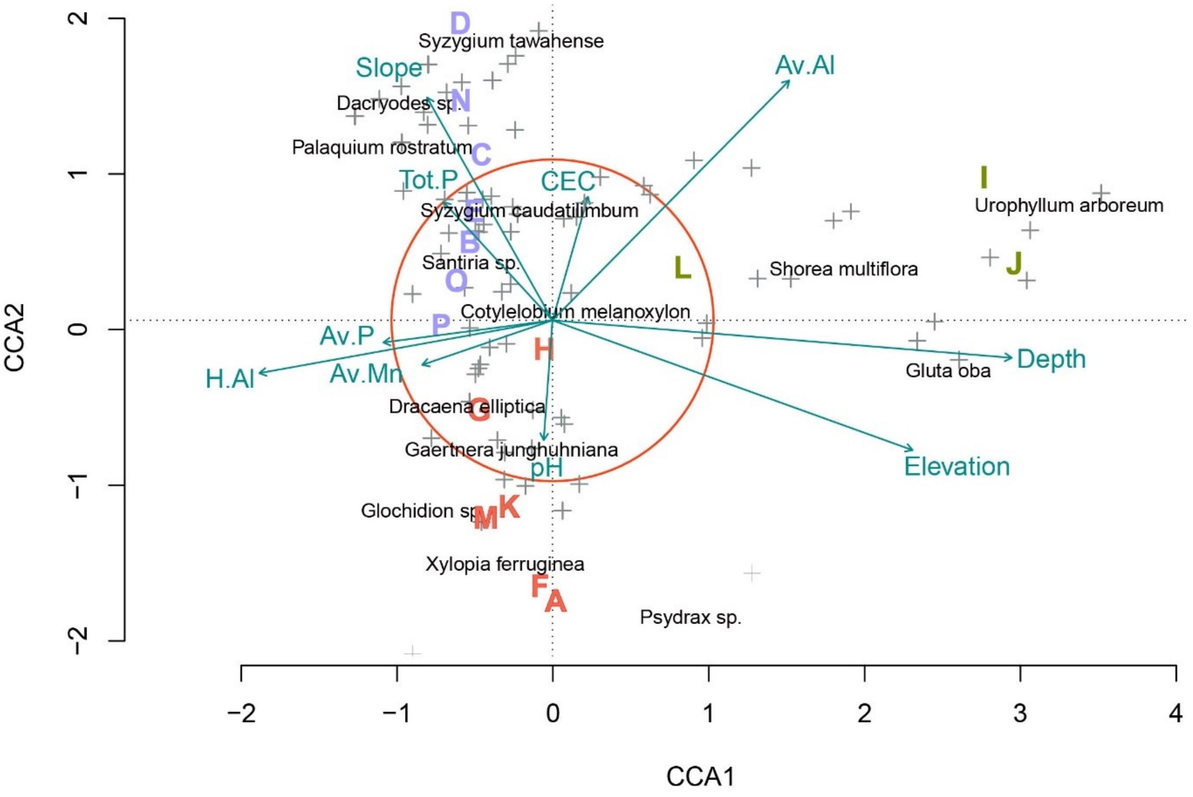

*Figure 3.4 CCA triplot with the tree species (represented as crosses) of all size classes in study plots (represented as letters) from the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The species whose name is written in full are the most abundant following the Shannon-Weiner diversity index and have a significant loading on the first two ordination axes. The red circle represent the standard deviation of the ordination centroid.*

The RDA first axis was characterised by a plot slope gradient (loading on the first axis: 0.99, $p<0.05$) showing that flatter plots to have less acidic pH, and lower exchangeable acidity and CEC. The second RDA axis was characterised by plot elevation (loading on the second axis: 0.99, $p<0.01$) and, to a lesser extent, by soil depth (loading on the second axis: 0.83, $p<0.05$) showing that higher elevation plots had deeper soil with high available aluminium, low H:Al ratio and total as well as available P (Figure 3.3). The PCA found seven variables exhibited collinearity (total Al, exchangeable acidity and available Fe, Na, K, Mg and Ca) so these were removed along with variables with non-significant loadings. The PCA first and second axes explained 40.8 % and 28.8 % of the variability in soil properties, respectively. The first axis was related to CEC, total and available P, pH and $NH_4^+$ whereas the second axis was linked to the H:Al ratio, available Al and Mn and the C:N ratio. The variables that exceeded the expected average contribution to the two first principal components were CEC, total P, available Al and P, H:Al ratio and pH (Table 3.3); these were retained for the CCA, Spearman and Mantel analyses along with topographic variables (elevation, slope) and soil depth.

### 3.3.3 Species distribution related to environmental variables:

From the CCA, we can see that species followed the first two axes of the ordination in agreement with topography and soil chemistry (Figure 3.4). Among the different tree DBH classes, soil chemistry and topography together explained between 68 % and 76 % of the floristic variation. In particular, soil depth and available Al were important for most size classes of trees but were less important for trees > 10 cm DBH ($X^2 = 0.24$, $p < 0.1$, and $X^2 = 0.25$, $p > 0.1$, for available Al and soil depth, respectively). Floristic variation in trees 5 - 10 cm DBH was influenced by CEC ($X^2 = 0.21$, $p < 0.05$) and total soil P ($X^2 = 0.23$, $p < 0.05$; Table 3.4). From the CCA ordination, we therefore identified two soil gradients along which species appear to be distributed. The first was the H:Al ratio-soil depth gradient and the second was the CEC-pH gradient (Figure 3.4). Although the CCA triplot's first axis was mainly driven by the H:Al ratio and soil depth gradients, available Al achieved high loadings on both the first (0.44; Table 3.4) and second axes (0.44) stressing the importance that Al retains in influencing species distributions.

*Table 3.2 Soil chemical and topographical characteristics of heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Values of chemical variables are means of four measurements whereas topographic variables consist of only one measurement.*

| Plot | pH | Moisture | Exchangeable | | H:Al | Total | | Available | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ($H_2O$) | Content | Acidity | Aluminium | Ratio | Al | P | P | Mn | Fe |
| | | (%) | cmol$_c$ kg$^{-1}$ | | | | | µg g$^{-1}$ | | |
| A | 3.89 | 5.37 | 1.51 | 0.18 | 7.7 | 178.7 | 40.8 | 10.7 | 2.4 | 20.2 |
| B | 4.05 | 8.74 | 2.02 | 0.32 | 9.1 | 148.6 | 61.1 | 21.5 | 6.3 | 18.1 |
| C | 3.75 | 5.79 | 2.42 | 0.55 | 3.5 | 216.8 | 42.5 | 10.7 | 0.9 | 33.1 |
| D | 3.56 | 13.90 | 4.26 | 0.76 | 4.7 | 271.8 | 70.2 | 16.6 | 2.3 | 29.7 |
| E | 3.68 | 6.67 | 2.10 | 0.37 | 5.2 | 153.0 | 36.7 | 8.2 | 0.9 | 17.8 |
| F | 3.82 | 4.00 | 1.47 | 0.26 | 4.6 | 106.5 | 28.2 | 8.6 | 0.7 | 14.4 |
| G | 3.63 | 9.40 | 2.77 | 0.42 | 3.4 | 287.9 | 59.3 | 15.4 | 4.2 | 42.8 |
| H | 3.56 | 6.49 | 4.31 | 1.13 | 2.8 | 365.1 | 56.9 | 12.4 | 1.1 | 33.7 |
| I | 3.80 | 6.11 | 2.18 | 0.68 | 2.2 | 402.5 | 42.8 | 10.7 | 1.1 | 44.6 |
| J | 3.72 | 7.02 | 2.53 | 0.80 | 2.8 | 535.0 | 38.8 | 9.5 | 1.2 | 42.3 |
| K | 3.68 | 5.80 | 2.36 | 0.63 | 2.9 | 260.4 | 57.6 | 15.4 | 1.0 | 22.5 |
| L | 3.43 | 13.60 | 3.74 | 0.60 | 5.3 | 285.9 | 70.1 | 15.2 | 1.3 | 21.5 |
| M | 3.74 | 4.62 | 2.50 | 0.40 | 5.2 | 173.7 | 54.2 | 19.8 | 2.7 | 18.2 |
| N | 3.82 | 6.20 | 1.64 | 0.31 | 4.7 | 133.8 | 38.1 | 9.4 | 0.7 | 15.5 |
| O | 3.64 | 7.04 | 2.28 | 0.39 | 4.9 | 209.0 | 65.6 | 18.1 | 3.0 | 22.7 |
| P | 3.58 | 8.43 | 2.77 | 0.47 | 5.2 | 236.3 | 76.2 | 22.9 | 6.2 | 28.8 |

*Table 3.2 Continued.*

| Plot | Exchangeable | | | | | | | C:N | Plot | Plot | Soil |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ca | K | Mg | Na | CEC | $NH_4^+$ | $NO_3^-$ | Ratio | ASL | Slope | Depth |
| | | | cmol$_c$ kg$^{-1}$ | | | μg g$^{-1}$ | | | m | % | cm |
| A | 0.30 | 0.20 | 0.61 | 0.12 | 2.37 | 4.9 | 0.0 | 26.6 | 55 | 9.5 | 23 |
| B | 0.13 | 0.07 | 0.11 | 0.03 | 3.59 | 4.2 | 0.0 | 26.3 | 49 | 12.3 | 19 |
| C | 0.16 | 0.12 | 0.37 | 0.07 | 3.36 | 9.6 | 0.2 | 24.5 | 69 | 13.7 | 23 |
| D | 0.14 | 0.19 | 0.44 | 0.08 | 6.03 | 11.7 | 1.1 | 25.2 | 53 | 14.6 | 24 |
| E | 0.14 | 0.13 | 0.32 | 0.05 | 2.59 | 6.4 | 0.4 | 23.7 | 50 | 14.8 | 27 |
| F | 0.16 | 0.10 | 0.21 | 0.04 | 2.00 | 6.2 | 0.6 | 17.7 | 73 | 13.3 | 29 |
| G | 0.19 | 0.20 | 0.38 | 0.09 | 4.68 | 10.0 | 0.8 | 26.0 | 66 | 13.1 | 32 |
| H | 0.21 | 0.17 | 0.82 | 0.23 | 5.67 | 5.4 | 0.5 | 19.5 | 64 | 14.1 | 39 |
| I | 0.16 | 0.13 | 0.35 | 0.07 | 2.64 | 7.8 | 0.8 | 21.7 | 83 | 13.3 | 100 |
| J | 0.13 | 0.20 | 0.33 | 0.12 | 3.11 | 7.6 | 0.2 | 16.7 | 74 | 12.8 | 49 |
| K | 0.19 | 0.18 | 0.50 | 0.07 | 3.47 | 11.6 | 0.7 | 24.6 | 61 | 14.3 | 39 |
| L | 0.17 | 0.37 | 0.75 | 0.09 | 6.00 | 9.8 | 0.0 | 21.9 | 64 | 14.8 | 48 |
| M | 0.34 | 0.17 | 0.58 | 0.06 | 3.96 | 8.9 | 0.8 | 27.0 | 60 | 14.9 | 32 |
| N | 0.12 | 0.12 | 0.23 | 0.05 | 2.25 | 1.6 | 0.3 | 21.7 | 51 | 14.1 | 21 |
| O | 0.49 | 0.20 | 0.65 | 0.07 | 3.66 | 9.0 | 2.0 | 22.7 | 42 | 15.8 | 27 |
| P | 0.51 | 0.20 | 0.78 | 0.07 | 4.62 | 20.8 | 1.1 | 21.5 | 48 | 15.4 | 33 |

*Table 3.3 Contribution on PCA first and second axis of soil chemical parameters from heath forest plots from the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The variables that scored a contribution higher than the expected one for both dimensions are noted in bold.*

| Variable | Contribution to PC1 | Contribution to PC2 |
|---|---|---|
| **Av.Al** | 6.89 | 15.41 |
| **Av.Mn** | 6.79 | 14.90 |
| **Av.P** | 12.75 | 7.88 |
| C.N | 1.20 | 14.57 |
| **CEC** | 17.36 | 2.38 |
| **H:Al** | 0.11 | 24.56 |
| MC | 11.58 | 0.58 |
| $NH_4$ | 11.47 | 0.81 |
| $NO_3$ | 0.84 | 9.26 |
| **pH** | 11.54 | 7.39 |
| **Tot.P** | 19.45 | 2.23 |

### 3.3.4 Species edaphic associations and soil gradients:

From the CCA analyses, 51 species retained both high importance for among-plot diversity and high scores on the first two ordination axes. Of these species, 19 were associated with a low H:Al ratio and deep soil, whereas no species was associated with shallow soil and a high H:Al ratio (CCA first axis, Table 3.5).

Furthermore, we identified another 18 species as generalists, but their association changed among the DBH classes considered. The only species that maintained a generalist species distribution among all DBH classes was *Cotylolebium melanoxylon* (Dipterocarpaceae). *Garcinia gaudichaudii* (Clusiaceae), *Gaertnera junghuhniana* (Rubiaceae), *Dracaena elliptica* (Asparagaceae), *Syzygium cauditilimbum* (Myrtaceae) and *Syzygium* sp. were generalists in at least two size classes (Table 3.5).

*Table 3.4 (Next page). Scores of soil and topographic variables on the first CCA axes (VSA1) in four tree size classes heath forest plots from the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant value ('***' < 0,001 '**' <0.01, '*' < 0.05, '+' < 0.1) are in bold.*

| Tree size | | Available Mn | CEC | Available Al | Total P | Available P | pH | H:Al ratio | Plot slope | Soil depth | Plot elevation | Number of individuals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| All | VSA1 | -0.24 | 0.07 | **0.44*** | -0.20 | -0.31 | -0.02 | -0.54 | **-0.23**$_{+}$ | **0.85*** | 0.67 | 3194 |
| | $X^2$ | 0.08 | 0.09 | 0.18 | 0.12 | 0.10 | 0.07 | 0.09 | 0.14 | 0.20 | 0.07 | |
| | *F-stat* | 0.99 | 1.08 | 2.19 | 1.43 | 1.27 | 0.85 | 1.07 | 1.68 | 2.51 | 0.89 | |
| <2cm | VSA1 | 0.21 | -0.01 | **-0.43*** | 0.25 | 0.34 | -0.08 | 0.58 | 0.35 | **-0.83*** | -0.67 | 1413 |
| | $X^2$ | 0.09 | 0.10 | 0.23 | 0.13 | 0.14 | 0.10 | 0.13 | 0.16 | 0.21 | 0.09 | |
| | *F-stat* | 0.86 | 0.92 | 2.11 | 1.16 | 1.30 | 0.95 | 1.21 | 1.43 | 1.89 | 0.78 | |
| 2-5cm | VSA1 | -0.25 | 0.13 | **0.41**$_{+}$ | -0.10 | -0.22 | -0.13 | -0.52 | -0.11 | **0.92*** | 0.67 | 1087 |
| | $X^2$ | 0.11 | 0.13 | 0.18 | 0.13 | 0.13 | 0.11 | 0.11 | 0.17 | 0.28 | 0.11 | |
| | *F-stat* | 0.90 | 1.11 | 1.50 | 1.08 | 1.06 | 0.89 | 0.92 | 1.39 | 2.36 | 0.90 | |
| 5-10cm | VSA1 | 0.09 | **-0.14*** | **-0.35*** | **0.07*** | 0.15 | 0.06 | 0.41 | **0.19**$_{+}$ | **-0.86**** | **-0.63**$_{+}$ | 353 |
| | $X^2$ | 0.17 | 0.21 | 0.25 | 0.23 | 0.13 | 0.17 | 0.18 | 0.20 | 0.34 | 0.19 | |
| | *F-stat* | 1.30 | 1.59 | 1.94 | 1.75 | 1.00 | 1.34 | 1.42 | 1.50 | 2.61 | 1.14 | |
| >10cm | VSA1 | -0.30 | 0.09 | **0.53**$_{+}$ | -0.19 | -0.35 | -0.08 | -0.58 | -0.06 | 0.83 | 0.64 | 341 |
| | $X^2$ | 0.15 | 0.15 | 0.24 | 0.15 | 0.11 | 0.10 | 0.12 | 0.14 | 0.25 | 0.10 | |
| | *F-stat* | 1.05 | 1.06 | 1.69 | 1.05 | 0.80 | 0.71 | 0.86 | 0.97 | 1.74 | 0.73 | |

### 3.3.5 Forest structure, Alpha- and beta- diversity:

Soil heterogeneity clearly influence forest structure although the Spearman and Mantel tests, consistent with the CCA, showed different influences of soil and topographic variables among DBH classes (Table 3.6 and Table 3.7). In particular, stem density and basal area decreased with high soil P. Density of all trees, and particularly those <2 cm DBH ($p<0.01$) were negatively correlated with available Mn and density and basal area of trees 5-10 cm DBH was negatively correlated with CEC, available Al and pH in addition to slope and soil depth (all $p < 0.05$).

A similar suite of elements also influenced α-diversity but correlations with soil chemistry and topography were mostly found in trees 5-10 cm DBH (CEC and pH: $p$ <0.01; total P, slope and depth: $p$ <0.05) whereas in trees > 10 cm DBH α-diversity correlated only with available Al and pH ($p$ <0.05).

The results of the Mantel test for β-diversity (Table 3.7) showed topography to be consistently significant among size classes, although at different degrees and with different variables. In particular, soil depth was most significant for trees 2-5 cm DBH ($p$ <0.01) and 5-10 cm DBH ($p$ <0.001) along with plot elevation for trees 5-10 cm DBH ($p$ <0.01). Soil chemistry was only correlated with β-diversity for trees 2-5 cm DBH (H:Al ratio at $p$ <0.05) and 5-10 cm DBH (pH and H:Al ratio at $p$ <0.05 and $p$ <0.01).

*Table 3.5 (Next page). Association of the 52 most important tree species for the first (H:Al ratio-soil depth) or second (CEC-pH) CCA axes ordination of heath forest study plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Columns are divided per size-class and axis considered. The species whose centroid was located within the triplot main centroid standard deviation have been called "generalists" (g in the table), whereas the species that had a positive or negative correlation with the indicated axis has been designated with a "+" or a "-", respectively. If a cell is empty it means that the individuals from that species in that size class were not important in determining inter plot variation.*

| Species | All |  | <2cm |  | 2-5cm |  | 5-10cm |  | >10cm |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH |
| *Anisophyllea disticha* |  |  | + |  | + |  |  |  |  |  |
| *Barringtonia sp.* | + |  |  |  |  |  |  |  |  |  |
| *Calophyllum sp.* |  |  |  |  |  |  |  | - | g | g |
| *Chionanthus pluriflorus* |  |  |  |  |  |  |  |  |  | + |
| *Cleistanthus gracilis* | + |  | + |  | + |  |  |  |  |  |
| *Cotylolebium melanoxylon* | g | g | g | g | g | g | g | g | g | g |
| *Dacryodes sp.* |  | + |  | + |  |  |  |  |  |  |
| *Diospyros fusiformis* |  |  | g | g |  |  |  |  |  |  |
| *Diospyros sp.* |  |  | + |  |  |  |  |  |  |  |
| *Dracaena elliptica* | g | g | g | g | g | g |  |  |  |  |
| *Elaeocarpus sp.* |  |  | + |  |  |  |  |  |  |  |
| *Euricoma longifolia* |  |  |  |  |  |  | + |  |  |  |
| *Gaertnera junghuhniana* | g | g | g | g | g | g |  | - |  |  |
| *Garcinia bancana* |  |  |  |  |  |  | g | g |  |  |
| *Garcinia gaudichaudii* |  |  |  |  |  |  | g | g | g | g |
| *Gluta oba* | + |  |  |  |  |  | + |  |  |  |
| *Glochidion sp.* |  | - |  |  |  |  |  |  |  |  |
| *Gnetum sp.* |  |  | g | g |  |  |  | + |  |  |
| *Gonystylus sp.* |  |  |  |  | g | g |  |  |  |  |
| *Hancea griffitihiana* |  |  |  |  |  |  | + |  |  |  |
| *Horsfieldia sp.* |  |  |  |  |  | + |  |  |  |  |
| *Ixonanthes reticulata* |  |  | g | g |  |  |  | + |  |  |
| *Ixora sp.* |  | - |  |  |  |  |  |  |  |  |
| *Koompassia malaccensis* |  |  |  |  |  | - |  |  |  |  |
| *Litsea cylindrocarpa* | g | g |  |  |  |  | g | g |  |  |
| *Madhuca pallida* | + |  | + |  |  |  | + |  |  | + |
| *Mangifera sp.* | + |  |  |  |  |  | + |  | + |  |

| Species | All | | <2cm | | 2-5cm | | 5-10cm | | >10cm | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH | Depth-H:Al | CEC-pH |
| *Memecylon sp.* | | | + | | | | | | | |
| *Mezzettia sp.* | | | + | | | | | | | |
| *Myristica sp.* | | | | + | | | | | | |
| *Myristica malaccensis* | | | | | + | | | | | |
| *Myrsine sp.* | | - | | - | | | | | | - |
| *Palaquium rostratum* | | + | | + | | + | | | | + |
| *Parinari sp.* | | + | | | | | | | | |
| *Parishia insignis* | | | | | + | | | | + | |
| *Pimeleodendron griffithianum* | | | | | | | | | g | g |
| *Psydrax sp.* | | - | + | | + | | | | | |
| *Rothmannia sp.* | + | | + | | | | | | | |
| *Santiria sp.* | g | g | | | | + | | | | |
| *Shorea felciferoides* | | | | - | | | | | | |
| *Shorea multiflora* | + | | | | | | + | | | |
| *Stemonurus sp.* | | | | | | | | + | | |
| *Syzygium cauditilimbum* | g | g | | | g | g | g | g | | + |
| *Syzygium sp.* | g | g | | | g | g | | | g | g |
| *Syzygium tawahense* | | | | | | + | | | | |
| *Ternstroemia aneura* | | | | | g | g | | | | |
| *Timonius flavesce* | | | g | g | | - | | | | |
| *Tristaniopsis obovata* | | | | - | | | | | g | g |
| *Urophylum arboreum* | + | | | | | | | | | |
| *Vatica micrantha* | | | | | + | | + | | | |
| *Xanthophyllum flavescens* | | | | | | | + | | | |
| *Xilopia ferruginea* | | - | | | | | | - | | |

### 3.4 Discussion:

Nutrient-poor tropical forests support high tree species diversity but the relative influence of environmental factors on these forests' floristic variability still needs further research. Our study site showed a typical heath forest floristic diversity, forest structure, and soil chemistry. We showed that soil acidity, topography and nutrient limitation act in concert to shape species distribution, structure and diversity of the Kabili-Sepilok heath forest ecosystem. The influences of these topo-edaphic factors change among size classes.

The heath forest in our study site had a basal area of trees > 5 cm DBH (34.4 $m^2$ $ha^{-1}$) and stem density of trees > 5 cm DBH (1997 stems $ha^{-1}$), similar to other Bornean heath forests (e.g. Proctor et al. 1983; Davies and Becker 1991; Miyamoto et al. 2007). When compared to the adjacent lowland evergreen rain forest, stem density was approximately doubled (1002 stems $ha^{-1}$; Nilus 2003) whilst basal area was very similar (35 $m^2$ $ha^{-1}$; Nilus 2003). The most abundant families were rather different to other Bornean tropical heath forests. In comparison to the extensive study undertaken by Newbery (1991) in Brunei and Sarawak heath forests, our site lacked Myrsinaceae, Annonaceae and Chrysobalanaceae.

This might be due to the limited area of our study (0.36 ha), requiring caution when comparing with results from other studies because such a small area might not be sufficient to exhaustively capture forest structure and biodiversity indices that are sample size dependent (Condit et al. 1996).

*Table 3.6 (Next page). Results of the Spearman correlation test among forest structure (i.e. Basal area and Stem density) and α- diversity (calculated with Shannon index) with edaphic and topographic variables in our heath forest study plots from the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. We performed the analysis splitting the individuals among four tree DBH size classes and grouping all the individuals together. Significant values ('***' < 0,001 '**' <0.01, '*' < 0.05) are in bold.*

| Size classes (cm) | Variable | Available Mn | CEC | Available Al | Total P | Available P | pH | H:Al ratio | Plot slope | Soil depth | Plot elevation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| All | Basal area | 0.3 | 0.15 | -0.05 | **0.61*** | 0.37 | -0.19 | 0.33 | 0.1 | -0.18 | -0.25 |
| | Stem density | **-0.7**** | -0.35 | 0.003 | **-0.54*** | **-0.6*** | 0.08 | -0.28 | -0.17 | -0.01 | 0.42 |
| | α- diversity | -0.34 | -0.2 | 0.01 | 0.009 | -0.19 | -0.02 | 0.08 | -0.02 | -0.4 | -0.02 |
| <2 | Basal area | -0.57 | -0.21 | 0.18 | -0.38 | -0.42 | 0.01 | -0.37 | -0.15 | 0.01 | 0.42 |
| | Stem density | **-0.64**** | -0.15 | 0.26 | -0.37 | -0.49 | -0.06 | -0.45 | -0.08 | 0.14 | 0.46 |
| | α- diversity | -0.31 | -0.22 | 0.04 | -0.06 | -0.13 | 0.01 | 0.08 | 0.05 | -0.38 | -0.15 |
| 2-5 | Basal area | -0.27 | -0.19 | -0.18 | -0.25 | -0.2 | 0.03 | 0.09 | -0.11 | -0.02 | 0.08 |
| | Stem density | -0.33 | -0.07 | -0.12 | -0.09 | -0.14 | -0.15 | 0.21 | 0.18 | -0.15 | 0.007 |
| | α- diversity | -0.36 | -0.17 | 0.06 | 0.03 | -0.06 | 0.03 | 0.06 | 0.1 | -0.39 | -0.08 |
| 5-10 | Basal area | **-0.5*** | **-0.7**** | **-0.49*** | **-0.74***** | **-0.62**** | **0.53*** | -0.09 | **-0.51*** | -0.4 | 0.26 |
| | Stem density | -0.45 | **-0.82***** | **-0.65**** | **-0.73**** | **-0.54*** | **0.69**** | 0.11 | **-0.51*** | **-0.58*** | 0.10 |
| | α- diversity | -0.47 | **-0.69**** | -0.37 | **-0.56*** | -0.46 | **0.66**** | 0.14 | **-0.54*** | **-0.61*** | 0.09 |
| >10 | Basal area | 0.36 | 0.32 | 0.13 | **0.69**** | 0.45 | -0.29 | 0.19 | 0.1 | -0.05 | -0.15 |
| | Stem density | 0.10 | 0.19 | -0.11 | 0.12 | 0.06 | -0.09 | 0.05 | -0.06 | 0.19 | 0.17 |
| | α- diversity | 0.02 | 0.44 | **0.49*** | 0.28 | -0.05 | **-0.54*** | -0.02 | 0.03 | 0.3 | 0.16 |

*Table 3.7 Results of the Mantel test between β- diversity (calculated as total dissimilarity matrix with Jaccard index) with edaphic and topographic variables in our heath forest study plots from the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. We performed the analysis splitting the individuals among four tree DBH size classes and grouping all the individuals together. Significant values ('***' < 0,001 '**' <0.01, '*' < 0.05) are in bold.*

| Size class (cm) | Available Mn | CEC | Available Al | Total P | Available P | pH | H:Al ratio | Plot slope | Soil depth | Plot elevation |
|---|---|---|---|---|---|---|---|---|---|---|
| All | -0.08 | -0.27 | 0.03 | -0.1 | -0.06 | -0.03 | 0.25 | 0.22 | 0.47 | **0.3*** |
| <2 | -0.09 | -0.23 | 0.01 | -0.05 | -0.04 | -0.006 | 0.2 | 0.21 | **0.39*** | **0.29*** |
| 2-5 | -0.09 | -0.17 | 0.1 | -0.05 | -0.09 | 0.09 | **0.34*** | **0.39*** | **0.48**** | 0.23 |
| 5-10 | -0.008 | -0.03 | 0.14 | -0.06 | -0.09 | **0.25*** | **0.32**** | **0.27*** | **0.45***** | **0.32**** |
| >10 | -0.11 | -0.12 | 0.06 | -0.02 | -0.07 | -0.07 | 0.06 | -0.09 | 0.38 | **0.35*** |

The soil (spodosol) underlying our plots had a greater concentration of available P and a lower concentration of Al compared with the heath forest plots (acrisol) of Nilus (2003) in the same KSFR, suggesting that the soils in our plots had likely gone through a longer or more intense podzolisation process.

During podzolisation, the soil is weathered and clay is eluviated (Bravard and Righi 1989) so Al and Fe are deposited in deeper layers of the mineral soil (Andriesse 1975), which often forms an indurated hardpan (Andriesse 1968). Usually, in tropical soils, available P is bound to Fe and Al, but the low concentration of these cations in spodosols increases P availability in the soil solution (as also seen by Medina and Cuevas 1989, Coomes 1997, Metali et al. 2015).

### 3.4.1 Influence of soil and topography on floristic distribution, diversity and forest structure:

Our results show that topography and soil chemistry have a strong influence on floristic distribution. Generally, it appears that, within our heath forest, the variation in species composition is driven by both edaphic and topographic variables, in particular available Al concentration and soil depth. On the other hand, soil nutrients (CEC and total P) along with soil pH play a major role only for tree (5 - 10 cm DBH) α-diversity, whereas an interaction of soil acidity, Al and topographic factors influences β-diversity. As Al is an important constituent of soil acidity, we argue that, in combination with its ratio with $H^+$, is important in shaping heath forest species composition as hypothesised by Proctor (1999). It is noteworthy that available Al covaries with soil depth and elevation and is directly linked to a decrease in the H:Al ratio. In Brazilian cerrado ecosystems, a similar pattern of increasing Al with elevation was observed to underpin species composition (Guidão et al. 2002, Abreu et al. 2012, Soares et al. 2015, Silva et al. 2016). Aluminium is abundant in clay-rich acidic soils and, together with $H^+$, is toxic for plants. Along a soil gradient with different clay content (e.g. ultisol to spodosol) Al is likely to create a species distribution gradient based on species' Al tolerance (Kidd and Proctor, 2001). On the other hand, within our sandy spodosol, the lack of Al-rich clay means low soil Al concentrations (as seen in the plots at the base of the slope). In such cases, a beneficial role of soil Al would be to reduce $H^+$ toxicity through its buffering action (Proctor 1999, Luizao 1996, Luizao et al. 2007). Hydrogen is more detrimental to plants than Al - experimental Al addition, for instance, enhanced growth of temperate (Kinraide 1993, Kidd and Proctor 2000) and tropical plants (Osaki et al., 1997) adapted to an extremely acidic Al-poor soil. In some acidic and sandy soils, it could be argued that plants accumulate Al in leaves to buffer $H^+$ toxicity through their litterfall with Al accumulators composing more than 30 % of the biomass in e.g. Brazilian cerrado (Goodland and Pollard 1973, Haridasan 1982, 2008). In our plots, *Gaertnera junghuhniana* (Rubiaceae) the most common species with a generalist distribution, is an Al accumulator (i.e. has a leaf Al concentration higher than 1000 $\mu g\ g^{-1}$; Sellan 2019). This further supports the importance of soil acidity, and Al, as a driver of species distribution in our study site. On the other hand, considering the emphasis given to low N availability in some studies as a theory to explain heath forest characters (e.g. see Vernimmen et al. 2013), N was too low to significantly explain differences among plots and thus was excluded from the analysis post PCA variable selection.

Soil P (available and total) influenced species richness of our plots for trees 5 - 10 cm DBH and structure (i.e. basal area and stem density) of trees > 5 cm DBH. Surprisingly, plots with high soil P concentrations had lower basal area and stem density (although this was largely driven by smaller trees < 10 cm DBH). We would have expected the contrary as P is often considered to be limiting in lowland rain forest (Cleveland et al. 2011; LeBauer and Treseder 2008), and evidence suggests that it might also be limiting in heath forest (Dent et al., 2006). High available P concentrations are found in plots with low exchangeable Al (as discussed above) where soil acidity is likely dominated by $H^+$ rather than Al (Proctor 1999). So, the negative relationship among soil P and forest structure is possibly due to $H^+$ toxicity rather than to soil P *per se*.

Interestingly, soil depth is a strong selective force for the distribution of trees 5 - 10 cm DBH with species as *Madhuca pallida* (Sapotaceae), *Shorea multiflora* (Dipterocarpaceae) and *Gluta oba* (Anacardiaceae) associated with deeper soil. This result seems to agree with the hypothesis proposed by Newbery (1991), and supported by Grainger and Becker (2001), that heath forests are composed of two ecophysiological and structural guilds: one with dominant deep-rooted trees and one with small shallow-rooted trees. Alternatively, soil depth is possibly important because a deeper soil has a greater volume and thus holds more nutrients per unit area.

### 3.4.2 Different influences of edaphic and topographic variables among size classes:

The diverse influence of nutrients and topography on tree species distribution, plot α- and β-diversity as well as community structure clearly changes among size classes. In particular, trees <5 cm DBH showed weak correlations among structure, floristic variation and diversity with edaphic and topographic variables when compared to individuals > 5 cm DBH. This differential effect among size classes was documented elsewhere in Asian forests (e.g. Paoli et al. 2008, Sukri et al. 2012, Xu et al. 2016, Yang et al. 2016) and we propose this dissimilarity to be the effect of light competition. Small understorey trees are primarily limited by light availability as they are growing below the forest canopy (Coomes and Allen 2007, Cai et al. 2008) and only secondarily from other resources. Despite heath forest's low leaf area index (Vernimmen et al. 2007) and high light availability at ground level (Richards 1936), leaves of understorey saplings (Cao 2000, Cao and Booth 2001) had adaptations to low light availability when compared to leaves of the same species growing in brighter environments. Based on our results, the smallest DBH size classes had a mean height of 2.9 m (< 2 cm DBH) and 5.7 m (2-5 cm DBH), well below the canopy height of 28 m, whereas trees 5-10 cm DBH had a mean height of c. 11 m, which might be sufficient to free them from light limitation. In this case, nutrient availability would have a greater influence on the distribution of trees >5 cm DBH. The poor correlation of tree species distribution with topo-edaphic factors for trees > 10 cm DBH might be explained by the dynamic nature of soil chemistry. In both tropical (Bauters et al. 2017) and temperate (Mueller et al. 2012; Vesterdal et al. 2008) forest plantations, changes in topsoil nutrient content and acidity have been recorded after just a few decades. Tropical trees can be as old as 1000 years (Chambers et al. 1998;

Kurokawa et al. 2003) and in heath forests trees, diameter growth is slow compared to lowland evergreen forest (Nilus 2003; Brearley et al. unpublished data). Although we have no information on tree age in our forest, it is likely that trees > 10 cm DBH developed in a soil with different nutrient characteristics from the ones we see today. Alternatively, the lack of correlation between trees > 10 cm DBH species distribution and topo-edaphic variables might be due to the random mortality of big trees in our plots. It is also interesting to note that trees > 10 cm DBH show an opposite correlation of basal area with soil total P and of α-diversity with soil pH if compared to trees 5-10 cm DBH. This might highlight different strategies to overcome soil acidity and absorb nutrients between different tree life stages.

### 3.4.3 Soil-species associations:

We acknowledge that our study plots are small but, comparing our results with existing literature, we found them to be consistent with other studies. For example, Baltzer et al. (2005) found *Shorea multiflora* to be a sandstone forest (humult ultisol) specialist in the same Kabili-Sepilok Forest Reserve. Our results thus agree with Baltzer et al. (2005) because sandstone soil is higher in Al than heath forest and we found *S. multiflora* to be more common in soil with low H:Al ratio, i.e. a soil with high available Al. The same is applicable to the results of Potts et al. (2002) who found *Pimelodendron griffithianum* (Euphorbiaceae) to be a generalist, *Vatica micrantha* (Dipterocarpaceae) and *Mangifera* sp. (Anacardiaceae) to favour Al- rich humult ultisols and two *Diospyros* (Ebenaceae) species to be specialists in udult ultisols (more nutrient rich soil). The dispersion of species around the ordination centroid in our analysis revealed that more than half of the species considered in this analysis followed a soil gradient (i.e. 16 species out of 23, considering all size classes grouped together).

The cumulative number of species following the soil depth- H:Al gradient through the split size classes (18 species) instead of the CEC-pH gradient (19 species) was very similar. However, the higher score of the first CCA axis gives us a further reasonable criterion to suggest a greater influence of the depth-H:Al gradient rather than the

CEC-pH gradient on species distribution. A secondary result is that, among the heath forest generalist species, we found *Gaertnera junghuhniana*, which is an Al accumulator. This characteristic might allow *G. junghuhniana* to succeed throughout our heath forest site because of its capacity of attenuate $H^+$ toxicity through Al-rich leaf litterfall.

### 3.5 Conclusion:

Our study demonstrated that there are complex interactions among topography, nutrient limitation and soil acidity that influence different aspects of forest tree species distributions and forest structure in this Bornean heath forest. These variables showed a greater importance for trees 5- 10 cm DBH, confirming a recently developed hypothesis suggesting that environmental filtering is almost absent in the early stages of plant development and become cumulative with age (Jabot et al., 2008). Generally, we suggest soil acidity to be a factor of primary importance in shaping this heath forest's floristic variation and structure. Given the high conservation value of this fragile forest type (Whitmore, 1984; Hattori et al. 2019) we underscore its susceptibility to changes in soil pH and encourage careful management and protection of heath forests.

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# 4 Influence of soil N and soil pH on productivity, soil and litterfall chemistry of a tropical heath forest.

**Abstract:** The productivity of tropical rain forests has been linked to soil nutrient availability and lowland rain forests are generally thought to be limited by soil phosphorus (P). Nonetheless, the soil spatial heterogeneity and differing plant species distribution found in the lowland tropics justifies the need for a more detailed testing of this hypothesis. Tropical heath forests are thought to be limited by low soil nitrogen (N) availability or soil acidity. In this study, we tested the effects of changes in soil N availability and pH on tree productivity, soil and litterfall chemistry, and leaf herbivory in a Bornean heath forest using a factorial N (urea) and $CaCO_3$ (lime) addition experiment. We also tested whether these treatments caused changes in relative growth rate in stem diameter among different stem size classes and species functional identities. Nitrogen fertilisation enhanced plant uptake of soil N and P. Nitrogen fertilisation also doubled stem diameter growth rate of trees 5-10 cm DBH. Stems 2-5 cm increased in growth rate but this was just less than significant, while tree 1-2 cm diameter did not respond suggesting that such small trees were limited by light availability rather than soil nutrients. On the other hand, the response to N fertilisation did not differ among species' functional strategies, suggesting that N limitation is widespread among all the species we tested. Litterfall mass was unaffected over one year of experimental fertiliser addition treatment, but changes in litterfall nutrient concentration suggested that trees in the $CaCO_3$ addition plots increased iron (Fe) uptake and quickly reached Fe saturation, indicating the possibility for Fe limitation in this heath forest. Herbivory of litterfall increased in the $CaCO_3$ plots but not in the N addition plots, suggesting that leaf palatability was more related to leaf toughness rather than nutrient concentration. The high sensitivity of this forest type to soil N availability suggests that the increasing rates of N deposition already occurring at tropical latitudes will promote heath forest productivity over the short term. Further long-term N addition experiments are required to understand the impacts of N pollution on tropical forests.

## 4.1 Introduction:

Tropical rain forests are globally among the most productive and carbon (C) dense ecosystems (Pan et al. 2011; 2013). Forest productivity is tightly linked to soil nutrient availability (Fernandez-Martina et al. 2014) and the traditional paradigm proposes that tropical lowland rain forest on weathered soils are limited by phosphorus (P) whereas rain forests on younger montane soils are nitrogen (N) limited (Tanner et al. 1998; Vitousek 1984). Nonetheless, recent research has cast doubts on the relative importance of these two soil nutrients for regulating tropical forest productivity (Wright et al. 2018). This uncertainty hampers the accuracy of predictive forest models that investigate the effects of human-induced perturbations (e.g. nutrient deposition and GHG emissions) on atmosphere-geosphere interactions, C cycling and the impact of future climate conditions on forests (Reed et al. 2015; Wang et al. 2010).

The increasing human population density (Bauters et al. 2018) and the expansion of agroindustry in the tropics (Albanito et al. 2017; Mackenzie et al. 2011) have intensified the input of reactive N in the atmosphere (Galloway et al. 2004; Kanakidou et al. 2016) and increased N deposition to ecosystems (Phoenix et al. 2006). This increase in N deposition has the potential to acidify soils (Bowman et al. 2013; Lu et al. 2014) and reduce species diversity (Bobbink et al. 2010; Stevens et al. 2004). Understanding tropical rain forests' nutrient limitation and responses to nutrient addition is therefore of primary importance to forecast future rain forest C storage capacity, and possible conservation strategies to prevent species loss. A powerful tool ecologists have to infer nutrient limitation of net primary production (NPP) are fertilisation experiments (Fayle et al. 2015; Sullivan et al. 2014), but few experiments have been conducted in the tropics (e.g. Homeier et al. 2012; Tanner et al. 1990; Walker et al 1996; Wright et al. 2018). Most evidence for rain forest nutrient limitation has been inferred from soil nutrient content (Vitousek and Farrington 1997; Walker and Syers 1976), organism nutrient content and stoichiometry (e.g. foliar N:P ratios; Aerts and Chapin 2000), laboratory based experimental nutrient manipulations (Sullivan et al. 2014) or correlational studies of edaphic habitat filtering. Given the extent of soil (Palm et al. 2007; Townsend et al. 2008) and plant (Slik et al. 2015) heterogeneity at tropical latitudes and among tropical regions, broad generalisations about rain forest nutrient limitation have to be considered carefully and more extensive experimentation is required (Cleveland et al. 2011; Tian et al. 2016).

Several studies have shown that the myriad of rain forest tree species have complex and sometimes contrasting responses to changes in soil nutrient availability (e.g. Cavelier et al. 2000; Homeier et al. 2012; Mayor et al. 2014). One promising approach to dealing with these contrasting responses and to improve the forecasts of rain forest responses to N deposition might lie in categorising species by their functional identity. Functional identity is a continuum of variation between 'acquisitive' and 'conservative' strategies. Species with an acquisitive strategy have fast growth rates and nutrient-rich leaves, whereas conservative species are longer-lived with slower growth rates and are more stress tolerant (Díaz et al. 2004; Reich 2014). Species' functional traits are good predictors for species distribution (Kraft and Ackerly 2010; Paine et al. 2011; Swenson and Enquist 2009) and species partitioning is often driven by soil variables such as fertility (Condit et al. 2013; Phillips et al. 2003). It follows that species with different functional strategies might have different responses to soil nutrient manipulation. Pioneering this approach in a study of Ecuadorian montane forest, Baez and Homeier (2018) found acquisitive species to increase their diameter growth rate after N+P fertilisation when compared to conservative species whereas P fertilisation enhanced growth rates of both acquisitive and conservative species.

Other proxies frequently used in studies of rain forest nutrient limitation are litterfall nutrient content and litterfall mass. Although, the nutrient concentration of leaf litterfall is generally higher in lowland rain forests compared to montane rain forests, the ratio of N:P in litterfall indicates N limitation in montane rain forests (low N:P ratio) and P limitation in lowland rain forest (high N:P ratio. Silver 1994; Vitousek 1984). The changes in litterfall nutrient concentration after fertilisation experiments mirror the resorption of nutrients from fresh leaves as well as possible nutrient saturation after fertilisation. For example, P soil addition increased litterfall P concentration in lowland tropical forest (Mayor et al. 2014) montane subtropical (Li et al. 2018) and montane rain forest (Homeier et al. 2012) whereas N addition increased litterfall N concentration in montane rain forest (Corre et al. 2010; Homeier et al. 2012). Changes in litterfall mass after fertiliser addition have supported this nutrient limitation pattern. Phosphorus fertiliser increased litterfall mass in lowland rain forest, and N fertilisation increased litterfall mass in montane rain forest (Benner et al. 2011; Kaspari et al. 2008; Tanner et al. 1998). It is clear that litterfall nutrient resorption suggests a more complex pattern of soil limitation rather than the simple paradigm of weathered lowland rain forest soils being limited by P and young montane rainforest soil being limited by N. For a comprehensive insight into soil nutrient limitation, therefore, it is necessary to combine analyses of soil nutrient dynamics, litterfall and tree growth rates.

Tropical heath forests are a unique forest formation scattered among the world's tropics growing on spodosol soil (FAO classification), one of the most intensely weathered soils found in the tropics (Andriesse 1968; Dubroeucq and Volkoff 1998; Palm et al. 2007). Tropical heath forests typically have low biomass and productivity (Miyamoto et al. 1997; Nilus 2003) and consist of short untapered trees (Proctor et al. 1983a) with thick sclerophyllous leaves (Richards 1936; Turner et al. 2000). Spodosols are typically acidic with low exchangeable cation capacity (CEC) and are very low in both N and P (Luizao 1994; Proctor et al. 1983a; Vernimmen et al. 2013). Although heath forests are generally found in lowland regions, soil P has only rarely been considered as a limiting factor for their productivity (as suggested by Dent et al. 2006), whereas the main limit to their productivity is thought to be soil N deficiency (Brearley et al. 2011; Luizao 1994), soil acidity (Luizao et al. 2007; Vernimmen et al. 2013; Proctor et al. 1983a) or an interaction of the two (Luizao 1996; Proctor 1999;). When investigating the reasons for stunted plant growth and leaf sclerophylly, paucity of soil nutrients is the most obvious cause to test for, whereas soil acidity might be a less intuitive driver of heath forests features. Nonetheless, in Chapter 3 we show an important role of soil acidity driving species distribution and forest structure in this forest. Furthermore, Proctor (1999) hypothesized that the high ratio between soil $H^+$ and Al leads to $H^+$ ion toxicity as the buffering capacity of Al is reduced in these sandy organic-rich soils. Given the acidifying properties of N deposition, it is important to test both the effects of altered soil pH and N availability on the productivity of heath forests. Furthermore, the sclerophyllous leaves of heath forest have been hypothesized to have developed as a trade-off between growing "expensive" leaves in a nutrient scarce environment, and produce leaves that discourage leaf herbivory (Fine et al. 2004; Janzen 1974; Turner 1994). Herbivores, for example, can decrease leaf litterfall mass by up to 20 % in lowland rain forest, converting coarse litterfall into more readily decomposable frass with clear impacts for nutrient cycling, (Metcalfe et al. 2014). We will therefore test whether nutrient addition increases leaf herbivory.

Heath forests have been overlooked by studies on the effects of human perturbations on ecosystems and C dynamics because of their low aboveground C density (Coomes et al. 2017) and relative scarcity. Nonetheless, heath forests store a considerable amount of belowground C. Montes et al. (2011), for example, estimated that throughout all Amazonian spodosols at least 13.6 ± 1.1 Pg of C lies in the deep ( 5-10 m) soil layer. Notably, this amount of C is five times the whole tropics' annual C emission from deforestation (Pan et al. 2011). As belowground C storage is directly connected with forest dynamics this underscores the need for detailed studies on heath forests nutrient limitation. Furthermore, heath forests host a highly endemic vegetation adapted to its acidic and nutrient poor soil (Anderson 1981; Fine et al. 2010; Newbery 1991); if the predicted N deposition do occur in the tropics, we might expect shifts in species composition and possibly changes in C storage.

In this chapter, we investigate the responses of a Bornean heath forest after a factorial N and calcium carbonate ($CaCO_3$) addition experiment. We focus on 1) changes in soil and soil leachate nutrient dynamics, 2) responses of stem diameter annual relative growth rates (RGRyr) and the influence of functional identity on RGRyr response and 3) changes in litterfall mass, leaf litter nutrient concentration and leaf herbivory after the treatments.

## 4.2 Methods:

### 4.2.1 Study site:

As described in Chapter 3, our study site is located in the heath forest at the eastern side of the Kabili-Sepilok Forest Reserve and is underlain by an infertile spodosols (USDA soil taxonomy), which develops from sandstone bedrock. The soil has acidic pH, low cation exchange capacity and low total and available N but available soil P content was higher than in the adjacent lowland evergreen rain forest (i.e. alluvial forest; Chapter 3 and Appendix). The forest is a characteristic tropical heath forest with basal area of 34.4 $m^2$ $ha^{-1}$ for trees > 5 cm DBH, high stem density (1997 stems > 5 cm DBH $ha^{-1}$) and an even canopy of ca. 28 m height (Chapter 3).

### 4.2.2 Experimental design:

In April 2016, we installed 16 forest plots of 225 $m^2$ (15 m x 15 m) in the Kabili-Sepilok heath forest. The plots were at least 30 m apart from each other to avoid cross-contamination from the chemicals spread over the plots. Within all plots we permanently tagged, identified to species level and measured DBH on all trees and lianas ≥ 1 cm DBH (Chapter 3). In order to assign the treatments among plots, we visualised plots' species composition with a detrended correspondence analysis (DCA. Axis 1 and 2 scores on the DCA of Figure 3.2, Chapter 3), compared plots' initial soil pH, $NH_4^+$ and $NO_3^-$ (data from Chapter 3) and allocated the treatments in the most homogeneous way possible across the floristic and soil gradients found, to ensure there were no significant differences in specis composition, pH, $NH_4^+$ and $NO_3^-$ among treatments. In July 2016, after the first tree census, we started a factorial experiment consisting of four treatments (control with no treatment, the addition of N or $CaCO_3$ and N+$CaCO_3$) with four replicate plots for each treatment. We applied 50 kg N $ha^{-1}$ $yr^{-1}$ in the form of urea and $CaCO_3$ (lime) at an initial rate of 5550 kg $ha^{-1}$ $yr^{-1}$ with the same amounts of each for the combined N+$CaCO_3$ treatment. The fertiliser was spread by hand as dry chemicals while walking across the plot. Chemicals were broadcast following two perpendicular directions to ensure even distribution. For the rest of the experiment we applied fertiliser approximately every six months, with the second application in February 2017 when we added the same amount of urea fertiliser as the initial treatment (resulting in an application rate of 25 kg N ha$^{-1}$ per time, which is equal to 1.21 kg urea plot$^{-1}$ per time). In the $CaCO_3$ alone and N+$CaCO_3$ treatment plots we reduced the $CaCO_3$ addition rate from 75 kg plot$^{-1}$ to 50 kg plot$^{-1}$ to avoid raising soil pH over the pH of the surrounding lowland evergreen rain forest. For the third application in July 2017 we further reduced the amount of $CaCO_3$ to 25 kg plot$^{-1}$ (see Figure 4.1).

To study the effect of treatments on litterfall mass, composition and leaf litterfall chemistry we installed three litterfall traps in each plot. In total, we installed 48 litterfall traps of 0.36 m$^2$ each (60 cm x 60 cm). We built the litterfall traps from 2.5 cm diameter PVC pipes and 1.8 mm x 1.8 mm plastic mesh. The traps were installed approximately 50 cm above the ground and at 5 m distance from the plot borders to minimize the chance of collecting leaves fallen from trees growing outside the plot and avoiding crown gaps. We also installed one suction lysimeter per plot built from PVC pipes and ceramic cups (N. 653X2-B3M3, Soil Moisture Equipment Co. Santa Barbara, CA, USA). Prior to lysimeter installation (September 2016) we sonicated them in deionised water; after installation the lysimeters were left to equilibrate for one month *in situ*.

### 4.2.3 Tree growth:

After the initial census before the start of the experiment in April 2016, in July 2017 and July 2018 we re-censused trees and lianas, and measured the DBH of all stems (individuals >1 cm DBH), which were permanently tagged and marked with point of measurement.

### 4.2.4 Soil, leachate and litter sampling:

We collected four soil samples per plot before the first treatment and sampled again every *ca*. six months for two years. We collected the top 5 cm of soil by removing the unconsolidated surface leaf material then digging a hole of approximately 10 cm x 10 cm x 5 cm deep with a knife. Roots and coarse undecomposed leaves were removed from the soil sample. Soil water leachate was collected from the lysimeters every month for one year following the first fertiliser treatment. Water was fully pumped out of the lysimeter at every sampling period to ensure we had separate monthly samples. After pH measurement, soil water samples were filtered with a 0.2 µm syringe filter, acidified to pH ~2 with a 50 % $H_2SO_4$ solution and stored at -20 $^{o}$ C.

We collected litterfall from the litterfall traps every month for one year after the start of the experiment. Litterfall samples were oven dried until stable weight at 50 $^{o}$C, separated into four fractions: i) twigs and bark, ii) debris particles <2 mm and unidentifiable parts, iii) leaves, and iv) reproductive parts, and weighted as suggested by Proctor (1984). To assess leaf herbivory we graded each leaf on a six-point scale (0, <20%, 20-40%, 40-60%, 60-80%, and 80-100%) by visually estimating missing leaf area presumed to have been removed by invertebrates. Prior to chemical analysis leaves from all three litterfall traps per plot were bulked together and ground for subsequent nutrient analysis.

### 4.2.5 Soil, leachate and leaf litter chemical analysis:

We conducted a full chemical analysis for soil samples collected at the start of the experiment before treatments were applied and at seven months and 12 months. At 17 and 23 months we repeated the soil sample analysis, but only analysed for moisture content, pH, $NH_4^+$ and $NO_3^-$ for the second year samples. Each soil sample was split in two subsamples. Immediately after field collection, a known amount of fresh soil (approximately 2 g) was added to 30 ml of 1 M KCl and shaken for one hour, allowed to equilibrate in a refrigerator for 18 hours, then filtered (Whatman No. 1) and analysed for $NH_4^+$ and $NO_3^-$ with a segmented flow analyser (Astoria-Pacific A2,USA). On further subsamples, we measured soil moisture content, pH, available and total nutrients, C and N as well as exchangeable acidity and Al as follows. Soil moisture content was determined gravimetrically after recording the fresh soil weight of approximately 3 g and drying the soil to constant weight at 105 ° C. To measure soil pH, we added 5 g of fresh soil to 12.5 ml of distilled water and shook it overnight; pH was then recorded with a Corning 240 pH meter. For total and available nutrients we oven dried at 50 ° C and then ground the dried samples. For total Al and P analysis we microwave-digested (CEM Mars Xpress 5, CEM Corporation, Matthews, NC) 0.25 g of soil with a solution of 8 ml $HNO_3$ + 2 ml deionised $H_2O$. For extractable P, Fe, Mn and available Ca, Na, Mg and K the oven dried and ground soil was extracted with a Mehlich I solution (2 g of soil shaken with 20 ml of Mehlich I solution for 5 minutes using a reciprocating shaker at 120 oscillations per minute. Wuenscher et al. 2015). Available and extractable nutrient concentrations in the Melich I solution were determined with inductively coupled plasma optical emission spectrometer (ICP-OES, iCAP Duo 6300, Thermo Scientific, USA). Exchangeable acidity ($H^+$ + Al) was measured through titration of a 1 M KCl extraction (5 g oven dried soil and 50 ml 1 M KCl) with 0.02 M NaOH and 0.01 % phenolphthalein (modified from Van Reeuwijk, 2002). We also measured exchangeable Al on the remaining (non-titrated) 1 M KCl extraction for H and Al using an iCAP 6300 ICP-OES (Thermo Scientific, USA). Cation exchange capacity was calculated as sum of bases and exchangeable acidity. Soil total C and N concentrations were determined by combusting 0.15 g of oven dried soil in an elemental CN analyser (Leco TruSpec, USA).

The filtered soil water leachate samples were analysed for $NH_4^+$ and $NO_3^-$ on a segmented flow analyser (Astoria-Pacific A2, USA), and soil water element concentration was determined with an iCAP 6300 ICP-OES (Thermo Scientific, USA).

Leaf litterfall samples were analysed for P, Al, Ca, Cu, Fe, K, Mg, Mn, Na and Ni. We added 0.25 g of ground sample to a mixture of 8 ml $HNO_3$ + 2 ml of deionised $H_2O$ and microwave-digested it (Mars Xpress 5, CEM Corporation, Matthews, NC). Then, we determined elemental concentration with the iCAP Duo 6300 ICP-OES (Thermo Scientific, USA). To determine C and N we combusted 0.1 g of ground leaf sample in the elemental CN analyser (Leco TruSpec, USA). Blanks and certified reference materials were added to all the batches to ensure the accuracy of the analyses.

We also analysed the $CaCO_3$ and urea used for the fertiliser addition treatments. Nutrient concentration of $CaCO_3$ and urea was determined using a Rigaku NEX-CG energy-dispersive (ED-XRF) spectrometer. The samples were prepared as loose powders supported on prolene film and data was collected under vacuum using a method employing Al, Mo, Cu, RX9 and Si as secondary target. Carbon and N concentrations were determined by combusting 0.1 g of ground sample in the elemental CN analyser (Leco TruSpec, USA).

### 4.2.6 Statistical analysis:

The analysis were performed with the package *nlme* in R 3.5.1 (R Development Core Team 2009). To infer significance of time-series data with many samples (the time series with monthly collection spanning one year i.e. soil leachate elements, litterfall weight, leaf litterfall nutrient concentrations and herbivory), we applied, for each response variable, linear mixed effect models with an interaction among treatments and month of collection as a fixed effect and plot with month of collection as random effects. Herbivory was calculated as the mean percentage of leaf area missing per litter trap. Furthermore, we included a first order autoregressive process accounting for an increasing divergence of measured values with increasing time difference (i.e. corAR1. Zuur et al. 2009). We also assessed the effect of treatments on time-series data with few samples, such as soil nutrients and pH, with linear mixed models. We used the interaction of treatment and month of collection as a fixed effect and only plot as a random effect and without the first order autoregressive process because it did not improved the overall model fit. If the mixed model's residuals were not normally distributed the response variables were log-transformed before analysis.

We calculated the annual relative stem diameter growth rate with the following formula: $(\ln(d_2)-\ln(d_1))/\ \ln(d_1))*\ 1/\ (\Delta t)$ where $d_1$ is the initial diameter, $d_2$ is the diameter at the end of the second year, and $\Delta t$ is the time interval between the two measurement expressed in years. To infer the significance of the treatments on diameter $RGR_{yr}$ we used a linear mixed model with treatment as a fixed factor and plot as a random factor. In addition, we determined whether RGRyr changed among treatment accordingly to species functional identity with a Bonferroni-corrected Spearman correlation analysis. We focussed on the 27 most common and widespread species throughout our plots. As functional traits we used specific leaf area (SLA, calculated as the quotient among fresh leaf area and dry leaf mass of approximately ten mature leaves per species collected in the control plots or around the study area) leaf C:N (as a proxy of leaf toughness) leaf P, leaf N, RGRyr from the control plots and tree wood density obtained from literature (i.e. Carsan et al. 2012; Zanne et al. 2009). When the wood density values of the target species were not present in literature we averaged all the available data for congeneric species from the same geographic area. We inferred species functional identity using a principal components analysis (PCA) with the scaled and centred values of functional traits averaged per species. We then extracted the scores of the species on the first and second PCA axis and performed the Spearman correlations.

## 4.3 Results:

### 4.3.1 Soil responses to fertiliser treatment:

Both $CaCO_3$ and N+$CaCO_3$ treatment increased soil pH by approximately 0.5 pH units every sampling ($p<0.001$; Table 4.1, Figure 4.1. Mean values per treatment are in Supplementary information Table 9.1) with a consequential decrease in exchangeable acidity of approximately 0.35 $cmol_c\ kg^{-1}$ every sampling ($p<0.001$).

The H:Al ratio increased in the $CaCO_3$ ($p<0.01$) and the N+$CaCO_3$ ($p<0.001$), treatments as a result of a lower concentration of exchangeable Al ($p<0.001$ for both the $CaCO_3$ and N+$CaCO_3$ treatment. Table 4.1). No change was detected in total N after the N addition treatments. In contrast, total N decreased by approximately 0.8 % after the $CaCO_3$ treatment ($p=0.02$) and the only changes in available N were a decrease in $NH_4^+$ after the N+$CaCO_3$ treatment ($p=0.004$), and a decrease in $NO_{3-}$ after N addition ($p<0.01$). Total soil C also decreased in the $CaCO_3$ treatment ($p<0.05$). Soil samples taken one year after fertiliser treatment showed that total soil P also decreased in the $CaCO_3$ and N+$CaCO_3$ treatment (both $p<0.05$), whereas available P decreased only after the N addition ($p<0.001$). Cation exchange capacity increased by ca. 0.5 $cmol_c\ kg^{-1}$, 0.2 $cmol_c\ kg^{-1}$ and 0.6 $cmol_c\ kg^{-1}$ every sampling in the $CaCO_3$ ($p<0.001$), N ($p<0.05$) and N+$CaCO_3$ ($p<0.001$) treatments, respectively. As was to be expected, both available and total Ca increased in the $CaCO_3$ and N+$CaCO_3$ treatment (all $p<0.001$). Interestingly, available Fe decreased by ca. 7.6 $\mu g\ g^{-1}$ every sampling after the N+$CaCO_3$ addition ($p<0.05$). The pH of soil leachate increased in both $CaCO_3$ and N+$CaCO_3$ treatment (both $p<0.001$ Table 4.1) whereas it slightly decreased after N addition ($p<0.05$). Soil leachate also showed a reduction in Fe after the N addition, with ($p<0.01$) or without ($p<0.05$) $CaCO_3$ and a ca. 0.01 µg $ml^{-1}$ monthly increase in P after the $CaCO_3$ addition ($p<0.05$). Surprisingly, Ca did not increase in soil leachate after the $CaCO_3$ addition. The addition of $CaCO_3$ both with and without N produced a decrease in Zn ($p<0.05$ and $p<0.001$ for $CaCO_3$ and N+$CaCO_3$, respectively).

*Table 4.1 Results of linear mixed models showing the change in soil leachate and soil nutrient concentrations after our experimental treatments (one year from the start of treatments for soil leachate, soil total and available nutrients as well as exchangeable acidity and ratios, two years after the start of the experiment for soil pH and mineral N) with respect to the control plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant value (‘***’ < 0,001 ‘**’ <0.01, ‘*’ <  0.05, ‘+’ < 0.1) are in bold.*

| Compartment | Treatment | Response variable | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Soil leachate | | pH | $NH_4^+$ | $NO_3^-$ | Tot. P | Av. P | Tot. Al | Av. Al |
| | | | | | µg $ml^{-1}$ | | | |
| | $CaCO_3$ | **0.074**$^{***}$ | 0.015 | -0.008 | **0.012**$^{*}$ | - | 0.05 | - |
| | N | **-0.032**$^{*}$ | -0.006 | 0.004 | -0.004 | - | 0.02 | - |
| | N+$CaCO_3$ | **0.066**$^{***}$ | -0.007 | -0.032 | -0.004 | - | -0.01 | - |
| Soil | | | | | µg $g^{-1}$ | | | $cmol_c$ $kg^{-1}$ |
| | $CaCO_3$ | **0.445**$^{***}$ | -0.46 | -0.04 | **-3.07**$^{*}$ | -0.69 | -25.8 | **-0.10**$^{***}$ |
| | N | 0.093 | -1.39 | **-0.43**$^{**}$ | -1.46 | **-3.71**$^{***}$ | -19.1 | -0.01 |
| | N+$CaCO_3$ | **0.525**$^{***}$ | **-3.36**$^{**}$ | -0.22 | **-3.44**$^{*}$ | 0.82 | **-53.5**$^{***}$ | **-0.19**$^{***}$ |
| | | Exc. Ac $cmol_c$ $kg^{-1}$ | H:Al | CEC $cmol_c$ $kg^{-1}$ | | C:N | C | N |
| | | | | | | | mg $g^{-1}$ | |
| | $CaCO_3$ | **-0.343**$^{***}$ | **7.2**$^{**}$ | **0.48**$^{***}$ | | -0.23 | **-1.16**$^{*}$ | **-0.27**$^{*}$ |
| | N | -0.090 | -1.1 | **0.20**$^{*}$ | | -0.89 | -0.77 | -0.04 |
| | N+$CaCO_3$ | **-0.379**$^{***}$ | **13.9**$^{***}$ | **0.60**$^{***}$ | | -0.27 | -0.63 | -0.14 |

*Table 4.1 Continued*

| Compartment | Treatment | Response variable | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Soil leachate | | Tot. Ca | Av. Ca | Tot. Fe | Av. Fe | Tot. K | Av. K | Tot. Zn |
| | | | | | μg ml$^{-1}$ | | | |
| | $CaCO_3$ | 0.50 | - | -0.031 | - | 0.02 | - | **-0.053**$^{*}$ |
| | N | 0.08 | - | **-0.045**$^{**}$ | - | 0.03 | - | -0.047 |
| | N+$CaCO_3$ | 0.90 | - | **-0.035**$^{*}$ | - | -0.04 | - | **-0.088**$^{***}$ |
| Soil | | | | | μg g$^{-1}$ | | | |
| | $CaCO_3$ | **71.3**$^{**}$ | **98.3**$^{***}$ | -9.76 | -2.19 | -3.57 | 6.11 | 0.03 |
| | N | -10.9 | 25.8 | -8.39 | -2.96 | -3.24 | 3.63 | 0.05 |
| | N+$CaCO_3$ | **105**$^{***}$ | **142**$^{***}$ | -28.4 | **-7.63**$^{*}$ | -3.45 | 6.83 | -0.04 |

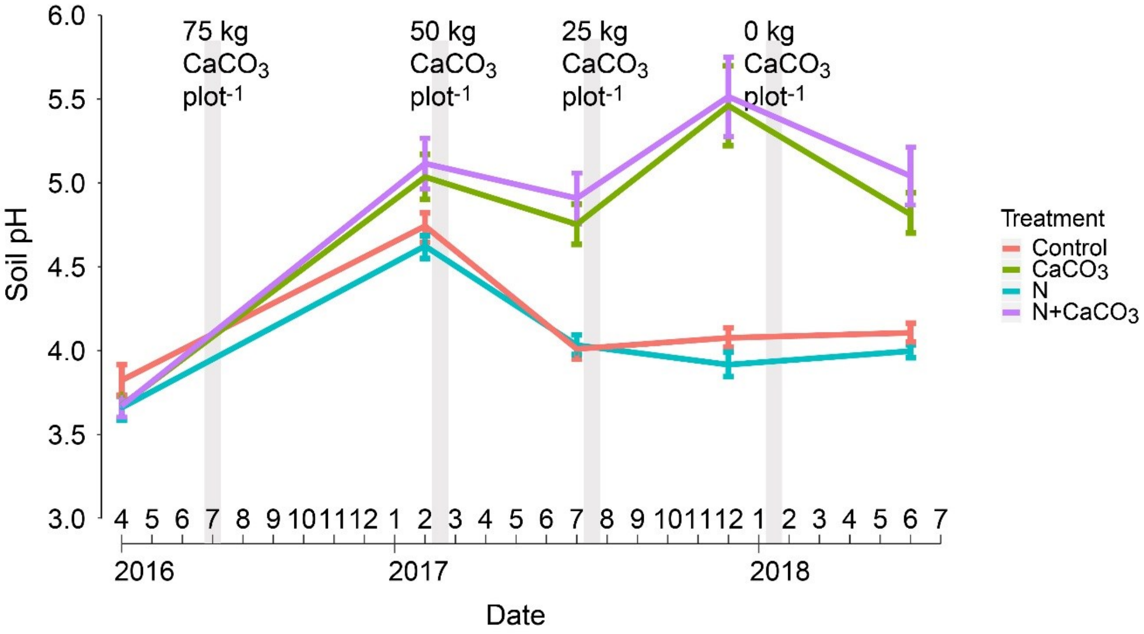

*Figure 4.1 Change in soil pH (mean ± SE) of our experimental plots through two years of N and $CaCO_3$ treatment in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The grey bars represent the period of treatment application. Nitrogen was added at the rate of 50 kg ha$^{-1}$ yr$^{-1}$ whereas the amount of $CaCO_3$ was progressively reduced at each application to avoid over-liming. In the first treatment we added 75 kg $CaCO_3$ plot$^{-1}$, in the second we added 50 kg $CaCO_3$ plot$^{-1}$, in the third we added 25 kg $CaCO_3$ plot$^{-1}$ whereas in the fourth treatment no lime was added.*

The nutrient concentration of urea was very low (from 0.001 to 0.7 mg g$^{-1}$ for elements other than N and C) whereas $CaCO_3$ had obviously a high concentration of Ca and C but had also unexpectedly high Mg, Fe and Al concentrations (Table 4.2).

### 4.3.2 Tree responses:

After two years of experimental treatments, only the addition of N affected mean stem $RGR_{yr}$. In trees 5-10 cm DBH $RGR_{yr}$ increased by 103 % ($p<0.001$) whereas in trees 2-5 cm DBH $RGR_{yr}$ increased 38 % and fell marginally short of significance ($p=0.056$, Figure 4.2). Tree species were divided by functional behaviour using a principal components analysis (PCA). The first two PCA axes explained 71 % of the total variance in species traits (Figure 4.3).

*Table 4.2 Mean (±SE) nutrient concentrations of the urea and lime used for our experimental treatments in the Kabili Sepilok Forest Reserve, Sabah, Malaysia. All concentrations are expressed in mg g*$^{-1}$.

| Element | Fertiliser | |
|---|---|---|
| | $CaCO_3$ | Urea |
| Al | 6.42 (±0.19) | 0.33 (±0.022) |
| C | 105 (±0.26) | 212 (±0.27) |
| Ca | 385 (±9.00) | 0.61 (±0.29) |
| Cu | 0.02 (±<0.00) | 0.004 (±<0.001) |
| Fe | 11.5 (±0.29) | 0.016 (±0.002) |
| K | - | 0.072 (±0.005) |
| Mg | 46.3 (±1.35) | 0.71 (±0.25) |
| Mn | 0.53 (±0.01) | - |
| N | 0.16 (±0.07) | 474 (±0.92) |
| Ni | 0.30 (±0.01) | - |
| P | 0.05 (±0.04) | - |
| S | 0.29 (±0.01) | 0.024 (±0.001) |
| Zn | 0.03 (±<0.001) | 0.001 (±0.002) |

The first axis (which explained 53 % of the variance) showed a gradient going from species with nutrient rich and tender leaves (e.g. *Maclurodendron* sp. - Rutaceae, *Dracaena elliptica* - Asparagaceae and *Pimeleodendron griffithianum* - Euphorbiaceae) to species with nutrient poor and tough leaves (i.e. with high C:N values as e.g. *Ternstroemia aneura* - Pentaphyllacaceae and *Myrsine* sp. - Primulaceae).

The second axis (which explained 18 % of the variance) was mainly characterized by a gradient going from slow growing and high wood density species (e.g. *Tristaniopsis obovata* – Myrtaceae) to fast-growing species with low density wood (e.g. *Timonius flavescens* - Rubiaceae and *Madhuca pallida* - Sapotaceae). Functional identity of the focal species in the first and second PC axis are listed in Table 4.3. The non-parametric Spearman correlation shows the second functional identity PCA axis to have more significant correlations (four significant correlations) with $RGR_{yr}$ through the different treatments rather than the first PCA axis (two significant correlations; Table 4.4).

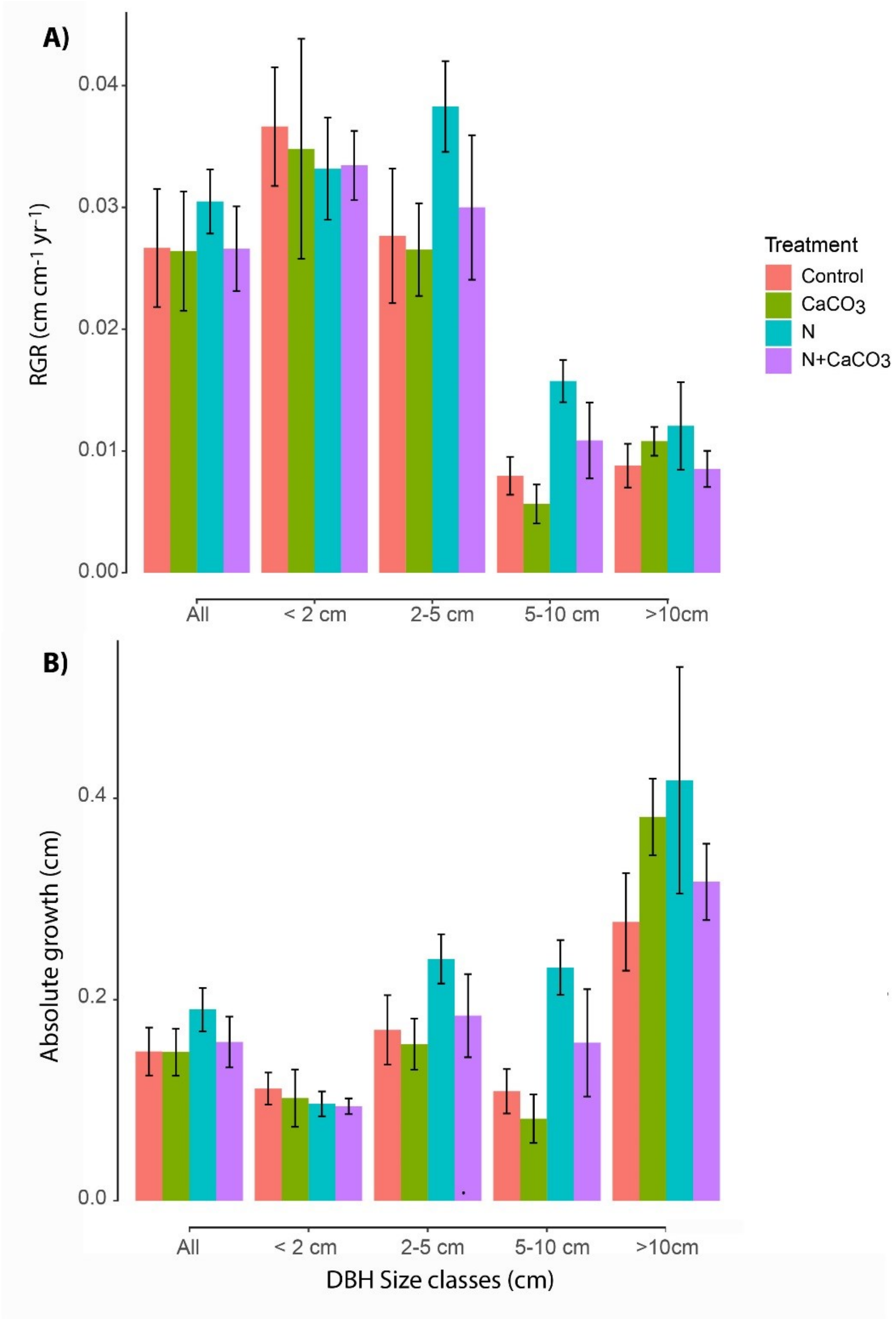

*Figure 4.2 Mean (± SE) stem growth of trees in four different size classes after two years of experimental N and CaCO3 addition in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. It is visible from both the a) annual relative growth rate as well as from the b) absolute stem growth that the addition of N increased the growth in trees 2-5 cm DBH (p=0.056) and 5-10 cm DBH (p<0.001). Standard error bars are calculated on the means of four replicate plots.*

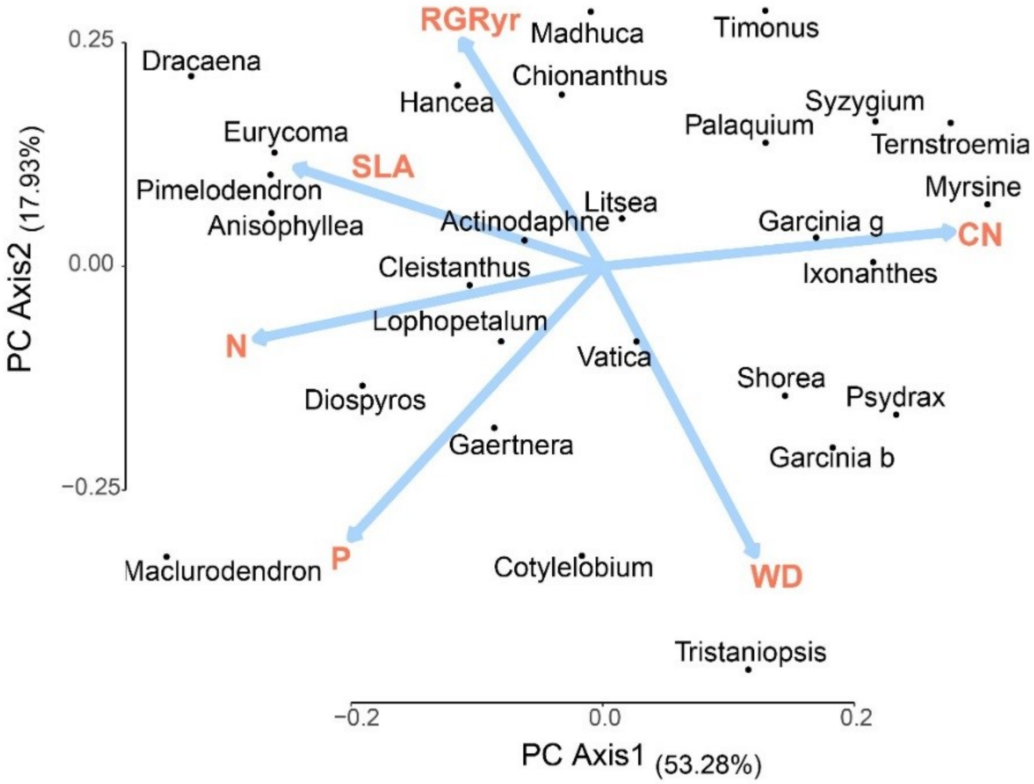

*Figure 4.3 Principal component analysis of functional traits among the 27 most abundant tree species in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. We used six functional traits for the analysis: foliar N (N) and foliar P (P) concentration, foliar C:N ratio (CN), specific leaf area (SLA), wood density (WD) and yearly relative growth rate (RGRyr).*

The only strong correlation was between functional identity PCA axis 2 and the growth of trees in the N+$CaCO_3$ treatment ($\rho = 0.6$, *p*-value < 0.01), whereas all the other significant correlations were only moderate ($40 < \rho < 59$. Table 4.4).

The annual litterfall, in order of importance, was composed of ca. 70 % leaves (3.69 ± 0.3 t $ha^{-1}$ $yr^{-1}$) with the remaining mass made up by twigs (0.91 ± 0.1 t $ha^{-1}$ $yr^{-1}$), reproductive materials (0.35 ± 0.09 t $ha^{-1}$ $yr^{-1}$) and debris (0.29 ± 0.04 t $ha^{-1}$ $yr^{-1}$). Among the treatments, only debris mass had a significant change, increasing 41 % ($p = 0.03$) in the $CaCO_3$ treatment (Table 4.5 Mean values of leaf litterfall chemistry are in Supplementary information Table 9.2).

*Table 4.3 Functional identity of the 27 most common species found in our heath forest in the Kabili- Sepilok Forest Reserve, Sabah, Malaysia. Functional identity is inferred from species' score on the first and second PCA axes that included six functional traits. Species are ranked according to scores on the first PCA axis that explained 53.3 % of the variation.*

| Functional Identity | Species | PC axis 1 | PC axis 2 |
|---|---|---|---|
| Acquisitive | *Maclurodendron* sp. | -3.23 | -1.85 |
| | *Dracaena elliptica* | -3.03 | 1.22 |
| | *Pimelodendron griffithianum* | -2.45 | 0.53 |
| | *Anisophyllea disticha* | -2.43 | 0.37 |
| | *Eurycoma longifolia* | -2.41 | 0.66 |
| | *Diospyros fusiformis* | -1.77 | -0.69 |
| | *Hancea griffithiana* | -1.06 | 1.06 |
| | *Cleistanthus gracilis* | -0.98 | -0.16 |
| | *Gaertnera junghuhniana* | -0.79 | -0.79 |
| | *Lophopetalum beccarianum* | -0.75 | -0.56 |
| | *Actinodaphne borneensis* | -0.57 | 0.07 |
| | *Chionanthus pluriflorus* | -0.29 | 1.07 |
| | *Cotylelobium melanoxylon* | -0.15 | -1.69 |
| | *Madhuca pallida* | -0.09 | 1.67 |
| | *Litsea cylindrocarpa* | 0.14 | 0.17 |
| | *Vatica micrantha* | 0.26 | -0.37 |
| | *Palaquium rostratum* | 1.04 | 0.39 |
| | *Tristaniopsis obovata* | 1.08 | -2.35 |
| | *Timonus flavescens* | 1.22 | 1.62 |
| | *Shorea atrinervosa* | 1.35 | -0.74 |
| | *Garcinia gaudichaudii* | 1.59 | 0.21 |
| | *Garcinia bancana* | 1.70 | -1.11 |
| Conservative | *Ixonanthes reticulata* | 2.01 | -0.06 |
| | *Syzygium* sp. | 2.03 | 0.92 |
| | *Psydrax* sp. | 2.18 | -0.87 |
| | *Ternstroemia aneura* | 2.59 | 0.86 |
| | *Myrsine* sp. | 2.86 | 0.41 |

The $CaCO_3$ treatment was also the only one to affect herbivory, which increased significantly but only by a monthly increase of 0.3 % (p=0.03. Table 4.5). With regard to leaf litterfall chemistry, $CaCO_3$ and addition of combined N + $CaCO_3$ led to lower C concentrations in litterfall ($p<0.01$; Table 4.6) and higher Ca ($p<0.001$) as well as Fe ($p<0.05$) concentration relative to the control. The N+$CaCO_3$ treatment resulted in a lower litterfall K concentration ($p<0.001$).

*Table 4.4 Spearman rho correlation and p-values of functional identity (principal component axes one and two of the PCA with functional traits for 27 target species) with RGRyr for our experimental treatments in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant values are listed in bold.*

| Treatment | | PC1 | PC2 |
|---|---|---|---|
| Control | rho | **-0.409** | **0.553** |
| | *p*-value | **0.047** | **0.005** |
| $CaCO_3$ | rho | -0.249 | **0.474** |
| | *p*-value | 0.262 | **0.027** |
| N | rho | -0.260 | 0.201 |
| | *p*-value | 0.267 | 0.392 |
| N+$CaCO_3$ | rho | -0.322 | **0.621** |
| | *p*-value | 0.125 | **0.001** |
| All trees | rho | **-0.484** | **0.577** |
| | *p*-value | **0.011** | **0.001** |

*Table 4.5 Results from the linear mixed models showing the mean (± standard deviation) monthly change in amount of the four litterfall fractions' production (in g per littertrap) with respect to the control treatment over one year after experimental nutrient manipulations in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Results from the linear mixed models showing the mean monthly change in herbivory is also reported (as a percentage calculated on the mean leaf herbivory per plot) as well as the overall production of litterfall (including the control). Significant values ('***' < 0,001 '**' <0.01, '*' < 0.05, '+' < 0.1) are in bold.*

| Treatment | Leaves | Reproductive parts | Twigs | Debris | Herbivory |
|---|---|---|---|---|---|
| | | g | | | % |
| $CaCO_3$ | -0.08 (±0.4) | 0.09 (±0.09) | 0.05 (±0.2) | **0.12 (±0.05)*** | **0.31 (±0.14)*** |
| N | -0.04 (±0.4) | 0.08 (±0.09) | -0.05 (±0.2) | 0.04 (±0.05) | 0.27 (±0.14) |
| N+$CaCO_3$ | 0.06 (±0.4) | 0.01 (±0.09) | 0.02 (±0.2) | 0.07 (±0.05) | 0.24 (±0.14) |
| Total annual mass (t $ha^{-1}$ $yr^{-1}$) | 3.69 (±0.3) | 0.35 (±0.09) | 0.91 (±0.1) | 0.29 (±0.04) | |

*Table 4.6 Results of linear mixed models showing the change in leaf litterfall nutrient concentrations (in % for N and C and mg $g^{-1}$for other leaf nutrients) through one year of experimental treatments with respect to the control plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant values are written in bold.*

| Element | Treatment | Change | *p*-value |
|---|---|---|---|
| N | $CaCO_3$ | -0.0008 | 0.9743 |
| | N | 0.0010 | 0.8555 |
| | N+$CaCO_3$ | 0.0012 | 0.7472 |
| C | $CaCO_3$ | **-0.1211** | **0.0051** |
| | N | -0.0216 | 0.6227 |
| | N+$CaCO_3$ | **-0.1281** | **0.0027** |
| P | $CaCO_3$ | 0.0002 | 0.8204 |
| | N | -0.0014 | 0.2471 |
| | N+$CaCO_3$ | -0.0012 | 0.2351 |
| Al | $CaCO_3$ | -0.0045 | 0.2875 |
| | N | 0.0009 | 0.9440 |
| | N+$CaCO_3$ | 0.0056 | 0.2570 |
| Ca | $CaCO_3$ | **0.1801** | **0.0001** |
| | N | -0.0332 | 0.4281 |
| | N+$CaCO_3$ | **0.2027** | **0.0001** |
| Fe | $CaCO_3$ | **0.0014** | **0.0248** |
| | N | -0.0002 | 0.6574 |
| | N+$CaCO_3$ | **0.0013** | **0.0294** |
| K | $CaCO_3$ | -0.0217 | 0.0749 |
| | N | -0.0239 | 0.0633 |
| | N+$CaCO_3$ | **-0.0476** | **0.0005** |

## 4.4 Discussion:

Nutrient limitation of forest productivity is widespread in weathered tropical soils (Vitousek 1984). Understanding forest nutrient limitation is necessary to forecast forest responses to human-induced modifications of nutrient cycles through pollution and N deposition. In this study, we assessed how soil nutrient dynamics, tree diameter growth, litterfall mass, leaf litterfall nutrient concentration and leaf herbivory changed in response to experimentally increased soil N availability and altered soil pH in a Bornean heath forest. We also tested whether the response to increased soil N availability and changes in soil pH were different among different tree stem size classes and species' functional identity. Soil chemistry and tree growth showed a swift response to the treatments and led us to hypothesize a strong soil N (and possibly Fe; see later) limitation in this heath forest ecosystem. The tree diameter growth response to the treatments was size class-related but functional identity only weakly affected the magnitude of the change in growth. Although litterfall production was not affected by the treatments, litterfall nutrient concentration changed significantly and there was a small, but significant, increase in herbivory, suggesting that soil pH may influence herbivory in this heath forest ecosystem.

### 4.4.1 Soil responses:

After only one application of lime we saw a clear increase in soil leachate pH, driven by the addition of Ca (Haynes and Naidu 1998), which also increased soil CEC. Liming also resulted in an increase in the H:Al ratio and decrease in exchangeable acidity which might be due to the precipitation (without leaching) of soil exchangeable Al – possibly as amorphous, positively charged hydroxyl-Al polymers (Alleoni et al. 2010; Haynes 1984). Lime might also have increased organic matter decomposition (Haynes 1982; see also Chapter 6). This would explain the decrease in total soil P, which would have been readily absorbed by trees and/or microbes, or lost in soil leachate (as suggested by the increased P in the $CaCO_3$ treatment's soil leachate). On the other hand, N addition decreased soil available P suggesting that P was absorbed by roots or microbes to maintain N and P stoichiometry in the tree biomass, as an increased biomass N concentration has been found to induce a higher P absorption (Marklein and Houlton 2012; You et al. 2018). The decrease in soil total C and N in the $CaCO_3$ treatment further supports the idea of increased mineralisation following liming (Haynes and Naidu 1998). The lime we used was rich in Mg and Fe so we expected to see an increase in soil total Mg and Fe throughout the $CaCO_3$ plots, as seen for total and available Ca, or an increased leaching of Fe. However, the leaching of Fe significantly decreased in both the N and N+$CaCO_3$ treatments, available Fe decreased in soil and showed no significant change in the $CaCO_3$ treatment. This suggests that Fe was absorbed by biomass and thus may also be a limiting nutrient.

Iron is known to limit marine phytoplankton photosynthesis (Behrenfeld et al. 1996) as well as other plant and microbial communities (e.g. Winbourne et al. 2017). Very low amounts of soil Fe can led to Fe chlorosis in plants due to depleted leaf chlorophyll (Brown 1961). Interestingly Kefahi et al. (2018) found indications that a Bruneian white sand heath forest's microbial community was Fe limited because genes associated with Fe-acquisition were abundant in the microbial community when compared with the surrounding lowland evergreen rain forest.

The input of extra N alone or with $CaCO_3$ reduced soil total N but did not affect N concentration in leached soil solution. In contrast to our findings, other N fertilisation experiments using similar or higher N addition rates, increased mineral N leaching in both temperate (140 kg N $ha^{-1}$ $yr^{-1}$; Corre et al. 2003) and montane tropical forest soil after one (50 kg N $ha^{-1}$ $yr^{-1}$; Homeier et al. 2012) and five years of addition (50 kg N $ha^{-1}$ $yr^{-1}$; Velescu et al. 2016) thus indicating ecosystem N saturation (Aber et al. 1998; Emmet, 2007; Matson et al. 1999). We speculate that the extra N added as fertiliser to our plots was readily absorbed by roots and/or immobilised by soil microorganisms. The Kabilli-Sepilok heath forest is, therefore, unlikely to undergo N saturation at low N deposition rates.

### 4.4.2 Effect of fertiliser and lime addition on trees:

Our results tend to favour the hypothesis of heath forest N limitation (Brearley et al. 2011; Luizao 1994; Moran et al. 2000; Proctor 1999; Proctor et al. 1983a) rather than the pH toxicity hypothesis. Nonetheless, it is possible that over a longer time period the change in soil pH or an interaction between pH and N treatment will produce significant outcomes for tree growth. The mean diameter growth rate in our control plots (0.13 ± 0.01 cm $yr^{-1}$ for trees > 10 cm DBH) was lower than that recorded in Bornean lowland rain forest (0.74 cm $yr^{-1}$ for trees > 10 cm DBH in Barito Ulu, Kalimantan Indonesia by Mirmanto et al. 1999) and similar to Barito Ulu heath forest (ca. 0.12 cm $yr^{-1}$ for trees > 10 cm DBH by Brearley et al. unpublished data). The higher $RGR_{Yr}$ in our N addition treatment supports our supposition of N being taken up by tree roots in the N addition treatment. The lack of a response in N+$CaCO_3$ treatment, however, might be due to the displacement of soil Al by the $CaCO_3$. This could have changed the soil pH buffer capacity and induced a high $H^+$ toxicity, hampering N assimilation (as proposed by Proctor 1999).

It is noteworthy that the increase in $RGR_{Yr}$ was significant only for stems in the 5-10 cm DBH size class and detectable ($p$=0.056) in the 2-5 cm DBH size class. Other researchers have also found size class-dependent responses to fertilisation treatments. Li et al. (2018), for instance, showed only trees 5-15 cm DBH responded to two years of fertiliser addition in subtropical as well as temperate forests in China and Alvarez-Clare et al. (2013) found that trees 5-10 cm DBH responded to 2.7 years of fertilisation in Costa Rica, but in both studies larger diameter trees did not respond to fertilisation. We can also consider investigations on changes of habitat filtering pressure through tree size classes and find an affinity between these two research fronts. Tree species distributions appear to be more clearly associated with soil variables as trees grow from saplings to adult trees (Yang et al. 2016 in temperate China, Baldeck et al. 2013 throughout the tropics, and Paoli et al. 2006 in Bornean lowland rain forest) and from plant forms of shrubs to canopy species (Xu et al. 2016). Though we must take into account that the variation explained by soil characteristics is sensitive to the number of individuals in the sample and the method chosen to select diameter size classes (Baldeck et al. 2013). From our results we suggest that very small trees (saplings <2 cm DBH) were limited by light, whereas small trees (2-5 cm DBH) and adult trees (5-10 cm DBH) may be progressively released from competition for light. For this reason, these trees 2-10 cm DBH responded to nutrient addition whereas larger diameter adult trees (> 10 cm DBH) may react to nutrient addition after a longer time period, when they have accumulated more N. Furthermore, adult trees might invest the added N in reproductive parts rather than in diameter growth (also note that the sample size for larger trees is much smaller than for smaller trees and it is more difficult to accurately measure small changes in diameter in larger trees).

The gradients derived from our PCA axes are similar to the ones observed by Baez et al. (2018) in Ecuadorian montane forest. We see a stronger relationship among the second PCA axis (driven by wood density and relative growth rate) rather than the first PCA axis (leaf gradient going from nutrient rich leaves to tough and nutrient poor leaves) with RGRyr growth after the treatments. The Spearman correlation led us to infer that in the control, $CaCO_3$ and N+$CaCO_3$ treatment, functional traits are important drivers of tree growth. In particular, acquisitive species have a significant response to $CaCO_3$ and N+$CaCO_3$ treatments if compared to conservative species. On the other hand, the lack of correlation among species functional strategy and growth in the N treatment led us infer that trees are responsive to the +N treatment irrespective of their functional identity, still underscoring the importance of soil N rather than pH in this forest.

Annual litterfall production in our control plots was similar to other heath forests. Proctor et al. (1983), for example, reported a leaf litterfall production of 5.6 t $ha^{-1}$ $yr^{-1}$ in Gunung Mulu heath forest (Sarawak, Malaysia) and Rahajoe and Kohyama (2003) reported a leaf litterfall production of 3.4 t $ha^{-1}$ $yr^{-1}$. Nonetheless Dent et al. (2006), in the same Kabili-Sepilok Forest Reserve heath forest, recorded 4.5 t leaf litterfall $ha^{-1}$ $yr^{-1}$. The differences might be due to the different location of Dent et al.'s (2006) plots which are characterised by a less podzolised soil and a greater tree basal area than in our location (Chapter 3). Overall, only the amount of debris retrieved from the litter traps in the $CaCO_3$ treatment plots has increased significantly probably due to the rather insoluble nature of the lime we used, which might have stuck to the leaves and detached after sample drying creating dust. We suppose that one year of fertiliser addition might be not enough to produce changes in litterfall production because of the long life span of heath forests' leaves (2.7 years in an Indonesian Borneo heath forest and 2.2 years in Amazon caatinga; Miyamoto et al. 2007; Jordan 1989). Other fertilisation studies, for example, obtained a significant increase in litterfall production after 19 months (225 kg N $ha^{-1}$ $yr^{-1}$ + 75 kg P $ha^{-1}$ $yr^{-1}$ fertilisation in Kalimantan lowland rain forest; Mirmanto et al. 1999), 20 months (300 kg N $ha^{-1}$ $yr^{-1}$ + 100 kg P $ha^{-1}$ $yr^{-1}$+ 100 K $ha^{-1}$ $yr^{-1}$ and micronutrient fertilisation in a Puerto Rican lowland forest; Walker et al. 1996) and four years (225 kg N $ha^{-1}$ $yr^{-1}$ + 75 kg P $ha^{-1}$ $yr^{-1}$ fertilisation in Venezuelan mountain forest; Tanner et al. 1992) of experimental treatments.

The $CaCO_3$ treatment increased leaf herbivory by a small proportion (an average monthly 0.3% increase in comparison to the control). Greater herbivory is possibly due to an increased palatability of less tough and more nutrient rich leaves (Sayer and Banin 2016). Coley (1983) showed leaf toughness to be the most important driver of leaf herbivory in lowland Panama, followed by leaf nutrient status. In Chapter 5 we analysed the changes in fresh leaf chemistry of the ten most common species and found that some species decreased their C:N ratio after $CaCO_3$ addition with and without N, and this is consistent with the significant decrease in C concentration for $CaCO_3$ plots' litterfall (possibly due to a dilution of C in leaf biomass). We thus surmise that $CaCO_3$ treatment made leaves softer and consequently increased leaf herbivory, whereas N deposition did not affect herbivory rates despite an increase in leaf N leading to more 'nutritious' leaves.

On the other hand, the $CaCO_3$ treatment, with and without N, led to an increase in Ca and Fe concentration in litterfall. These responses possibly reflect the increased availability of these two elements in the soil directly due to the lime we used. Trees growing in nutrient- poor soil tend to reduce resorption of elements from senescing leaves if the element becomes abundant (Haynes et al. 2014; Tsuji et al. 2017). The lower K concentration in leaf litterfall in N+$CaCO_3$ plots might be due to the competition between Ca and K for root absorption (Lucas and Davies 1961). From the resorption perspective, there is a noteworthy lack of response of litterfall N concentration in the +N plots. Possibly, the experimentally added N was not enough to induce a decrease in N resorption from senescent leaves (saturation level not reached), implying again that N limitation is rather important in this soil (but could also be not clearly detected due to long leaf life spans). This underscores that tropical heath forests' tree growth is sensitive to changes in N availability. Whether the expected increases in N deposition predicted for tropical areas should happen, this heath forest would be likely to undergo N saturation over a longer timeframe.

## 4.5 Conclusion:

Nutrient limitation of forest productivity is widespread in weathered tropical soils and broad generalisations are used when forecasting rain forest responses to human-driven alterations of nutrient cycles. Nonetheless, in tropical areas, substantial differences in soil fertility and species composition can occur over just a few kilometres. Understanding how edaphic factors shape trees communities may allow more fine-scale predictions of rain forest responses to human driven soil nutrient alterations.

In tropical heath forest we found that liming decreased soil acidity and decreased total soil P, C and N. Nitrogen fertilisation was also associated with a decrease in total soil N, available P and decreased Fe leaching. These responses suggested N, P and Fe are important for this forest ecosystem. The response of the trees corroborated the fundamental role of soil N availability, as the N treatment significantly increased relative diameter growth rate by more than 100 %, for some size classes. This effect was strongest in trees 5-10 cm DBH and almost significant ($p=0.056$) in trees 2-5 cm DBH.

Both acquisitive and conservative tree species had a strong response to N fertilisation, whereas there was a trend of faster DBH growth after $CaCO_3$ and N+$CaCO_3$ for conservative species. We did not find any change in leaf litterfall mass after the treatments, although an increased concentration of Fe in litterfall in both $CaCO_3$ and N+$CaCO_3$ treatments suggests that the Fe added with lime was absorbed by trees and quickly saturated the tree's Fe requirements. Addition of $CaCO_3$ also correlated with an increased herbivory, suggesting a link between soil pH and investment

# 5 Leaf stoichiometry and tree species functional identity in response to lime and nitrogen fertilisation in a Bornean heath forest.

**Abstract:** Soil nutrients often limit productivity in forest ecosystems with leaf nitrogen (N) and phosphorus (P) stoichiometry often used as a proxy to infer ecosystem nutrient limitation. Nonetheless, the leaf N:P ratio is subject to considerable variation among cohabitant species as well as along edaphic gradients. Furthermore, very few researchers have studied dynamics of other leaf nutrient apart from N and P. In this study, we investigate the effects of increased soil N availability and soil pH with a factorial N and $CaCO_3$ addition experiment on a wide range of leaf nutrients in a Bornean heath forest. Furthermore, we determine how the functional identity (i.e. the combination of different characteristics from one tree species defining this species' growth strategy) of ten common species influences the response of leaf nutrients to the experimental treatments. Leaf stoichiometry varied among species but, overall, we found a 21% increase of leaf N concentration after N addition treatments; leaf N:P ratios were not affected by the treatments. Another ubiquitous response was the increased concentration of leaf Fe and Cu, most likely originating from the lime we used. The change in leaf nutrient concentrations after treatment correlated with species functional identity; in particular, conservative species (i.e. slow growing species with nutrient poor leaves) increased their concentrations of Fe, Al, Cu and Na. We hypothesise that these micronutrients (Fe, Al, Cu and Na) might be especially valuable for conservative species, because they could use them as a form of biochemical stress-tolerance strategy. From our results, we propose a N and P co-limitation in this tropical heath forest. Given the increased leaf Fe and Cu concentration after liming, we also advocate that these two nutrients might be important and possibly limiting in this forest environment. The lack of correlation of functional identity with increased leaf N shows that N is fundamental irrespective of a tree's functional strategy.

## 5.1 Introduction:

Plants are closely adapted to the environment they live in because of their sessile nature and the low mobility of nutrients they rely upon. In addition to light and water availability, nutrient absorption and storage play a fundamental role in competition among species and individuals in plant communities (Craine and Dybzinski 2013). Globally, terrestrial ecosystem productivity is thought to be mainly limited by two soil nutrients, which are nitrogen (N) and phosphorus (P; Elser et al. 2007). Soil N is mainly derived from biological fixation by heterotrophic microorganisms, which are widespread and find optimal conditions at tropical latitudes (Hedin et al. 2009). On the other hand, P is integrated in the soil mainly by mineral dissolution and, in comparison to N, is quickly lost through leaching and weathering (Porder et al. 2007). In young temperate soils, productivity is thus limited by N, whereas in old weathered tropical soils productivity is limited by P (Vitousek 1984; Vitousek and Howarth 1991). This dichotomy has been inferred from fertilisation experiments and changes in leaf stoichiometry, among other methods (Sullivan et al. 2014).

Both soil and leaf N and P concentrations generally decrease from temperate to equatorial latitudes whereas leaf N:P ratios increase along the same gradient (Hedin 2004; Reich and Oleksyn 2004). The seminal work of Redfield (1934; 1958) on the constrained nature of C:N:P stoichiometry in marine systems, triggered the idea that leaf N:P ratios could be used as a tool to assess soil nutrient deficiencies. Koerselman and Meuleman (1996) proposed a foliar N:P ratio <14 and >16 to be indicative of a generalised N and P limitation, respectively. The decrease in leaf N:P ratio along a latitudinal gradient support the hypothesis of lowland rain forests being limited mainly by soil P availability (Cleveland et al. 2011; LeBauer and Treseder 2008). Nonetheless, a recent meta-analysis of nutrient manipulation experiments proposed a P and N co-limitation in lowland tropical rain forests (Wright et al. 2018). It thus becomes clear that, despite the solid applicability of Koerselman and Meuleman’s (1996) thresholds to global soil gradients, soil-leaf N and P relationships are not straightforward at local scales in the tropics (Alvarez-Clare and Mack 2015). Leaf N:P ratios, for example, varies greatly among species (Güsewell 2004) as well as across short gradients of soil nutrient availability (Sullivan et al. 2014) given the high diversity of tropical soilscapes (Palm et al. 2007; Townsend et al. 2008).

We propose that this ambiguous relationship among leaf N:P ratios and soil nutrient limitation (Ostertag and Dimanno 2016) can be explained by species functional identity. Functional traits have been shown to predict species' performance along environmental gradients (such as aboveground biomass increment throughout South America; Finegan et al. 2014) as well as species' responses to nutrient manipulation (such as community composition shift and plant biomass; Baez and Homeier 2018; Dickson et al. 2014). Species functional identity is a continuum of variation from "acquisitive" to a "conservative" strategies (Reich 2014). Acquisitive species typically have low wood density and high leaf nutrient concentrations with a high specific leaf area (SLA). These species grow fast and quickly acquire the available resources. Conservative species, on the other hand, have an opposite set of traits and are comparatively long lived and drought tolerant (Chapin 1980; Van der Sande et al., 2016; Wright et al. 2004). We thus would expect acquisitive species to change their N:P ratio more promptly after a nutrient manipulation experiment in comparison to conservative species.

Another tool to infer tree nutrient limitation was recently proposed by You et al. (2018). Their approach relies on the response of leaf stoichiometry to nutrient manipulations. After N addition in N limited environments, leaf N should increase and leaf P should decrease. The decrease in leaf P concentration is likely due to the dilution of P in the newly produced biomass. In P limited environments both leaf N and P should increase after N addition. This co-increase of P with N is likely due to the effect of added N that stimulates the activity of phosphatase-producing micro-organisms in soil (Marklein and Houlton 2012). Furthermore, P resorption from leaves can increase after N addition (Kozovits et al. 2007; Mayor et al. 2014; Yan et al. 2015). In N and P limited environments, leaf N should increase and leaf P should not change. The stable concentration of leaf P after N addition in N and P co-limited environment might be due to the interaction between a slightly higher P absorption from soil (because of the stimulant effect of N on phosphatase-producing microorganisms) with P dilution in the newly produced biomass (You et al. 2018). We will use also the You et al. (2018) approach to assess nutrient limitation in our study.

In addition to N and P, other leaf nutrients have important eco-physiological functions in plants. Calcium, (Ca) for example, is fundamental for signal conduction and cell structure, magnesium (Mg) for the regulation of cellular pH as well as cation-anion balance, potassium (K) maintains tissue water content whereas manganese (Mn) is important in enzyme activation. Iron (Fe) and copper (Cu) are necessary enzymatic components that detoxify superoxide radicals and are mainly present in photosystem 1, whereas sulfur (S) is integrated in many amino acids (Marschner 1995). Most of these macro- and micro-nutrients have shown an even wider global variation when compared to N and P in leaves (Metali et al. 2012) such as Al, Ca, K and Mg - in descending order of magnitude. It is accepted that these differences in leaf elemental concentrations are due to both environmental and genetic factors (Masunaga et al. 1998; Watanabe et al. 2007; White et al. 2012).

Among the environmental factors regulating leaf nutrient concentrations, soil pH plays a key role by regulating soil organic matter decomposition and mineralisation (Chapin et al. 2002; Elliott et al. 2002) hence influencing the availability of nutrients in the soil. Soil pH is generally positively correlated with available N and P content in soil and cation exchange capacity (i.e. exchangeable Ca, Mg, Na, K), which allows plants to absorb, store and invest in these nutrients (Aluko 1990; Wright et al. 1991). A neutral soil pH decreases available Mn and Al, which are toxic to plants at high concentration (Lavelle and Spain 2001; Wright et al. 1990). Despite a body of literature investigating the effects of liming on crop stoichiometry in agricultural tropical soils (e.g. Fageria et al. 1995; Fageria and Filho 1998; Sarker et al. 2000), we are not aware of studies investigating tropical forest trees stoichiometric responses - other than leaf N and P - to experimental pH manipulations. A few studies exist for temperate acidic forests: Moore and Ouimet (2006), for example, found increased leaf N, P, Ca and Mg concentrations but decreased K in maple trees growing over acid soil (pH 4.3, Ndzangou et al. 2006) after liming with $CaMg(CO_3)_2$ (i.e. dolomitic limestone). Similar results were observed by Forey et al. (2015) for senescent beech leaves except for K and Mg (due to the fact that they used calcitic lime, $CaCO_3$, that lacks Mg). The Forey et al. (2015) experiment showed an effect on K, Na and Mg only as a reduced resorption rate from senescing leaves. So, the relation among tropical forest plant leaf nutrient and pH requires further investigations.

A case of interest for nutrient limitation, as well as tropical soil and plant relationships, are tropical heath forests. These forests are found throughout tropical South America, South-east Asia and possibly also Africa (Whitmore 1990). They are characterised by a unique tree species composition with a high proportion of endemic species (Fine et al. 2010; Newbery 1991). The trees here have low productivity (Miyamoto et al. 1997; 2007) and leaves with low N (Luizao et al. 2004; Turner et al. 2000), P (Aoyagi and Kitayama 2015) and K concentrations (Peace and Macdonald 1981). These stunted forests' characteristics have been proposed to be due to low soil pH (Luizao et al. 2007; Proctor 1999), low N availability (Brearley et al. 2011; Luizao 1994; Moran et al. 2000; Proctor et al. 1983a; Proctor 1999) or to an interaction of the two (Luizao 1996). More recently, co-limitation by both N and P has been proposed for tropical heath forests (Dent et al. 2006).

In the last decades, agro-industrial expansion (Carrasco et al. 2014) and increasing population densities (Tyukavina et al. 2018) has shaped whole landscapes around the tropics (Lewis et al. 2015) leading to high atmospheric nitrogen input (Albanito et al. 2017; Castanheira et al. 2014; MacKenzie et al. 2011), with consequent deposition (Bauters et al. 2018; Reay et al. 2008). Nitrogen deposition has long been identified as a driver for species loss (Bobbink et al. 2010; Stevens et al. 2004) mainly shifting the competitive dynamics of species within nutrient limited ecosystems. Given heath forests' susceptibility to disturbance (Whitmore 1990), slow N cycling and possible N limitation, they might be highly sensitive to increased nutrient input driven by atmospheric deposition. Understanding how these rare and fragile forest ecosystems will react to an increased availability of resources is crucial to foresee the effects of global change.

In this chapter, we analysed the nutrient concentration of leaves from trees of a Bornean heath forest subjected to a factorial liming and N fertilisation experiment. In particular, we investigated the following questions: 1) is this tropical heath forest tree growth limited by N, P or an interaction of the two? For this quesion we followed the approaches of Koerselman and Meuleman (1996: leaf N:P ratio thresholds) and You et al. (2018: N and P concentration changes after N fertilisation), 2) how do foliar nutrient concentrations change after an experimental increase of soil N and pH? and 3) does species functional identity mediate the response of leaf stoichiometry to soil nutrient manipulation?

## 5.2 Methods:

### 5.2.1 Study site:

We performed this study in the Kabili-Sepilok Forest Reserve, Sabah, Malaysian Borneo (5° 51'N, 117° 58'E). The forest reserve hosts four forest typologies and we focussed on the heath forest in the eastern side of the reserve (Chapter 3). The climate is equatorial, with an average annual temperature of 26 $^{0}$ C and precipitation of ~3000 mm per year. Only in the dry season (approximately from March to May) does the precipitation drop below 100 mm per month (Fox 1973 Nilus, 2003). The soil underlying our plots is an infertile spodosol with low concentration of mineral nitrogen and low pH (mean of 3.7. Chapter 3). In this heath forest, we installed sixteen 15 m x 15 m experimental plots. The plots were fertilised using a factorial design with N (50 kg N $yr^{-1}ha^{-1}$) and $CaCO_3$ (approximately 5550 kg $yr^{-1}ha^{-1}$ of $CaCO_3$; see Chapter 4 for full details) to increase soil pH by approximately 1 pH unit.

### 5.2.2 Sampling:

We identified the 10 most common tree species throughout our plots. These were: *Actinodaphne borneensis* (Lauraceae), *Chionanthus pluriflorus* (Olaceae), *Cotylelobium melanoxylon* (Dipterocarpaceae), *Diospyros fusiformis* (Ebenaceae), *Dracaena elliptica* (Asparagaceae), *Gaertnera junghuhniana* (Rubiaceae), *Pimelodendron griffithianum* (Euphorbiaceae), *Syzygium* sp. (Myrtaceae), *Ternstroemia aneura* (Pentaphyllacaceae) and *Tristaniopsis obovata* (Myrtaceae). In every plot, we collected around ten fresh leaves from one individual of each focal species, although not every species was present in all plots. We collected leaves once before the treatments (April 2016) and three times after the treatments throughout the two years of the experiment (January 2017, July 2017 and June 2018). We sampled the same trees at every collection if possible. After the first collection, if the tree was dead, we sampled leaves from another tree of the same species. Leaves were collected with a pruner at a height of ~ 7 m. The canopy of heath forests is quite open, so the leaves were not in full shade. We oven dried the fresh leaves at a temperature of 50 $^{0}$ C until stable weight (approximately one week). We then ground the leaves for each individual before analysis. We determined specific leaf area (SLA) only for leaves from the last leaf collection; it was calculated as the quotient between fresh leaf area and dry leaf mass.

### 5.2.3 Leaf Chemical Analysis:

We determined foliar Al, Ca, Cu, Fe, K, Mg, Mn, Na, Ni and P by digesting 0.25 g of ground leaf material with a mixture of 8 ml $HNO_3$ + 2 ml of deionised $H_2O$ using a microwave digestor (Mars Xpress 5, CEM Corporation, Matthews, NC) and measured the elemental concentration with an inductively coupled plasma-atomic emission spectrometer (iCAP 6300, Thermo Scientific, USA). To measure C and N concentration, we analysed 0.15 g of ground leaf with a Leco TruSpec CN elemental analyser.

### 5.2.4 Functional traits:

As functional traits, we used SLA, leaf C:N (as a proxy of leaf toughness), and total leaf N and P concentrations from trees in control plots. Tree wood density was obtained from literature (i.e. Carsan et al. 2012; Zanne et al. 2009); when wood density values of the target species were not present in literature we averaged all of the available data for congeneric species from the same geographic area. We also included the yearly stem diameter growth rates of trees from the control plots. This was calculated with the following formula: $((d_2 - d_1)/ d_1)* 1/ \Delta t$ where $d_1$ is the initial diameter, $d_2$ is the diameter at the second year, and $\Delta t$ is the time interval between the two measurements expressed in years.

### 5.2.5 Statistical analysis:

We checked variables for normality with Shapiro-Wilk tests, and due to the non-normality of the models' residuals, values were log-transformed. We then assessed whether leaf nutrient concentration differed among species before the treatments with Kruskal Wallis tests. Variables were then ranked with a HSD Tukey test. We inferred the effect of treatments on leaf stoichiometry with linear mixed models (LMM) where the interaction among treatment and month of collection was a fixed effect and plot was a random effect. Linear mixed models were run separately for all individuals together as well as for single species.

### 5.2.6 Identification of functional strategies:

To identify species' functional strategies, we performed a principal components analysis (PCA) with the log values of the six functional traits. We then inferred the functional behaviour of species in the PCA multidimensional space extracting individual scores on the first axis and averaged them for each species. We tested the correlation among species' functional identity and species' response to the treatments with a Spearman correlation analysis with Bonferroni correction.

## 5.3 Results:

### 5.3.1 Leaf stoichiometry before the treatments:

All leaf nutrients were significantly different among species before the treatments (the highest Kruskal Wallis p-value was <0.01; Table 5.1) and that which had the greatest variance was Ni (overall mean concentration of 1.44 ± 2.80 SD µg $g^{-1}$ dry weight), followed by Al (0.38 ± 1.02 SD mg $g^{-1}$), Na (0.58 ± 0.89 SD mg $g^{-1}$), Mn (177 ± 146 SD µg $g^{-1}$), Mg (3.4 ± 2.0 SD mg $g^{-1}$), K (8.19 ± 5.01 SD mg $g^{-1}$), and Zn (18.2 ± 20.8 SD µg $g^{-1}$). On the other hand, the most stable concentrations among species were leaf C (overall mean concentration of 46.2 ± 2.12 SD %), N:P ratio (27.9 ± 6.07 SD), N (1.2 ± 0.31 SD %) and C:N ratio (39.7 ± 10.8 SD; Table 5.1). Overall, the mean P concentration was 0.45 ± 0.09 SD mg $g^{-1}$. Interestingly *Gaertnera junghuhniana* had a high concentration of Al (greatest value of 5.6 mg $g^{-1}$, mean value of 2.72 ± 1.65 SD mg $g^{-1}$). Specific leaf area was also significantly different among species (p-value <0.001).

### 5.3.2 Response of leaf stoichiometry to the treatments:

The linear mixed models showed that the response of leaf stoichiometry to N, $CaCO_3$ and N + $CaCO_3$ treatments varied greatly among our target species.

*Table 5.1 Mean (±SD) values of initial leaf nutrient concentration from ten species in heath forest plots in Kabilli-Sepilok Forest Reserve, Sabah, Malaysia. Mean values sharing the same superscript letter within a row are not significantly different, P>0.05, Tukey's HSD test. All variables had p-value <0.001 except Fe and Ni, which had p-value <0.01.*

| Species | *n* | Al | Ca | S | Na | K | Mg |
|---|---|---|---|---|---|---|---|
| | | (mg g$^{-1}$) | | | | | |
| *Actinodaphne borneensis* | 12 | 0.03 (±0.10)$^{c,d}$ | 3.15 (±1.40)$^{b,c}$ | 1.71 (±0.25)$^{b,c}$ | 0.14 (±0.15)$^{c,d}$ | 7.11 (±0.9)$^{b}$ | 1.09 (±0.30)$^{e}$ |
| *Chionanthus pluriflorus* | 14 | 0.05 (±0.02)$^{b,c,d}$ | 2.72 (±1.11)$^{c}$ | 1.21 (±0.24)$^{c,d}$ | 0.55 (±0.33)$^{a,b,c}$ | 4.41 (±2.2)$^{c}$ | 2.59 (±0.68)$^{d}$ |
| *Cotylelobium melanoxylon* | 15 | 0.03 (±0.03)$^{c,d}$ | 3.53 (±1.28)$^{b,c}$ | 0.92 (±0.47)$^{d,e}$ | 0.32 (±0.24)$^{b,c,d}$ | 4.07 (±1.1)$^{c}$ | 1.27 (±0.79)$^{e}$ |
| *Diospyros fusiformis* | 14 | 0.02 (±0.02)$^{d}$ | 3.67 (±0.97)$^{a,b,c}$ | 1.74 (±0.45)$^{b,c}$ | 1.10 (±1.13)$^{a,b}$ | 15.9 (±2.9)$^{a}$ | 6.60 (±1.30)$^{a}$ |
| *Dracaena elliptica* | 14 | 0.02 (±0.01)$^{c,d}$ | 3.81 (±1.29)$^{a,b,c}$ | 3.16 (±1.26)$^{a}$ | 0.13 (±0.08)$^{b,c,d}$ | 16.6 (±4.7)$^{a}$ | 4.33 (±1.21)$^{b,c}$ |
| *Gaertnera junghuhniana* | 16 | 2.71 (±1.65)$^{a}$ | 5.85 (±2.69)$^{a}$ | 1.53 (±0.77)$^{c}$ | 0.25 (±0.71)$^{d}$ | 6.09 (±3.1)$^{b,c}$ | 3.18 (±0.89)$^{c,d}$ |
| *Pimelodendron griffithianum* | 14 | 0.06 (±0.44)$^{b,c}$ | 4.52 (±1.38)$^{a,b}$ | 2.15 (±0.44)$^{a,b}$ | 0.39 (±0.27)$^{a,b,c,d}$ | 6.15 (±1.5)$^{b,c}$ | 3.61 (±0.83)$^{b,c,d}$ |
| *Syzygium* sp. | 15 | 0.04 (0.03)$^{c,d}$ | 7.21 (±5.83)$^{a}$ | 1.60 (±0.48)$^{b,c}$ | 2.19 (±1.37)$^{a}$ | 6.69 (±3.2)$^{b,c}$ | 4.33 (±1.72)$^{b,c}$ |
| *Ternstroemia aneura* | 14 | 0.31 (±0.14)$^{b}$ | 4.70 (±1.26)$^{a,b}$ | 1.29 (±0.31)$^{c}$ | 0.12 (±0.11)$^{c,d}$ | 8.47 (±2.8)$^{b}$ | 5.32 (±1.22)$^{a,b}$ |
| *Tristaniopsis obovata* | 10 | 0.02 (±0.02)$^{c,d}$ | 4.16 (±1.56)$^{a,b,c}$ | 0.79 (±0.19)$^{e}$ | 0.19 (±0.14)$^{b,c,d}$ | 7.85 (±3.1)$^{b}$ | 1.39 (±0.38)$^{e}$ |

*Table 5.1 Continued.*

| Species | Cu | Fe | Mn | Ni | Zn |
|---|---|---|---|---|---|
| | | | (µg g$^{-1}$) | | |
| *Actinodaphne borneensis* | 4.3 (±0.5)$^{b}$ | 54.0 (±2.8)$^{a,b}$ | 275 (±13.7)$^{a,b}$ | 0.7 (±0.12)$^{a,b}$ | 28.8 (±0.70)$^{a}$ |
| *Chionanthus pluriflorus* | 4.2 (±0.2)$^{b}$ | 39.1 (±1.7)$^{a,b}$ | 186 (±11.3)$^{a,b}$ | 2.5 (±0.53)$^{a,b}$ | 22.8 (±0.66)$^{a,b}$ |
| *Cotylelobium melanoxylon* | 4.7 (±0.1)$^{b}$ | 48.6 (±2.1)$^{a,b}$ | 230 (±14.4)$^{a,b}$ | 0.9 (±0.09)$^{a,b}$ | 25.0 (±1.07)$^{a,b}$ |
| *Diospyros fusiformis* | 8.7 (2.6)$^{a}$ | 40.5 (±9.8)$^{a,b}$ | 314 (±174)$^{a}$ | 2.4 (±2.9)$^{a}$ | 13.3 (±7.20)$^{b,c,d}$ |
| *Dracaena elliptica* | 3.9 (±0.9)$^{b}$ | 67.0 (±38.6)$^{a}$ | 73.8 (±17.8) $^{c,d}$ | 1.1 (±0.69)$^{a,b}$ | 21.8 (±7.52)$^{a,b}$ |
| *Gaertnera junghuhniana* | 3.9 (±1.2)$^{b}$ | 55.9 (±25.1)$^{a,b}$ | 229 (± 123)$^{a,b}$ | 1.4 (±3.8)$^{b}$ | 24.7 (±55.8)$^{b,c}$ |
| *Pimeleodendron griffithianum* | 4.0 (±1.0)$^{b}$ | 57.1 (±27.4)$^{a,b}$ | 127 (±73.6)$^{b,c}$ | 1.7 (±1.2)$^{a}$ | 11.9 (±5.27)$^{b,c,d}$ |
| *Syzygium* sp. | 3.3 (±1.3)$^{b}$ | 38.0 (±35.1)$^{b}$ | 47.0 (±25.9)$^{d,e}$ | 0.7 (±0.85)$^{a,b}$ | 7.4 (±4.39)$^{d}$ |
| *Ternstroemia aneura* | 2.0 (±0.9)$^{c}$ | 38.6 (±27.7)$^{a,b}$ | 43.5 (±48.1)$^{e}$ | 0.7 (±0.61)$^{a,b}$ | 9.1 (±5.30)$^{c,d}$ |
| *Tristaniopsis obovata* | 5.2 (±1.9)$^{b}$ | 35.8 (±23.4)$^{a,b}$ | 294 (±165)$^{a}$ | 2.5 (±5.0)$^{a,b}$ | 18.3 (±8.72)$^{a,b,c}$ |

*Table 5.1 Continued.*

| Species | N | C | P | C:N | N:P | SLA |
|---|---|---|---|---|---|---|
| | (%) | | (mg g$^{-1}$) | ratio | | (cm$^2$ g$^{-1}$) |
| *Actinodaphne borneensis* | 1.29 (±0.13)$^{c,d}$ | 48.1 (±0.39)$^{b}$ | 0.44 (±0.06)$^{a}$ | 37.6 (±3.5)$^{b,c,d}$ | 29.1 (±2.7)$^{a}$ | 115 (±8.3)$^{cd}$ |
| *Chionanthus pluriflorus* | 1.10 (±0.14)$^{d}$ | 46.0 (±0.59)$^{c}$ | 0.39 (±0.09)$^{a,b,c}$ | 42.4 (±5.9)$^{b}$ | 28.3 (±5.1)$^{a,b}$ | 133 (±28.6)$^{bcd}$ |
| *Cotylelobium melanoxylon* | 1.31 (±0.18)$^{c}$ | 50.0 (±2.32)$^{a}$ | 0.51 (±0.19)$^{a}$ | 38.9 (±4.4)$^{b,c}$ | 25.7 (±5.2)$^{a,b}$ | 107 (±8.3)$^{de}$ |
| *Diospyros fusiformis* | 1.60 (±0.11)$^{a,b}$ | 46.7 (±0.84)$^{b,c}$ | 0.50 (±0.11)$^{a}$ | 29.2 (±2.0)$^{e,f}$ | 32.1 (±5.9)$^{a}$ | 123 (±10.3)$^{bcd}$ |
| *Dracaena Elliptica* | 1.67 (±0.27)$^{a}$ | 43.7 (±0.99)$^{e}$ | 0.50 (±0.14)$^{a}$ | 26.8 (±4.2)$^{f}$ | 33.7 (±4.1)$^{a}$ | 140 (±9.2)$^{ab}$ |
| *Gaertnera junghuhniana* | 1.28 (±0.20)$^{c,d}$ | 44.5 (±1.22)$^{d,e}$ | 0.52 (±0.59)$^{a,b}$ | 35.5 (±5.2)$^{c,d}$ | 24.5 (±8.7)$^{a}$ | 115 (±9.4)$^{bc}$ |
| *Pimeleodendron griffithianum* | 1.40 (±0.16)$^{b,c}$ | 45.4 (±0.73)$^{c,d}$ | 0.53 (±0.14)$^{a}$ | 32.8 (±3.6)$^{d,e}$ | 26.5 (±4.6)$^{a,b}$ | 162 (±33.6)$^{a}$ |
| *Syzygium* sp. | 0.90 (±0.14)$^{e}$ | 45.8 (±1.85)$^{c,d}$ | 0.31 (±0.09)$^{b,c}$ | 52.1 (±7.9)$^{a}$ | 29.4 (±5.5)$^{a,b}$ | 72 (±7.6)$^{e}$ |
| *Ternstroemia aneura* | 0.79 (±0.11)$^{e}$ | 45.2 (±0.94)$^{c,d}$ | 0.27 (±0.05)$^{c}$ | 58.6 (±8.2)$^{a}$ | 28.8 (±3.9)$^{a,b}$ | 91 (±12.0)$^{e}$ |
| *Tristaniopsis obovata* | 1.09 (±0.13)$^{d}$ | 46.4 (±0.76)$^{b,c}$ | 0.50 (±0.11)$^{a}$ | 43.1 (±4.6)$^{b}$ | 21.6 (±5.2)$^{b}$ | 89 (±19.2)$^{cde}$ |

*Table 5.2 (Next page). Leaf nutrient concentration changes (which are in mg g$^{-1}$ for all elements except C and N which are in % and C:N and N:P which are ratios) after two years of N, $CaCO_3$ and N+$CaCO_3$ addition in the tropical heath forest of Kabili-Sepilok Forest Reserve, Sabah, Malaysia. We reported the results for all species grouped together and for each of the different species. * $P < 0.05$; ** $P < 0.01$; ***$P<0.001$.*

| Element | Treatment | Species | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | All | *Act.bor.* | *Chi.plu.* | *Cot.mel.* | *Dio.fus.* | *Dra.ell.* | *Gae.jun.* | *Pim.bor.* | *Syz.*sp | *Ter.ane.* | *Tris.obo.* |
| N:P | $CaCO_3$ | -0.27 | -0.82 | -2.3 | -1.45 | 0.67 | 0.45 | 0.81 | -1.17 | -0.73 | **-3.50**$^{*}$ | 0.43 |
| | N | 1.74 | 0.66 | -1.38 | -1.09 | 1.21 | 3.62 | 2.99 | 0.99 | 2.40 | 2.27 | -0.37 |
| | N+$CaCO_3$ | 2.09 | 1.25 | 0.95 | -0.65 | **5.52**$^{*}$ | **10.17**$^{*}$ | 0.18 | 0.38 | 1.63 | -0.95 | -2.83 |
| C:N | $CaCO_3$ | -2.50 | -3.06 | -2.58 | -0.85 | 1.05 | 1.23 | **-6.28**$^{**}$ | **-3.21**$^{+}$ | **-7.03**$^{**}$ | 0.84 | -0.63 |
| | N | **-3.09**$^{*}$ | -0.44 | 1.94 | -2.68 | 1.38 | -1.85 | **-7.68**$^{***}$ | -0.47 | -3.72 | -1.89 | **-9.11**$^{*}$ |
| | N+$CaCO_3$ | -2.50 | 0.79 | -0.68 | -0.57 | 0.04 | -2.05 | **-8.34**$^{***}$ | -1.95 | -2.41 | 3.99 | -4.46 |
| N | $CaCO_3$ | 0.07 | 0.11 | 0.09 | 0.05 | -0.04 | -0.07 | **0.17**$^{**}$ | 0.13 | **0.16**$^{**}$ | -0.005 | -0.01 |
| | N | **0.09**$^{*}$ | 0.02 | -0.04 | 0.07 | -0.06 | 0.12 | **0.22**$^{***}$ | 0.01 | 0.05 | 0.04 | **0.20**$^{*}$ |
| | N+$CaCO_3$ | **0.08**$^{+}$ | -0.02 | 0.02 | -0.0003 | 0.02 | 0.18 | **0.26**$^{***}$ | 0.04 | 0.06 | -0.04 | 0.07 |
| C | $CaCO_3$ | 0.11 | -0.33 | 0.12 | 0.59 | 0.38 | -0.01 | -0.83 | **-0.84**$^{**}$ | 1.28 | **1.00**$^{+}$ | -0.24 |
| | N | -0.05 | **0.52**$^{*}$ | -0.22 | -0.36 | 0.41 | 0.53 | -0.46 | 0.15 | -1.07 | 0.83 | -0.17 |
| | N+$CaCO_3$ | -0.22 | 0.19 | -0.02 | **-1.06**$^{+}$ | 0.17 | **1.06**$^{*}$ | -0.22 | **-0.94**$^{***}$ | 0.79 | 0.59 | -0.18 |
| P | $CaCO_3$ | 0.03 | 0.06 | 0.08 | 0.06 | -0.02 | -0.03 | 0.04 | 0.09 | **0.06**$^{*}$ | 0.03 | -0.02 |
| | N | 0.004 | -0.001 | -0.01 | 0.04 | -0.05 | -0.01 | 0.03 | -0.001 | -0.003 | -0.004 | 0.08 |
| | N+$CaCO_3$ | 0.03 | -0.02 | -0.01 | 0.02 | **-0.07**$^{+}$ | -0.05 | **0.26**$^{*}$ | 0.05 | 0.01 | -0.01 | 0.06 |
| Al | $CaCO_3$ | 0.057 | -0.0044 | -0.01 | -0.001 | -0.006 | -0.004 | 0.41 | -0.14 | 0.001 | -0.20 | 0.02 |
| | N | 0.017 | -0.0057 | -0.01 | -0.011 | 0.006 | 0.006 | 0.15 | -0.15 | 0.011 | -0.08 | -0.009 |
| | N+$CaCO_3$ | -0.113 | 0.0007 | -0.02 | -0.009 | -0.013 | -0.003 | -0.79 | -0.16 | **0.026**$^{+}$ | -0.07 | -0.007 |
| Ca | $CaCO_3$ | -0.2 | **2.559**$^{**}$ | 0.13 | -0.38 | -0.73 | 1.18 | -0.05 | 1.53 | -2.14 | -0.47 | -0.39 |
| | N | 0.09 | -0.229 | 0.21 | -0.62 | -0.58 | -0.54 | 0.91 | 0.88 | 1.40 | -0.17 | -1.02 |
| | N+$CaCO_3$ | -0.003 | -0.427 | 0.43 | -0.02 | -0.32 | -0.01 | 0.21 | 0.89 | -1.53 | -0.66 | **-1.36**$^{*}$ |
| Cu | $CaCO_3$ | **0.005**$^{*}$ | 0.0002 | 0.001 | **-0.0014**$^{*}$ | 0.0008 | 0.0005 | 0.00026 | 0.0005 | **0.00168**$^{***}$ | **0.0011**$^{**}$ | 0.000006 |
| | N | 0.001 | -0.0003 | -0.0004 | -0.0007 | -0.001 | -0.0001 | 0.00005 | 0.0001 | 0.00030 | **0.0008**$^{*}$ | 0.001737 |
| | N+$CaCO_3$ | 0.002 | -0.0001 | -0.0004 | **-0.0017**$^{**}$ | -0.001 | -0.0007 | 0.00007 | **0.0009**$^{*}$ | -0.00001 | **0.0012**$^{*}$ | **0.001987*** |

*Table 5.2 Continued.*

| Element | Treatment | Species | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | All | *Act.bor.* | *Chi.plu.* | *Cot.mel.* | *Dio.fus.* | *Dra.ell.* | *Gae.jun.* | *Pim.bor.* | *Syz.*sp | *Ter.ane.* | *Tris.obo.* |
| Fe | $CaCO_3$ | **0.005**$^{*}$ | -0.009 | **0.11**$^{*}$ | **0.01**$^{+}$ | -0.0004 | -0.013 | 0.0003 | -0.002 | **0.021**$^{*}$ | **0.022**$^{**}$ | 0.0008 |
| | N | **0.004**$^{*}$ | -0.007 | 0.01 | 0.003 | 0.0037 | 0.003 | 0.0052 | 0.006 | 0.002 | 0.004 | 0.0053 |
| | N+$CaCO_3$ | **0.003**$^{+}$ | -0.006 | 0.01 | 0.006 | -0.0005 | **-0.017**$^{+}$ | 0.0075 | **0.010**$^{*}$ | 0.006 | 0.001 | **0.0144**$^{**}$ |
| K | $CaCO_3$ | -0.116 | **-1.46**$^{**}$ | 1.2 | 0.13 | -1.69 | -1.32 | 0.22 | -0.66 | 1.17 | 0.94 | -0.39 |
| | N | 1.04 | 0.09 | 0.79 | 0.3 | 2.2 | -0.72 | -0.10 | 0.78 | -0.13 | 0.18 | 2.82 |
| | N+$CaCO_3$ | -0.009 | 0.46 | -0.3 | 0.28 | -0.98 | **-5.5**$^{*}$ | **0.86**$^{+}$ | 0.41 | -0.59 | 1.14 | 2.67 |
| Mg | $CaCO_3$ | 0.38 | **0.81**$^{***}$ | 0.003 | 0.34 | 0.46 | 0.4 | 0.73 | 0.84 | -0.54 | 0.09 | 0.14 |
| | N | 0.2 | -0.06 | 0.596 | -0.15 | -0.38 | 0.32 | -0.47 | 0.15 | -0.89 | 0.26 | 0.06 |
| | N+$CaCO_3$ | 0.5 | 0.02 | 0.061 | 0.08 | -0.23 | -0.28 | 0.59 | **0.95**$^{+}$ | 1.43 | 0.02 | -0.05 |
| Mn | $CaCO_3$ | -0.06 | 0.04 | -0.073 | **-0.17**$^{*}$ | -0.18 | 0.018 | -0.1234 | 0.007 | -0.005 | -0.03 | -0.07 |
| | N | -0.03 | 0.02 | -0.035 | -0.09 | -0.13 | -0.003 | -0.0005 | 0.007 | -0.002 | -0.02 | -0.09 |
| | N+$CaCO_3$ | -0.03 | -0.07 | 0.008 | -0.07 | -0.11 | 0.012 | -0.0653 | -0.014 | 0.006 | -0.03 | -0.10 |
| Na | $CaCO_3$ | 0.15 | 0.007 | 0.29 | 0.009 | 0.18 | -0.023 | -0.14 | 0.09 | -0.06 | 0.007 | 0.03 |
| | N | -0.06 | **-0.08**$^{*}$ | 0.27 | -0.001 | 0.27 | -0.005 | -0.20 | **0.14**$^{+}$ | -1.02 | 0.043 | 0.02 |
| | N+$CaCO_3$ | 0.31 | -0.04 | 0.03 | 0.076 | 0.73 | 0.795 | 0.05 | **0.43**$^{**}$ | -0.08 | 0.036 | 0.06 |
| Ni | $CaCO_3$ | **0.0001**$^{+}$ | -0.0002 | -0.001 | -0.0001 | 0.0006 | -0.0003 | 0.0012 | **0.001**$^{*}$ | 0.00004 | 0.0007 | -0.0008 |
| | N | -0.0002 | 0. 0002 | -0.002 | -0.0001 | -0.0001 | -0.0001 | -0.0003 | -0.0002 | 0.00016 | 0.0001 | -0.0008 |
| | N+$CaCO_3$ | 0.000004 | -0.0003 | -0.001 | -0.0003 | 0.0006 | **-0.0004**$^{*}$ | 0.0002 | 0.0001 | 0.00048 | 0.0006 | -0.0004 |
| S | $CaCO_3$ | 0.02 | **0.27**$^{*}$ | 0.14 | 0.09 | -0.25 | -0.4 | 0.17 | 0.20 | 0.04 | -0.15 | 0.05 |
| | N | -0.07 | 0.04 | -0.19 | -0.05 | -0.37 | **-0.91**$^{+}$ | -0.15 | 0.06 | 0.07 | -0.09 | 0.06 |
| | N+$CaCO_3$ | -0.09 | 0.15 | **-0.29**$^{*}$ | -0.07 | -0.3 | 0.41 | -0.04 | -0.15 | -0.02 | **-0.282**$^{+}$ | -0.02 |
| Zn | $CaCO_3$ | 0.0009 | 0.0051 | 0.004 | 0.0006 | 0.001 | 0.004 | 0.0004 | -0.0003 | 0.0010 | -0.001 | -0.003 |
| | N | 0.0013 | -0.0009 | 0.002 | 0.0031 | -0.002 | 0.004 | 0.0036 | 0.0011 | 0.0013 | -0.001 | **0.007**$^{+}$ |
| | N+$CaCO_3$ | 0.003 | **-0.0088**$^{*}$ | 0.002 | **0.0097**$^{+}$ | 0.004 | 0.005 | 0.0189 | 0.0011 | -0.0003 | -0.003 | **0.008**$^{**}$ |

Nonetheless, a few elements increased consistently (although not significantly in some cases) across all species following treatments (Table 5.2). We examined these patterns with linear mixed models that grouped all of our focal species together and found an increase in leaf N concentration with respect to the control, for trees subjected to N-addition treatments (we consider a p-value < 0.05 significant) and, consequently, a significant decline in the C:N ratio (in the N treatment only). Although there was a trend towards increasing N:P ratios in both N and N+$CaCO_3$ treatment, this was not significant.

With regard to the other elements, only leaf Cu and Ni increased significantly in the $CaCO_3$ treatment and leaf Fe increased significantly in all three treatments. The linear models run with single species allowed us to infer a more detailed stoichiometric response to nutrient additions. Among all species, *Actinodaphne* and *Gaertnera* were the most responsive species because seven of their leaf elements changed significantly after the treatments. The species with least number of significant responses were *Diospyros* with one (N:P ratio) and *Chionanthus* with two (Fe and S) respectively. The most dynamic element was Cu, which increased significantly in leaves of *Tristaniopsis* (N+$CaCO_3$ treatment), *Ternstroemia* ($CaCO_3$ treatment and N+$CaCO_3$ treatment) and *Syzygium* ($CaCO_3$ treatment), whereas it decreased significantly in *Cotylolebium* leaves after the $CaCO_3$ and N+$CaCO_3$ treatments. As expected, the N+$CaCO_3$ treatment caused the greatest number of significant responses in leaf nutrients (19 species x elements intractions changed significantly) followed by $CaCO_3$ addition (18 significant changes). The N addition alone, on the other hand, had fewer significant changes (six).

### 5.3.3 Species functional identity and its correlation with species responses to the treatments:

The first two PCA axes explained 84 % of the variation in the data (Fig. 1). The first axis (which explained 61.5 % of the total variance) was characterised by a gradient going from species with high leaf C:N ratios (proxy for leaf toughness) on the negative values to species with high N and P leaf concentration (and SLA with relative growth rate to a lesser extent) on the positive values. The second axis was characterised by a gradient going from species with high wood density to species with fast growth and high SLA gradient. We extracted the individuals' scores on the first axis as it had the highest explanatory power and, by doing so, we obtained a species' functional identity gradient, which varied from negative values, indicating the most conservative species (such as *Syzygium* and *Tristaniopsis* from the Myrtaceae family and *Ternstroemia* from the Pentaphyllacaceae family) to positive values (indicating acquisitive species such as *Pimleodendron* from the Euphorbiaceae family, *Diospyros* from the Ebenaceae family and *Dracaena* from the Asparagaceae family. Table 5.3).

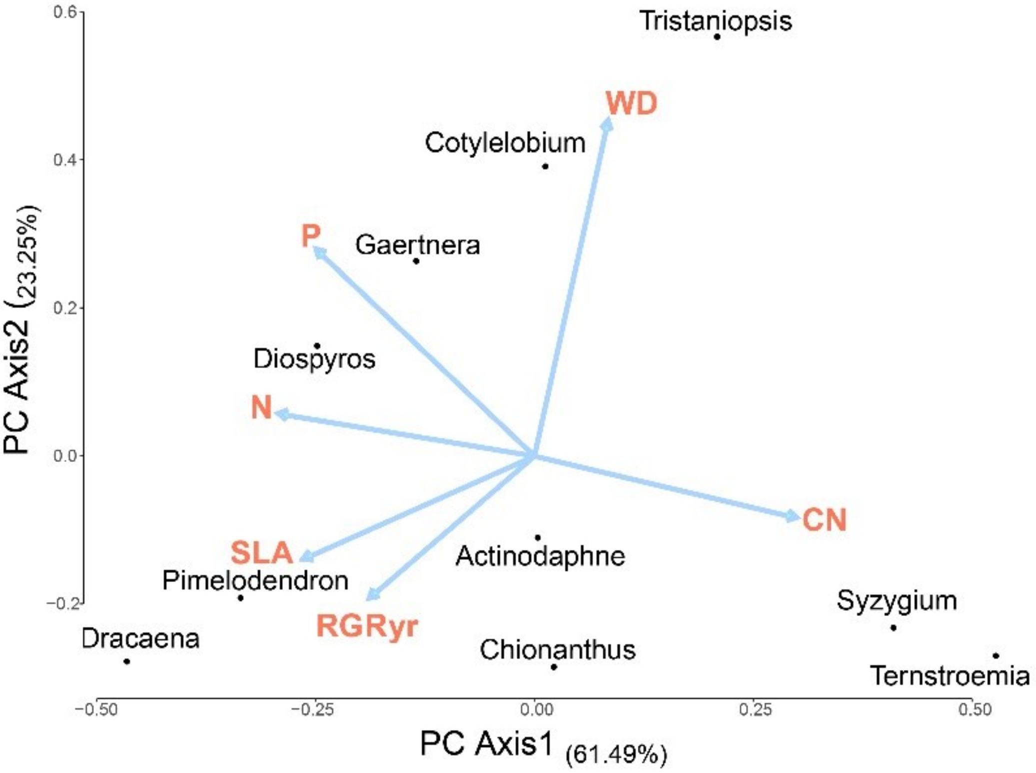

*Figure 5.1. Principal component analysis of six functional traits among ten target species from the heath forest in the the Kabili-Spilok Forest Reserve, Sabah, Malaysia. WD= wood density, P= leaf P concentration, N= leaf N concentration, CN= leaf C:N ratio, SLA= specific leaf area, RGRyr= yearly relative stem diameter growth rate.*

*Table 5.3 Functional identity of ten target species from the heath forest in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. We inferred functional identity from species' score on the first axis of the principal component (PC) analysis built with six functional traits (see Figure 5.1).*

| Functional strategy | Species | Score on PC1 |
|---|---|---|
| Acquisitive | *Dracaena elliptica* | -2.83 |
| | *Pimelodendron griffithianum* | -2.04 |
| | *Diospyros fusiformis* | -1.51 |
| | *Gaertnera junghuhniana* | -0.82 |
| | *Actinodaphne borneensis* | 0.02 |
| | *Cotylelobium melanoxylon* | 0.07 |
| | *Chionanthus pluriflorus* | 0.13 |
| | *Tristaniopsis obovata* | 1.27 |
| | *Syzygium* sp. | 2.49 |
| Conservative | *Ternstroemia aneura* | 3.20 |

The Spearman correlation analysis (Table 5.4) revealed that changes in leaf stoichiometry after the treatments were related to plant functional identity for half of the elements analysed. The element with the strongest relationship between stoichiometric change and plant functional identity was Fe, which increased in conservative species after $CaCO_3$ addition. Aluminium and Na changes were also strongly related to species functional identity (Al: $\rho=-0.73$, p-value $< 0.0003$; Na: $\rho= -0.71$, p-value $< 0.0003$) whereas C, Cu and Ni had a moderate correlation (C: $\rho=-0.55$, p-value $< 0.0003$; Cu: $\rho=-0.66$, p-value$<0.0003$; Ni: $\rho=0.50$, p-value$<0.0003$. Table 5.4). All these negative correlations indicate an increase in elemental concentration in conservative species' leaves.

On the other side of the spectrum we see that only Ca and Mn have moderate correlations with acquisitive species (Mn: $\rho=0.50$, p-value$<0.0003$; Ca: $\rho=0.50$, p-value$<0.0003$). The remaining variables (K, P, N, S, Zn, Mg, as well as N:P and C:N ratios) showed only weak or no correlation with functional identity ($\rho<0.5$ and $\rho>-0.5$).

*Table 5.4 Spearman correlation coefficients of leaf nutrient responses to our three experimental treatments with the species functional strategy (obtained extracting species scores from the first axis of a PCA performed with species functional traits before the treatment). Moderate to strong correlations (ρ≥0.5) are indicated in bold. Thresholds for p-values were calculated with Bonferroni correction. The figures are as follows: * P < 0.016; ** P < 0.003; ***P<0.0003.*

| Element | Treatment | | |
|---|---|---|---|
| | $CaCO_3$ | N | N+$CaCO_3$ |
| Fe | **-0.83***** | -0.41*** | -0.17* |
| Al | **-0.73***** | -0.10 | **-0.65***** |
| Na | **-0.71***** | -0.05* | -0.08 |
| C | **-0.55***** | 0.15 | -0.20 |
| Cu | **-0.54***** | **-0.66***** | -0.49*** |
| Ni | **-0.50***** | -0.26* | -0.41*** |
| K | -0.43*** | -0.14* | -0.38*** |
| P | -0.38** | -0.01 | -0.15 |
| N | -0.27 | -0.05 | 0.37** |
| Mn | 0.05 | 0.49*** | **0.50***** |
| C:N | 0.15 | 0.19 | -0.34* |
| S | 0.19 | -0.33* | 0.02 |
| Ca | 0.38*** | 0.01 | **0.50***** |
| Zn | 0.39*** | 0.07 | 0.36 |
| Mg | 0.42*** | 0.26** | -0.17 |
| N:P | 0.45*** | 0.25* | 0.33*** |

## 5.4 Discussion:

Understanding tropical forest nutrient limitation is fundamental to forecast these forests' responses to human perturbations of their nutrient cycles. Here, we studied the effects of a factorial N and $CaCO_3$ addition experiment on trees' foliar stoichiometry in a Bornean heath forest. We also assessed whether changes in leaf stoichiometry were related to species' functional strategies.

### 5.4.1 Species nutrient status before the treatments and N-P limitation:

When compared with South-east Asian heath forests from the literature (Metali et al. 2012; Peace and MacDonald 1981; Vitousek and Sanford 1986) Kabili-Sepilok heath forest mean leaf N, P, K and Mg concentration are quite high while Ca is rather low. As expected, the nutrient status of leaves at our site was consistently lower than Amazonian and South-east Asian lowland evergreen rain forests (Asner et al. 2014; Vitousek 1986). The mean N:P ratio of our leaves (28) was similar to the N:P ratio found in Badas and Sawat heath forests (Brunei; N:P of 24; Metali et al. 2015) but lower than Bako National Park heath forest (Sarawak, Malaysia; N:P of 40; Peace and MacDonald 1981). We compared our N:P ratio to lowland evergreen rain forest leaves, and find our N:P ratio to be consistently higher than both Bruneian (N:P of 25; Metali et al. 2015) and Costa Rican (N:P of 22; Alvarez-Clare and Mack. 2015) lowland forest leaves. Our heath forest N:P ratio, along with the values obtained in other heath forests, are well above the proposed threshold of 16 that Koerselman and Meuleman (1996) suggest to indicate soil P limitation. This contrasts with the general vision of heath forests being mainly limited by soil N (Proctor 1999; Proctor et al. 1983a). Nonetheless, Dent et al. (2006) proposed tropical heath forests are co-limited by both N and P soil concentration by the means of a high phosphorus-use efficiency in heath forest in the same Kabili-Sepilok Forest Reserve. It is true that if leaves have a low N concentration (e.g. 11 mg $g^{-1}$, indicating a clear N deficiency) and a comparatively low P concentration (e.g. 0.39 mg $g^{-1}$), the resulting quotient (i.e. 28) will indicate a P deficiency and overlook N limitation (Townsend et al. 2007; Yan et al. 2017). So, given our heath forest leaves low nutrient concentrations, there is a clear chance to misunderstand nutrient limitation using Koerselman and Meuleman's (1996) approach alone. Thus, we will rely on the effect of our nutrient manipulation experiment on leaf chemistry to infer plant nutrient limitation (You et al. 2018; see section 5.1).

Our Kabili-Sepilok heath forest mean SLA was also in the range reported from the literature for tropical heath forest and lower than lowland evergreen rain forest (Miyamoto et al. 2007; Paoli 2006; Turner et al. 2000) and peat swamp forest (Nishimura and Suzuki 2001). From the point of view of functional identity, we saw clear differences among our focal species, which showed a wide spectrum of functional strategies.

### 5.4.2 Response of leaf stoichiometry to the treatments:

The experiment highlighted an overall clear response of leaf chemistry after just two years of treatment. Nonetheless, several nuances in response to the treatment among different species were also visible. The overall response with all species grouped together showed a rapid increase in foliar N after N addition. This might indicate that the trees are limited by soil N or that trees absorbed N in excess and store it as a form of luxury consumption. Luxury consumption usually occurs in shade-tolerant species (Lawrence 2003), which are ecologically comparable, in our analysis, to “conservative” species. As we show both acquisitive and conservative species to increase their N concentration in leaves, and given the increased tree growth rate assessed in Chapter 4, we propose that the response of trees in our study highlights an ubiquitous N limitation. This result contrasts with the P limitation inferred from the N:P ratio. Nonetheless, as we did not treat the plots with P we are not able to say whether N or P is the principal nutrient limiting the tree growth in these heath forests. Following the approach of You et al. (2018) we lean towards the N and P co-limitation hypothesis for heath forest tree growth. In the case of N and P co- limitation, You et al. (2018) showed an increase in leaf N and an unchanged leaf P content after N addition, as also seen in our experiment.

When all species were grouped together, only leaf Cu and Fe increased significantly following $CaCO_3$ addition. Few results on the effects of liming on Cu are available from the literature, but in North American acid soils, liming has been shown to not affect, or even reduce the foliar Cu and Fe concentration of tall fescue (*Festuca arundinacea*; Hamilton 2006) possibly due to soil Fe sequestration by carbonates (Brown 1961). Our results might indicate a scarcity of Cu and Fe in our study site soil as well as an important role of these nutrients for our heath forest trees. Iron has been found to be possibly limiting Bruneian heath forest bacterial communities (Kerfahi et al. 2018) and Belizean calcareous forest soil microbial community (Winbourne et al. 2017). Generally spodosols are depleted not only in N but also low in cation exchange capacity and other – beneficial or not – elements such as Al and Fe due to clay eluviation (Andriesse 1970; Sobrado 2013). Copper, on the other hand, is generally low in sandstone, which is the bedrock of our study site (Nilus 2003). In particular, our plots have a mean available Cu and Fe concentration of 0.05 µg $g^{-1}$ and 26 µg $g^{-1}$ respectively (Chapter 3). The $CaCO_3$ we used had a total concentration of 20 µg Cu $g^{-1}$ and 11530 µg Fe $g^{-1}$ (Chapter 4), so it is likely that the importance of Cu and Fe for free radical detoxification (i.e. superoxide dismutase) and for plant enzyme architecture (Uchida 2000; Yamasaki et al. 2008) drove the increased storage of these nutrients in our trees after liming.

Another unexpected result is the lack of a significant response of leaf Ca and K to our treatments. In a Canadian soil liming experiment, Ca increased in *Acer saccharum* leaves (Moore et al. 2000) whereas K decreased in both soil (Magdoff and Bartlett 1980) and leaves (Moore et al. 2000). The decrease in plant K content after liming reported in the literature is usually ascribed to the competition for root uptake of Ca and Mg with K (Hamilton 2006). The lack of response in Ca and K leaf concentrations suggests that neither of these nutrients limit our forest community. Furthermore, liming is known to reduce soil Al concentration (Badalucco et al. 1992) unlocking soil P, which then become available to plants (Fageria and Filho 1998). The lack of response of leaf Al and P is possibly due to the already low amount of soil Al in our study site (tropical spodosols' acidity is thought to be dominated by soil $H^+$ rather than soil Al; Proctor 1999). So, at our site, soil P is unlikely to be bound with Al. Thus, the P limitation inferred from N:P ratio in our heath forest could be the result of root stoichiometry. Plants' roots absorb P preferentially as orthophosphates ($H_2PO^-_4$ and $HPO_4^{-2}$; Raghothama 1999) but this uptake requires the co-transport of $H^+$, which exerts a toxic effect on roots (Foy 1984). Plants thus might limit the absorption of orthophosphates to avoid a toxic root concentration of $H^+$.

### 5.4.3 Species functional identity correlates with response to nutrient addition:

We detected a differential ability of plants with contrasting functional strategies to acquire soil nutrients in our heath forest. Despite the common understanding that acquisitive species have a higher rate of nutrient uptake than conservative species (Van der Sande et al. 2018), we see conservative species increasing the uptake of soil elements such as Fe, Al, Na, Cu, and Ni, and increasing leaf C content (possibly because of a faster photosynthetic rate) relative to acquisitive species. Acquisitive species perform slightly better than conservative ones for only a couple of elements, which are Mn and Ca. The low Spearman correlation coefficient and p-values of residual variables (i.e. K, N, P, S, Zn and Mg as well as N:P and C:N ratios) with species functional identity leads us to two hypothesis. The first entails that the leaf concentration of these elements have been changing (although not significantly in Table 5.2) irrespectively of species' functional strategy. The second is that there is no real change in the stoichiometry of these elements in our leaves. We inspected the scatterplots of species identity with the variables and inferred that the first hypothesis applies to our situation. Magnesium, N, Ni, P, Zn and N:P generally increased among all treatments irrespective of plant functional strategy whereas S and C:N ratio generally decreased.

Species with conservative traits are known to be long lived and stress tolerant (Lohbeck et al. 2013; Poorter and Bongers 2006; Ruger et al. 2012) resisting drought (Van der Sande et al. 2016) and shade (Baltzer and Thomas 2010). The increased uptake of micronutrients observed in our conservative species might indicate that conservative plants growing in a nutrient depleted soil such as our heath forest spodosol, adopt a form of biochemical stress tolerance. As discussed above, Fe and Cu are fundamental for free radical detoxification, and free radical production is exacerbated by adverse environmental stresses such as drought and high irradiance (Bowler et al. 1994), which both occur frequently in heath forests. Aluminium, on the other hand, can improve tree growth in extremely Al poor acidic soils (Kidd and Proctor 2000; Kinraide 1993). So, it appears reasonable for conservative species to absorb extra Al with the scope to enrich the soil nearby the rooting zone through litterfall, so reducing $H^+$ toxicity (see also Chapter 3).

## 5.5 Conclusion:

In this study, we assessed the response of leaf stoichiometry in a tropical heath forest after a factorial N fertilisation and liming experiment. Our initial questions were whether this tropical heath forest is limited by soil N or P as well as what effect N fertilisation and liming would have on leaf stoichiometry. Despite the high N:P ratio of our leaves before the experiment suggesting P limitation, the change in foliar N and P concentration after N fertilisation after the treatment leads us to hypothesise that N and P co-limit this tropical heath forest. A factorial N and P addition experiment would be necessary to fully test this hypothesis, however. After the treatments, Fe and Cu increased in the leaves of our target species, suggesting an important role of these elements for plant physiology. We saw that liming had a greater influence on changes in leaf stoichiometry rather than N fertilisation, but we suggest that the response is more related to the input of new elements in the soil from the lime itself, rather than from the effect of increased soil pH. Our other question was whether species functional identity had any influence on the species' response to N and lime addition. The results show that changes in leaf stoichiometry had a marked correlation with species functional identity. Iron, Al, Na, Cu and Ni (in order of the strength of the correlation) increased only in conservative species and especially after $CaCO_3$ addition alone. On the other hand, the most important elements, such as N, increased throughout all the species, regardless of their functional strategy. This suggests that the predicted increase in N deposition throughout the tropics might increase heath forest trees N uptake irrespective of functional identity. Anyhow, due to the faster growth of acquisitive species, these might increase in biomass, reproductive rate and eventually drive a change heath forests' species composition.

# 6 Impact of soil nitrogen availability and pH on tropical heath forest organic matter decomposition and decomposer activity.

**Abstract:** Decomposition is a key process for rain forest nutrient cycling. Heath forests are high conservation-valued forests characterised by slow litter decomposition rates due to low quality litter, along with acidic soil pH and low availability of soil nitrogen (N). To investigate which of these is most important in the regulation of tropical heath forest organic matter decomposition, we used a factorial N and $CaCO_3$ addition in the Kabili-Sepilok Forest Reserve (Sabah, Malaysia) to measure wood and unfertilised leaf litter decomposition rates, the abundance of culturable fungi, and mesofaunal activity. Our heath forest site had a slower decomposition rate in comparison to lowland evergreen rainforest and similar to that of temperate forest soils. The experimental modification of both soil pH and available N had weak effect on decomposition rates and fungal counts although there was a clear, but transient, increase in worm casts in the $CaCO_3$ and N+$CaCO_3$ treatment. The general lack of a response of decomposition processes to changes in N and pH was surprising given the rapid response of trees 2 - 10 cm DBH; it may take longer than one year for the decomposer community and associated processes to be influenced by the altered edaphic conditions.

### 6.1 Introduction:

Tropical rain forests generally develop on infertile soils but, paradoxically, they are the most productive forest ecosystems on earth (Bonan 2008). Decomposition of wood and leaf litter is a key process ensuring the efficient cycling of nutrients needed to achieve such productivity (Cleveland et al. 2013; Xu et al. 2013) but the factors influencing decomposition rates are still poorly understood (Powers et al. 2009). In order to better understand forest productivity, it is essential to understand the influence of local environmental factors on decomposition. Although tropical rain forests develop in warm and moist regions, local climatic and soil characteristics can be different. Mean annual precipitation and temperature influence leaf litterfall and wood decomposition and are considered the most important factors within tropical regions (Chambers et al. 2000; Powers et al. 2009; Salinas et al. 2011; Weedon et al. 2009). Further factors influencing tropical litter decay rate are litter quality (e.g. nutrient concentration and lignin concentration; Pietsch et al. 2014) and the decomposer community (Maynard et al. 2016; Waring 2012) but the relative importance and interaction among these factors are still debated (Lavelle et al. 1993; Powers et al. 2009; Sayer 2006). Decomposer community composition, abundance and activity, and thus decomposition rates of organic matter, are in turn affected by soil chemistry (Cleveland et al. 2002; Hobbie and Vitousek 2000; Swift et al. 1979).

Throughout the tropics, soils have very different physical structure and nutrient composition. Among the least fertile tropical soils are spodosols (Palm et al. 2007; Vitousek and Sanford 1986) that can be as acidic as pH 3 (Andriesse 1968) and low in available nitrogen (N; Moran et al. 2000) or both N and phosphorus (P; Dent et al. 2006). Tropical spodosols often host a unique forest formation known as “heath forest”. Despite tropical heath forests’ low primary productivity (Dent et al. 2006; Proctor et al. 1983a) their high conservation value lies in their high species endemism (Anderson 1981; Garcia 2016) and belowground C stock (Montes et al. 2011). The low quality of litter produced and rapid nutrient uptake by roots suggests that nutrient cycles in these forest systems are very efficient (Medina and Cuevas 1989; Vitousek 1984). Heath forests typically host tree species with long-lived, small thick leaves (Becker et al. 1999; Peace and Macdonald 1981; Turner 1994) with low N and P concentrations (Aoyagi and Kitayama 2016; Luizao 1994; Turner et al. 2000) and high phenolic and tannin content (Dent et al. 2006; Janzen 1974; Whitmore 1990). Tree wood also has low nutrient content (Aoyagi and Kitayama 2016) and these wood and leaf characteristics make heath forests’ litter a poor substrate for decomposition (Dent et al. 2006). The influence of soil characteristics on heath forest ecology - such as tree growth and leaf stoichiometry - have been discussed extensively (see Coomes 1997; Luizao 1996; Moran et al. 2000; Vernimmen et al. 2013) but, to our knowledge, only Luizao (1994) studied the influence of heath forest soil chemistry on decomposition. Luizao (1994) performed a laboratory experiment using a manipulative approach and found that N addition significantly increased soil microbial activity (measured as soil respiration) as well as net nitrification, but net nitrification was only affected if N was combined with P. A temporary increase in soil respiration was found after the addition of $CaCO_3$, but they argued that the amount of $CaCO_3$ added was too low to change the soil pH.

Fertilization experiments usually test the effects of soil N and P limitation on decomposition and only rarely are other nutrients considered (e.g. Kaspari et al. 2008 who tested for B, Ca, Cu, Fe, Mg, Mn, Mo, S, Zn limitation). The recent review by Camenzind et al. (2018), for instance, reported that soil P limited lowland rain forest microbial activity while soil N limited montane rain forest microbial activity (especially mineralization and nitrification rates, e.g. Baldos et al. 2015). This dichotomy is consistent with the long-standing paradigm of rain forest tree productivity limitation (Tanner et al. 1998) which suggest lowland rain forest being limited by soil P and montane rain forest being limited by soil N. Nonetheless, new evidence (Wright et al. 2018) challenges this theory and suggests lowland rain forest nutrient limitation is more complex and probably influenced by both N and P (LeBauer and Treseder 2008; Wright et al. 2018). This widened perspective on soil nutrient limitation of rain forest tree productivity might also apply to the soil decomposer community. It is conceivable that the lack of widespread experimental evidence in tropical areas (e.g. Camenzind et al. 2018 reviewed experiments from 16 tropical areas) allowed an oversimplified generalisation of decomposer nutrient limitation (Kaspari et al. 2008). Another generally accepted limit to decomposition is soil pH (Chapin et al. 2002; Haynes 1986), which acts as a selective force for the decomposer community. Low soil pH was associated with a) lower bacterial diversity (Tripathi et al. 2012), b) low biomass of soil bacteria (Anderson and Domsch 1993), and c) increased abundance of fungi (Högberg et al. 2007) thus lowering the bacteria-to-fungi ratio (Blagodatskaya and Anderson 1998) in both temperate and tropical forest soils. Further evidence that soil pH influences organic matter decomposition comes from work in temperate forest (Corre et al. 2003; Nyborg and Hoyt 1978) and lowland evergreen rain forests (Luizao et al. 2007), which showed how liming forest soils increase soil N mineralization. This increase in mineralization results from an increase in the bacteria-to-fungi ratio, which also affects the abundance of earthworms (Moore et al. 2013; Potthoff et al. 2008) that feed on bacteria.

Here, we advance understanding of the influence of soil chemistry on decomposition and decomposer activity by investigating whether soil pH, N availability or an interaction between both of these limits 1) the rate of wood and leaf litter decomposition, 2) the abundance of soil fungi, and 3) the soil mesofaunal activity in a Bornean heath forest using a factorial N and $CaCO_3$ addition experiment.

## 6.2 Methods:

### 6.2.1 Study site:

This study was undertaken in the Kabili-Sepilok Forest Reserve, in the state of Sabah, Malaysian Borneo (5° 51' N, 117° 58' E). The climate is equatorial, with an average temperature of $26^0$ C and rainfall of ~3000 mm year. There is a short dry season - usually in April - with less than 100 mm monthly precipitation, whereas almost 45 % of annual precipitation occurs from November to February (Fox 1973). The reserve consists of four forest-soil associations: the coastal Mangrove forest, the Alluvial forest which lies in valleys, the Sandstone forest on steep slopes and the Heath forest on moderate slopes (Jucker et al. 2018; Nilus 2003). Our study side is located in the heath forest at the eastern side of the reserve and is underlain by an infertile spodosol (USDA soil taxonomy) which develops from a sandstone bedrock. The soil has acidic pH, low cation exchange capacity and total as well as available N but available soil P content was higher than in the adjacent lowland evergreen rainforest (i.e. alluvial forest. Chapter 3 and Appendix). The forest is a characteristic tropical heath forest with low basal area (34.4 $m^2$ $ha^{-1}$ for trees > 5 cm DBH), high stem density (1997 stems > 5 cm DBH $ha^{-1}$) and an even canopy of ca. 28 m height (Chapter 3).

### 6.2.2 Experimental setup:

In April 2016, we installed 16 forest plots of 225 $m^2$ (15 m x 15 m. Chapter 3). We conducted a factorial experiment consisting of four treatments (control, N, $CaCO_3$

and N+$CaCO_3$) with four replicates (Chapter 4). We applied N at a rate of 50 kg ha$^{-1}$ yr$^{-1}$ in form of urea and $CaCO_3$ at an initial rate of 5550 kg ha$^{-1}$ yr$^{-1}$. In the subsequent $CaCO_3$ additions, we reduced the amount of lime per plot to avoid raising the soil pH above pH 5 (as specified in Chapter 4). The addition rate of $CaCO_3$ was almost twice the amount added by Luizao (1994) in Brazilian heath forest. We studied how the increased soil pH and N availability affected decomposition of organic matter by incubating teabags, tree leaves, wooden sticks and cubes on the forest floor and examined the abundance and activity of soil decomposers (fungi, mesofauna and earthworms).

### 6.2.3 Teabag experiment:

For this experiment, in September 2016, we dried, weighed and tagged Lipton Green teabags (EAN 87 22700 05552 5) and Rooibos teabags (EAN 87 22700 18843 8). We then buried three teabag of each type in every plot below the mineral soil surface, ca. 8 cm depth. After two months of incubation (Tea Bag Index protocol. http://www.teatime4science.org/wp-content/uploads/scientific.pdf), we collected, dried at 50$^{o}$ C and removed soil debris from the teabags. We then weighed them to obtain a decomposition constant ($k$) and litter stabilization factor ($s$) as described in Keuskamp et al. (2013).

### 6.2.4 Leaf litter decomposition:

To account for decomposition of local leaf litter material, litter of mixed species was collected weekly from eight large mesh sheets suspended over the forest floor. The litter was oven dried at 50$^{o}$ C until a stable weight was reached and 5 g (±0.005 g) of dry litter was placed in litterbags (20 cm x 20 cm) with 1.8 mm mesh. In September 2016, we laid 15 litterbags per plot on the soil surface; three litterbags were collected from each plot after 1, 3, 6 and 12 months, and their content was oven dried at 50$^{o}$ C, brushed free of roots and soil and weighed.

### 6.2.5 Wood decomposition:

We studied wood decomposition using local timber wood cubes (*Terminalia catappa* (L.) sapwood, a paleotropical species obtained from the local sawmill) as well as flat wooden sticks (*Betula pendula* bought form Baker Ross, Essex, UK; AG206). We dried, bored with a hole, weighed, tagged and tied to trees, six 5 cm x 5 cm wood cubes in every plot totalling 96 cubes. Tying the wood cubes to trees made the retrieval easier but the cubes were lain on the soil surface. After one and two years, we collected and weighed three wood cubes per plot. The wooden sticks were oven dried at $50^{o}$ C, tagged and weighed. We placed 25 wood sticks per plot for a total of 400 wood sticks. The sticks were lain on the soil surface and secured to nearby trees with string. We then sampled, dried and weighed five sticks per plot after 3, 6 and 12 months. Wood cubes incubation started in September 2016 whereas wood sticks were placed in the plots in October 2016.

### 6.2.6 Culturable fungi:

We assessed culturable soil fungi in each plot. In July 2018, we divided each plot into four quadrats and collected one surface soil sample (0-5 cm) for each quadrat totalling 64 samples. For each sample, we put 1 g of soil in 9 ml of sterilised water and serially diluted it to $10^{-4}$. One ml from each $10^{-4}$ solution was plated onto potato dextrose agar petri dishes with streptomycin (30 µg $ml^{-1}$) to control the growth of bacteria and actinomycetes. After a two days incubation ($25^{o}$ C) the colony forming units (CFU) were counted.

### 6.2.7 Mesofaunal activity:

To assess the effects of treatments on mesofaunal activity, we incubated lamina bait sticks (Kratz, 1998) and counted the worm casts present in every plot. The lamina bait sticks (Terra Protecta GmbH, Berlin, Germany) are plastic strips with 16 small holes spaced ~ 5 mm from each other. The holes are filled with a standard bait of cellulose powder, bran flakes and activated carbon. In May 2017, lamina bait sticks were inserted vertically into the soil and incubated for two different periods: two sticks per plot were incubated for 6 days, and three sticks per plot were incubated for 14 days. After incubation, we removed the sticks and counted how many holes had their bait eaten, assigning a score per bait hole of 1 for fully-eaten baits and a score of 0.5 for half-eaten baits. We assessed the activity of earthworms in August 2017 by counting the worm casts in four 1 $m^2$ quadrats located at the corners of a central 5 m x 5 m square in each plot. Dry worm casts were excluded from the counting and only the fresh moist ones, assumed to be deposited on the soil surface in the last week, were counted.

### 6.2.8 Statistical analysis:

After teabag retrieval, we calculated the *s* and *k* values for each bag (see Keuskamp et al. 2013 and below), took the mean value for each plot and compared *k* and *s* variance among treatments with an ANOVA. The stabilisation factor *s* depicts the inhibiting effect that environmental variables have on the decomposition rate. Decomposition rates of local leaf litter, wood sticks and wooden cubes were compared across the treatments using the daily decay coefficient *k* obtained by the following formula: $Y \sim e^{kX}$ (Olson 1963). This is the exponential regression relating the quotient of the incubated sample weight to the original sample weight (Y) and the days of incubation (X). Hence, *k* can be derived as the slope of a linear regression of log(Y) against X. To obtain the yearly decay rate we multiplied *k* by 365. We calculated the number of days required to decompose half the mass of the sample ($t_{0.5}$) with the following formula: $t_{0.5}= (\ln(0.5)/k)*365$ (Bockheim et al. 1991). We then assessed the effect of the treatments on the decomposition rates of leaf litter in litterbags, wood sticks and wood cubes using linear mixed models where percentage mass loss was the explanatory variable, an interaction of treatment with days of incubation as fixed factor and plot as a random factor. We checked the normality of model's residuals by screening residuals' histograms. We also tested whether the fungal CFUs per gram of soil, the number of worm casts and the cumulative lamina bait score were significantly different among treatments using linear mixed models but with only treatment as a fixed factor for both counts of fungal CFU and worm casts, and with the interaction among treatment and time for the lamina bait scores.

## 6.3 Results:

Around three-quarters of the teabags retrieved from field incubation were pierced by termites and tea was likely lost, so we had to discard them. Across the treatments, for undamaged tea bags, the weight loss was higher for green tea (74.9% of the original weight) than for rooibos tea (42.6%). All treatments (N, $CaCO_3$ and N+$CaCO_3$) decreased the stabilisation factor *s* and increased the decomposition constant *k* relative to the control (Table 6.1), although these were not significant (p value > 0.05 in both cases).

*Table 6.1 Stabilisation factor (s) and decomposition rate (k) mean values and confidence intervals calculated from green tea and rooibos teabags incubated in plots with four treatments in the Kabili-Sepilok Forest Reserve heath forest, Sabah, Malaysia*

| Treatment | *s* | | *k* | |
|---|---|---|---|---|
| | Mean | 95 % CI | Mean | 95 % CI |
| Control | 0.073 | 0.01-0.13 | 0.021 | 0.017-0.025 |
| $CaCO_3$ | 0.034 | -0.06-0.13 | 0.028 | 0.027-0.029 |
| N | 0.049 | -0.05-0.14 | 0.024 | 0.019-0.028 |
| N+$CaCO_3$ | 0.068 | 0.03-0.11 | 0.026 | -0.012-0.065 |

The linear mixed models shown a significant reduction in leaf litter decomposition rates in the $CaCO_3$ and N+ $CaCO_3$ treatments (with $p < 0.05$ and confidence intervals for the decomposition constant *k* not overlapping; Table 6.2) but no significant effect of N on decomposition rate. A slow decomposition rate at high pH (~5) is counterintuitive and we argue that this is due to an experimental bias. Calcium carbonate has a low solubility in water and thus, despite brushing our samples, $CaCO_3$ stuck on the litterbags' decaying leaves resulting in an experimental artefact. Wood decomposition (sticks and cubes) was not statistically significantly different from the control for any treatment (all p values >0.05; Figure 6.1). Despite the lack of significance we believe a trend can be seen, with a decreased decomposition rate (low *k* and high $t_{0,5}$) for wood cubes in the N treatment (Table 6.2).

In all other cases (i.e. teabags, wood sticks and wooden cubes but excluding the litterbags under $CaCO_3$ and N+$CaCO_3$ treatments) both increased pH and available N showed a non- significant promotion of decomposition rates (Table 6.3).

*Table 6.2. Annual decomposition rate (k) with confidence intervals, regression parameters and half-life of samples (t0.5 ) for litterbags, wood sticks and wood cubes incubated in plots with four treatments in the Kabili-Sepilok Forest Reserve heath forest, Sabah, Malaysia.*

| | Treatment | $r^2$ | F | Intercept | Coefficient | $k$ (yr) | 95% CI | $t_{0.5}$ (days) |
|---|---|---|---|---|---|---|---|---|
| Litterbags | Control | 0.64 | 84 | 0.84 | 0.0014 | 0.51 | 0.40-0.63 | 491 |
| | $CaCO_3$ | 0.41 | 31 | 0.84 | 0.0007 | 0.27 | 0.17-0.36 | 949 |
| | N | 0.82 | 215 | 0.90 | 0.0017 | 0.64 | 0.55-0.73 | 393 |
| | N+$CaCO_3$ | 0.38 | 28 | 0.84 | 0.0009 | 0.35 | 0.21-0.48 | 720 |
| Wood sticks | Control | 0.53 | 64 | 1.11 | 0.0024 | 0.89 | 0.67-1.11 | 283 |
| | $CaCO_3$ | 0.39 | 37 | 1.03 | 0.0026 | 0.90 | 0.66-1.29 | 258 |
| | N | 0.39 | 38 | 1.19 | 0.0040 | 1.48 | 1.00-1.95 | 170 |
| | N+$CaCO_3$ | 0.48 | 51 | 1.08 | 0.0033 | 1.22 | 0.88-1.56 | 207 |
| Wood cubes | Control | 0.28 | 8 | 1.23 | 0.0014 | 0.52 | 0.15-0.90 | 478 |
| | $CaCO_3$ | 0.46 | 18 | 1.12 | 0.0017 | 0.63 | 0.32-0.93 | 403 |
| | N | 0.30 | 10 | 1.09 | 0.0011 | 0.41 | 0.15-0.68 | 609 |
| | N+$CaCO_3$ | 0.30 | 9 | 1.52 | 0.0020 | 0.75 | 0.25-1.26 | 334 |

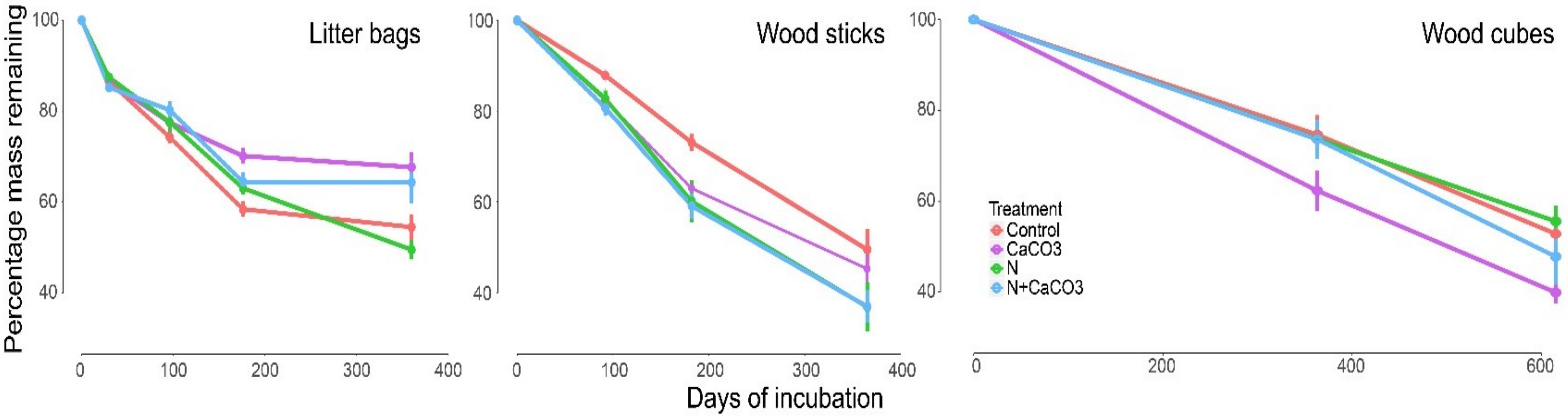

*Figure 6.1. Percentage of the original mass remaining after one (litterbags and wood sticks) and two years (wood cubes) of incubation in the four experimental treatments in the Kabili-Sepilok Forest Reserve heath forest in Sabah, Malaysia. All values are means ± standard error.*

*Table 6.3. Overall effect of increased soil N and pH in relation to control plots for our experiments in the Kabili-Sepilok Forest Reserve heath forest in Sabah, Malaysia. The "+" and "-" sign indicate that the treatment increased and decreased: decomposition rate (for teabags, litterbags, wood sticks and wood blocks) and abundance/activity of soil decomposers (for fungal CFUs, feeding activity measured with lamina bait sticks and number of worm casts). Significance symbols are as follows: '***' < 0.001 '**' <0.01, '*' < 0.05, '.' < 0.1.*

| Treatment | Teabags | Litterbags | Wood sticks | Wood cubes | Fungal CFUs | Feeding activity | Worm casts |
|---|---|---|---|---|---|---|---|
| $CaCO_3$ | + | - | + | + | + | + | $+^{***}$ |
| N | + | + | + | - | - | + | + |
| $N+CaCO_3$ | + | - | + | + | - | + | $+^{**}$ |

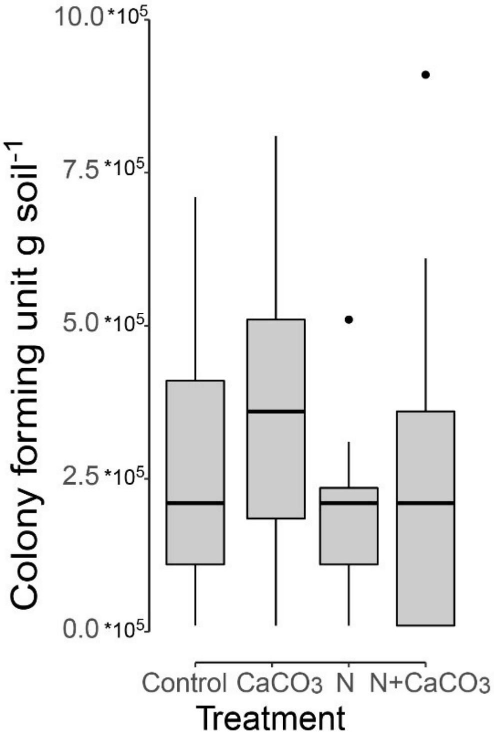

*Figure 6.2 Number of fungal colony forming units in four treatments in the Kabili-Sepilok Forest Reserve heath forest in Sabah, Malaysia. The black bar represent the median value, first and third quartiles are at the top and bottom of the plot, respectively, and the maximum and minimum values excluding outliers are the whiskers. Dots indicate outliers.*

The difference in fungal CFUs among treatments was not significant but we could see a trend of increasing CFUs in the $CaCO_3$ treatment (*Figure 6.2*). The feeding activity calculated with the lamina bait slightly increased in the $CaCO_3$ (p value = 0.055) and N+$CaCO_3$ (p value =0.069) *treatments (*Figure 6.2*;* Figure 6.3*)* The density of worm casts increased in both $CaCO_3$ (p value < 0.001) and N+$CaCO_3$ (p value < 0.05) treatments (Figure 6.4).

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## 6.4 Discussion:

Organic matter decomposition is an essential process in forest nutrient cycling. Nonetheless, few studies have addressed the influence of tropical forest soil chemistry in regulating organic matter decomposition. In this chapter, we studied whether soil pH, soil available N or an interaction of the two limits organic matter decomposition in the tropical heath forest of Kabili-Sepilok, Sabah, Malaysia. From an overall point of view, we speculate that decomposition might be regulated by both soil pH and N availability, whereas mesofauna activity appears to be more strongly regulated by soil pH, although these relationships were generally weak.

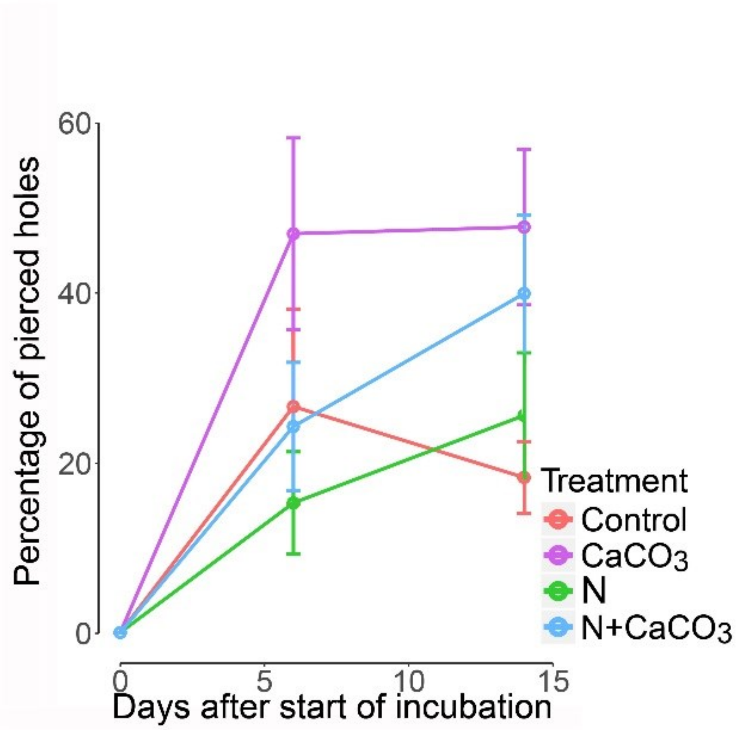

*Figure 6.3 Effects of the experimental treatments on mesofaunal activity, accounted for by feeding activity with lamina bait test stick in the Kabili-Sepilok Forest Reserve heath forest in Sabah, Malaysia. All values are mean ± standard error.*

### 6.4.1 Organic matter decomposition:

The teabag experiment was established as a part of the international teabag experiment instigated by Judith Sarneel (http://www.teatime4science.org/). The advantage of the teabag approach is that, using standardised material, it allows comparisons of decomposition constants throughout the globe. Our teabag stabilization factor (*s*) fits well into the global trend found by Keuskamp et al. (2013).

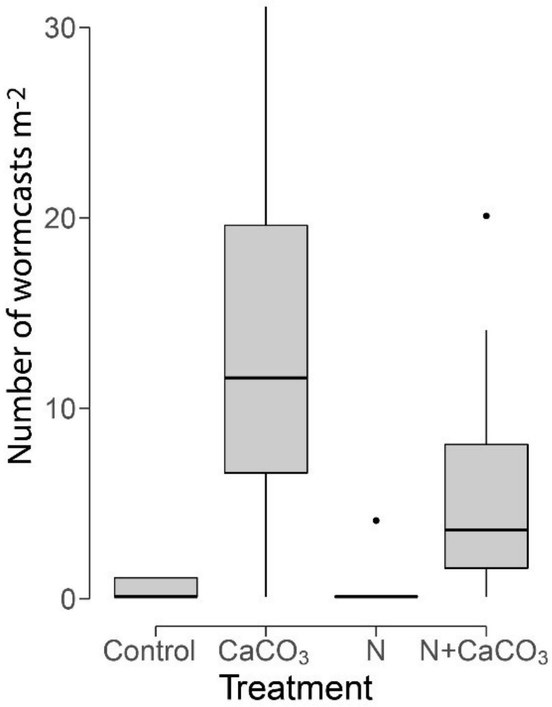

*Figure 6.4 Number of worm casts among the four treatments in the Kabili-Sepilok Forest Reserve heath forest in Sabah, Malaysia. The black bar represent the median value, first and third quartiles are at the top and bottom of the plot, respectively, and the maximum and minimum values excluding outliers are the whiskers. Dots indicate outliers.*

The stabilization factor *s* is expected to decrease with increasing precipitation and temperature and our results are in the range of lowland rain forest values (Djukic et al. 2018; Keuskamp et al. 2013) indicating a low long-term soil surface carbon storage. On the other hand, our decomposition rate (*k*) is rather slow and closer to temperate rather than tropical forest values highlighting the slow decomposition dynamics at our site. The confidence intervals of the *k* and *s* values are large partly because of the low number of samples we were able to include in the analysis after termites punctured the tea bags. Possibly, shorter incubations are necessary in tropical soils inhabited by termites. Alternatively, we advise the use of termite-resistant bags.

The decomposition constant *k* of local leaf litter also had overlapping confidence intervals among treatments so its rate of change following the treatments was not significant. Nonetheless, if we consider only the mean *k* values, N shows a positive trend of increasing leaf decay rate in line with other studies on N limited environments (Camenzind et al. 2018). Overall, our leaf litter *k* values were lower than reported in the literature for tropical heath forest (e.g. Anderson et al. 1983; Dent et al. 2006). Dent et al. (2006) undertook a litter decomposition experiment in a different location of the same Kabili-Sepilok Forest Reserve heath forest. In comparison to other studies (e.g. Dent et al. 2006), our study site is located on a more podsolized soil (Chapter 3) with a typical sandy texture (Andriesse 1975; Bravard and Righi 1988). A large amount of sand was found in our litterbags and this accumulation of sand may also have contributed to the final weight and thus biased the *k* value and making it lower than other studies.

Sand and $CaCO_3$ accumulation did not affect our wood decomposition experiments. Wood cubes had a slower decomposition rate than wood sticks. Generally, studies on wood decomposition use local wood which prevents clear comparison among studies, due to the differences in wood nutrient content and wood density among species (Weedon et al. 2009). Nonetheless, the mean wood stick decomposition rate in our control plot ($k = 0.52 \pm 0.37$ 95% CI) was in the range detected by Chambers et al. (2000) in Amazonia for large wood (minimum $k = 0.015$, maximum $k = 0.67$) as well as similar to the results of Anderson et al. (1983) for small ($k = 1$) and large ($k = 0.3$) wood in Gunung Mulu heath forest, Sarawak, Malaysia. The difference in decomposition rates between our large and small wood might be explained by two facts. Firstly, the wood used for the cubes (*Terminalia catappa*) has antifungal properties (Gandhi et al. 2015; Goun et al. 2003) but a similar wood density to *Betula pendula* (Chave et al. 2009), which is used for the sticks. Secondly, the wood cubes had a lower surface-to-mass ratio than the sticks. Decomposers start their process from the surface, thus a larger surface exposed to the primary attack leads to a faster decomposition rate (Winandy and Morrell 1992).

Wood cubes showed a statistically non-significant trend of an increasing decomposition rate with liming, and wood sticks had a statistically non-significant trend of an increasing decomposition rate after the N addition. Previous studies have shown that as soil pH increases, the bacteria-to-fungi ratio increases, suggesting that bacteria become relatively more abundant and outcompete fungi at higher pH (Baath and Andeson 2003). Soil fungi and gram+ (G+) bacteria rely on more recalcitrant organic matter with low nutrient content (Kramer and Gleixner 2008) such as wood. So, the trend of a faster rate of wood cube decomposition in the $CaCO_3$ treatment is possibly due to an increased G+ bacterial biomass in the soil. On the other hand, experimental N fertilization generally increases the abundance of fungi in relation to bacteria in rain forest soils (Fanin et al. 2015; Liu et al. 2013; Zhang et al. 2018) and also reduces the overall microbial biomass (Compton et al. 2004; Treseder 2008), but not all soil fungi react the same way. Morrison et al. (2018) showed that N fertilization favours yeasts (which have low importance for wood decomposition) but decreases the relative abundance of wood decomposing fungi. We speculate that the opposite response of wood sticks and wood cubes to N addition may therefore be due to the different response of yeasts and wood-decomposing fungi. In the N addition treatment *Terminalia catappa* wood showed a slower decomposition trend when compared to the controls because of a possible lower abundance of lignolytic fungi whereas *Betula pendula* wood sticks might have had a trend of faster decomposition in comparison to control wood sticks because of the hypothesised increased abundance of yeasts. However, this theory is not supported by the fungal CFU counting experiment, which, in contrast, sees no change (a non-significant increasing trend) in soil fungi with increased pH. If we only look at the mean values of variables of this study, heath forest organic matter decomposition appears to be limited by both nitrogen and soil pH. We cannot exclude, though, that other nutrients such as P might be limiting decomposition. From our findings, we can speculate that should human-induced N deposition increase, heath forest soil might experience an increased accumulation of less readily decomposable wood litter but a decrease in leaf litter due to a change in the microbial community, and this possibly applies for every heath forest, given the similarity of these forests' vegetation and soil. Nonetheless, clearer effects of the treatments on decomposition rate might be seen after a longer treatment time.

### 6.4.2 Mesofauna activity:

Along with microbes, meso- and macro- fauna also have a prominent role in soil organic matter decomposition process (Hattenschwiler et al. 2005; Henegan et al. 1999; Powers et al., 2009) grinding organic matter and redistributing nutrients through the soil (Tinsley and Darbyshire 1984). In the alluvial forest of the Kabili-Sepilok Forest Reserve, for instance, earthworms can process between 18 and 87 kg of soil $m^{-2}$ $yr^{-1}$ (Gould et al. 1987) and in Danum Valley (Sabah, Malaysia) the casts they produce contain twice the concentration of nitrate in comparison to the bulk soil (Johnson et al. 2012). In our study, overall mesofaunal activity was greater at higher soil pH with the addition of $CaCO_3$ and N+$CaCO_3$ for lamina baits and with the addition of only $CaCO_3$ for earthworms, whereas N did not have any effect on mesofaunal or earthworm activity. The literature reports contrasting results, detecting a positive (Jacquemin et al. 2012; Sayer 2006) and negative (Jandl et al. 2003) influence of nutrient inputs on arthropod abundance. This highlights that any change in soil fauna in response to fertilization depends upon the initial soil nutrient status (Wang et al. 2016). On the other hand, other studies detected increased activity and abundance of earthworms after soil liming (Moore et al. 2013; Potthoff et al. 2008). This might be due to the increased availability of earthworm's nutrient sources, which are bacteria. Interestingly, the increase in worm casts seen in our plots happened straight after the $CaCO_3$ addition and declined within a couple of months, indicating a transient response to the treatments despite a continued increase in soil pH during the experiment.

In agreement with Luizao (1994), we propose an important role of soil acidity shaping this rare forest typology due to its negative effect on decomposition through controlling mesofaunal activity, and thus nutrient mobility. We can foresee that the expected increase in human induced atmospheric N deposition (Phoenix et al. 2006) will have detrimental effects on this forest type. Nitrogen addition rates as moderate as ours significantly decreased a deeply weathered Chinese tropical soil pH (Lu et al. 2014). Furthermore, in our N treatment plots soil leachate was more acidic than the control plots after only one year of treatment (Chapter 4). We also believe that the trend in our results suggest increased N deposition could produce a shift in the decomposer community, hampering the decay of recalcitrant woody debris, and leading to an accumulation of organic substance on the forest floor and locking-up considerable amounts of nutrients. Despite the scattered distribution and low productivity of tropical heath forests, their biodiversity value and fragile nutrient dynamics need further studies.

## 6.5 Conclusion:

With our study, we asked whether soil pH or soil N availability affects the decomposition of organic matter in a nutrient-poor tropical heath forest. Throughout our experimental work, we found several problems in carrying out the experiments as described above such as the sandy nature of the soil, undissolved $CaCO_3$ sticking to leaves and termite activity that potentially resulted in the large confidence intervals and few statistically significant results. Taking into account only the mean values of the results, overall, we found a stronger trend in the effect of soil pH than soil N on the decomposition of large wood. The N treatment increased only small wood decomposition and hampered large wood decomposition. Also earthworm (primarily) and soil fauna activity (secondarily) were stimulated by liming. We suspect that the responses of decomposition to the fertilizer treatments is mediated by a change in the microbial community. However, no statistically significant results were found from the fungi CFU counts. From the literature we know that heath forests in Brunei have a higher soil fungal diversity but a similar bacterial diversity when compared to mixed dipterocarp forest soil (Tripathi et al. 2016), but no data is available on absolute abundance, functional strategies (e.g. yeasts *vs.* white rot fungi) or fungi-to-bacteria ratios. Thus, to advance our understanding about drivers of organic matter decomposition and its effect on soil biotic community, we need to apply metabarcoding techniques to detect fine-scale changes in bacterial and fungal community composition among our experimentally-treated heath forest spodosol plots. If the expected increase in N deposition will occur in our study area we might expect a shift in the decomposer community. Another useful approach would be to construct the litterbags with thin mesh that would avoid infiltration of powdered $CaCO_3$ although this might exclude also mesofauna.

# 7 General conclusions.

Tropical heath forests are characterised by trees with stunted physiognomy (Davies and Becker 1996; Miyamoto et al. 1997; Miyamoto et al. 2007; Proctor et al. 1983) growing on acidic and nutrient poor soil (Herrera et al. 1978; Tanaka et al. 2013; Richards 1936). Heath forests occupy only a small area of the forested tropics, but are spread throughout all tropical regions (Adeney et al. 2016; Anderson 1981; Proctor 1999; Whitmore 1984) and sustain great floral (Anderson 1981; Garcia et al. 2016; Kartawinata 1980; Low et al. 2016; Ong et al. 1998; Wood 1984), faunal (Borges et al. 2016; Woxvold and Noske 2011) and fungal (Roy et al. 2016) biodiversity. Tropical heath forests also store high amounts of belowground C (Montes et al. 2011). Despite the important role of this unique forest formation for rain forest C storage and biodiversity, it remains unresolved whether soil acidity (Luizao et al. 2007; Proctor et al. 1983; Proctor 1999; Vernimmen et al. 2013; Whitmore 1984) or low soil N availability (Brearley et al. 2011; Dent et al. 2006; Moran et al. 2000) influences the development of these forests and/or limits their primary productivity.

The economic development of countries in tropical areas is leading to local increases in N emissions - mainly from agriculture (Bowman et al. 1997; Galloway et al. 2004; Sutton et al. 2015) and biomass burning (Andreae et al. 1988; Curtzen and Andreae 1990; Lobert et al. 1990; Bauters et al. 2018). Consequently, this is increasing the rate of local N deposition (Chen et al. 2012; Dentener et al. 2006; Matson et al. 1999; Reay et al 2008), which reduces the competitive ability of low soil N-adapted plant species, leading to documented declines in plant biodiversity in temperate regions (Bobbink et al 2010; Phoenix et al. 2006; Matson et al. 2002; Midolo et al. 2018; Stevens et al. 2004). Nitrogen deposition can also acidify the soil in non N-limited environments (Duan et al. 2016; Lu et al. 2014; Matson et al. 2002; Matson et al. 1999). Nonetheless, when compared to temperate areas, just a few studies have characterised the atmospheric N input, deposition and effects on ecosystems in the tropics (Chen et al.

2010; Duan et al. 2016; Lu et al. 2010; Lu et al. 2014; Matson et al. 2009; Phoenix et al. 2006).

Given the uncertainty regarding the abiotic controls of tropical heath forests' species distribution and productivity, and the increasing human-induced modification to N cycles in tropical areas, it is fundamental to gain insights into heath forests' ecological responses to increased N availability. Such insights will ultimately provide policy makers with evidence-based information, allowing the development of conservation strategies as well as management of tropical heath forests.

With this research, I recorded the amount of wet inorganic N deposition in a Malaysian site located nearby the pristine Kabili-Sepilok Forest Reserve (KSFR; Sabah, Malaysia) and characterised the influence of edaphic and topographic factors on a KSFR heath forest's species distribution and structure. Furthermore, I assessed the sensitivity of this forest's primary productivity, soil nutrient dynamics, organic matter decomposition rate and leaf stoichiometry to increased soil N availability and soil pH by setting up a factorial N and $CaCO_3$ addition experiment.

At the start of my study, I collected evidence that tree species distribution, diversity and stand structure of this heath forest are influenced by both soil characteristics and forest topography. Nonetheless, among the edaphic characteristics, available Al was the factor that most correlated with species distributions (Chapter 3). The importance of soil available Al in shaping floristic associations is still debated among researchers and is likely to vary among sites. Aluminium was found as important as N, P and other nutrients on influencing species distributions in central and South American rain forests (John et al. 2007), but was much less important in comparison to soil P when restricting the analysis to lowland rain forests in Panama (Condit et al. 2013) or when comparing rain forests in different continents (Baldeck et al. 2012). My results support the hypothesis of Proctor (1999) who proposed heath forest productivity is limited by soil acidity ($H^+$ + Al). The $H^+$ ion is extremely toxic to plants and $H^+$ toxicity is prominent where soil lacks the buffering activity of Al, as it is the case in extremely weathered spodosols developed on Al-poor sandstone. In these heath forest soils, plant roots limit the absorption of nutrients to avoid the co-transport of toxic $H^+$ ions (Proctor 1999; Luizao et al. 2007; Vernimmen et al. 2013). Interestingly, I found the most common tree species in my plots (*Gaertnera junghuhniana*; Chapter 3) to be an aluminium accumulator (Chapter 5). Aluminium accumulation have been proposed to develop as a response to Al toxicity (Jansen et al. 2002) especially in tropical soils where Al is frequently abundant (Haridasan 1982; Metali et al. 2012, 2014). Nonetheless, the striking ubiquity of this Al accumulating species in my plots along with the low amount of available aluminium and the high H:Al ratio in my plots' soil allows me to propose a new hypothesis explaining Al accumulation. Accumulation of Al allowes *Gaertnera junghuhniana* to ameliorate soil $H^+$ toxicity through leaf abscission of high Al material, which increases soil available Al.

Following the fertilisation experiment, trees had a clear and significant increase in DBH relative growth rate only in the N addition plots, whereas the plots with added $CaCO_3$ and N+$CaCO_3$ the growth rate was not statistically different from the control plots (although there was a non-significant trend of increased growth rate in the N+$CaCO_3$ plots; Chapter 4). The change in leaf stoichiometry showed the same pattern, with an increase in leaf N concentration and a decrease in the leaf C:N ratio in 10 focal species being significant in the N treatment and having a non-significant similar trend in the N+$CaCO_3$ plot (Chapter 5) highlighting the N-limited status of heath forest trees. Although the addition of N should have increased soil $H^+$ (as seen in both tropical and temperate forest environment; Matson et al. 1999; Matson et al. 2002) decreasing the uptake of available N, this was not observed, possibly due to the small amount of N added, or to the quick eluviation of the newly freed $NH_4^+$-derived protons. Furthermore, in Chapter 4, I showed that the addition of $CaCO_3$ induced a decrease in soil Al concentration. This explains why the DBH growth rate and leaf stoichiometry did not change after the N+$CaCO_3$ addition because ubiquitous Al decrease after $CaCO_3$ addition increased the H:Al ratio in the soil, further hampering root uptake of N despite it being added with the fertiliser.

I also calculated the plots' above ground biomass (AGB) of trees > 5 cm DBH before the treatments and projected how AGB would vary after one year of growth in two scenarios: one with N deposition and one without N deposition. I calculated aboveground biomass for all the censused trees with the equation of Chave et al. (2014) which requires trees' wood density (WD), tree height (H) and tree DBH. I used the same WD from the literature cited in Chapter 4 for the 27 most abundant tree species in my plots, and used a weighted mean of WD for the rare species. I derived H for all the censused trees using an allometric scaling among tree H and DBH following the formula: $H \sim \alpha\ DBH^{\beta}$, where α is the allometric constant and β is the scaling exponent. For this calculation, I used tree height data of a subset of trees from my plots (Chapter 4). I then simulated one year of DBH growth without N deposition by applying to all individuals > 5 cm DBH the mean size-class annual DBH relative growth rates derived from the control plots (Chapter 4). I re-calculated all the individuals' H from the new "grown" DBHs using the same α and β parameters as described above and, subsequently, the AGB across all the plots. For the N deposition scenario, I applied the annual relative growth rate derived from the N treated plots to the trees 5-10 cm DBH, whereas I applied the same control plots' DBH relative growth rate for the trees > 10 cm DBH (as they were not significantly different). Then I calculated H and AGB for this N deposition scenario. The AGB of trees > 5 cm DBH before the treatments was 377.2 Mg ha$^{-1}$, which is similar to AGB estimates from other Bornean heath forests (Budiharta et al. 2014; Proctor et al. 1983; Miyamoto et al. 2015). The AGB production after one year of growth in the N deposition scenario (9.1 Mg ha$^{-1}$) was around 5 % greater than the one in non-deposition scenario (8.7 Mg ha$^{-1}$) depicting a difference in AGB production of 446 kg ha$^{-1}$ yr$^{-1}$ under N deposition. It has to be noted that this is just a rough calculation, as I did not include tree mortality, and this will have an impact on the estimate of AGB as N-depositionmay increase the rate of tree mortality in N limited systems (Ibanez et al. 2016; Wallace et al 2007). Nonetheless, other fertilisation experiments confirmed that N deposition induced an increase in productivity in allegedly N poor tropical montane forests (Tanner et al. 1998; Homeier et al. 2012) as well as in temperate forests (LeBauer and Treseder 2008; Matson et al. 2002). At temperate latitudes, increasing tree growth rates after N addition are suggested to be only temporary as, over the long term, tree growth (Emmet 1999; Matson 1999) and biodiversity (Midolo et al. 2018) declined due to soil acidification and cation losses (Bobbink et al. 2010; Matson et al. 2002). Although lowland rain forests already cycle high amounts of N, experimental N additions showed tree growth to increase after fertilization (see the review by Wright et al. 2018). Nonetheless, low N deposition readily induces N saturation in lowland evergreen rain forest (i.e. when N is not absorbed by living biomass), possibly resulting in a faster – if compared to temperate soils – soil acidification (Lu et al. 2014; Lu et al. 2018) and species loss (Lu et al. 2010; Matson et al. 1999). Due to the N poor nutrient status of the Kabili-Sepilok heath forest soil, I speculate that, similarly to temperate forests, a decrease in biodiversity and AGB is likely after an increase and long-term N deposition. Nonetheless, the species rich nature of this heath forest (compared to temperate forests) drives the coexistence of a wide range of functional strategies within the same system. This, over the long term, will allow me to identify different responses of species with contrasting functional strategies to N deposition, leading to intriguing predictions on biodiversity changes under N deposition. Heath forest sensitivity to N deposition has become clear both from DBH growth rate as well as fresh leaf nutrient concentration. Nonetheless, the effect on species composition was not clear, as both species with acquisitive and conservative functional strategies responded strongly to the two years of moderate N addition (Chapters 4 and 5). I suspect, though, that with longer spans of N addition it will lead to a differential response of species with different functional strategies (Sayer and Banin 2016), shifting competitive success of low N-adapted plants and eventually leading to changes in species distribution and, potentially, biodiversity loss (Bobbink et al. 2010). On the other hand, my results indicate that this heath forest is unlikely to undergo N saturation due to N deposition over the short term. This highlights the value of small projects like the one undertaken in this thesis to understand the ecology of forests and the responses of tropical tree species composition to human induced N deposition.

From my experiment, it remains unclear how soil C stocks will change under N deposition. The effects of N deposition on decomposition are contrasting, as some studies support the hypothesis of N limitation of microbial activity in N poor environments (e.g. montane rain forests; see the review of Camenzind et al. 2018) but, conversely, some other studies find negative effects of N deposition on microbial abundance and respiration in temperate zones (Janssens et al. 2010) and at a global scales (Zhang et al. 2018). From the (non-significant) decline of soil C:N and soil total C concentration in N treatment plots (Chapter 4), I could speculate that N deposition will decrease soil C storage in this heath forest. Nonetheless, the results obtained from my decomposition experiments (Chapter 6) are not clear and prevent me from the formulating any new hypotheses. Given the important amounts of C stored in heath forests soil (Montes et al. 2011), more detailed studies are needed to understand the influence of N deposition on microbial activity and soil C storage.

I did not obtain significant changes in decomposition rates following the treatments, possibly due to experimental biases (Chapter 6), although the addition of $CaCO_3$ decreased the amount of total P and C in soil (Chapter 4), suggesting an effect of acidity on organic matter mineralisation. Other experiments are needed to provide information about the role of soil N availability and soil acidity in heath forests' organic matter decomposition, such as a comparison of soil respiration rates among treatments, incubation experiments to assess nitrification, and denitrification rates, and tracing of marked isotopic N.

From this work, I also suggested the possibility that forest productivity is limited by a) low soil P, due to the response of leaf N:P ratio (Chapter 5) along with a decrease in soil available P after N addition (Chapter 4) and b) low soil Fe, due to its general decrease in soil and soil leachate after the treatments (indicating uptake by the trees) with consequent increase in fresh leaves (Chapter 5). Nonetheless, Fe concentration also increased in leaf litterfall (Chapter 4) indicating that Fe was not resorbed from the leaves by the tree before leaf abscission, suggesting that Fe limitation was only transitory or of marginal importance. Both P and Fe are limiting for other ecosystems, such as lowland rain forests in the case of P (Porder et al. 2007) and oceans in the case of Fe (Behrenfeld et al. 1996). Despite the general idea of heath forests being limited by soil N, my results on nutrient co- limitation are supported by recent studies reporting KSFR heath forest trees' high P use efficiency (Dent et al. 2006) and Bruneian heath forest's microbial communities being rich in genes associated with Fe acquisition (Kerfahi et al. 2019). This supports the views of Kaspari et al. (2008), Kaspari and Powers (2016) and Wright et al. (2018) who stated that equatorial forests are actually limited by multiple soil elements rather than just soil P, and broaden this hypothesis to tropical heath forests as we show that different forest ecosystem processes respond differentially to N and lime. In view of a potential heath forest nutrient co-limitation, it is likely that increased N deposition might shift the limitation of forest productivity from N to P or Fe. I thus point out the need for more holistic approaches to study nutrient limitation in forest systems, with further experiments testing a wider set of nutrients. Micro- and macro-nutrient limitation on tree growth has usually been tested by adding nutrients to pot-grown seedlings in shaded greenhouses (e.g. Burslem et al. 1995; Hall et al. 2003) or testing root mass production inside vermiculite bags imbibed with different nutrients and inserted in forest soil (Cuevas and Medina 1988). Despite the valuable aspects of nutrient limitation bioassays on seedlings or with nutrient-imbibed bags (these are non-expensive experiments that quickly deliver results), I argue that species' plasticity in nutrient investment under different conditions (e.g. different light competition, as seen in Chapter 4) might bias the results of pot bioassays. Furthermore, the vermiculite bag approach might be biased by microsite soil characteristics and by the species composition of trees directly surrounding the bag. This would eventually hamper the holistic view that one could obtain by using nutrient addition in small forest plots.

To deepen the understanding of N deposition effects on this rare forest's C stock, other further experiments are needed. Changes in trees' belowground carbon investment, for example, might be assessed measuring root biomass, whereas the characterisation of microbial functional groups by metagenetic screening could allow to infer microbial nutrient limitations (e.g. Kerfahi et al. 2019). The effect of treatments on organic matter decomposition might be assessed by measuring soil respiration. Another fundamental line of research is to assess N mineralisation and nitrification rates, and N loss in the form of $N_2O$ emissions after fertilisation.

Although this heath forest cannot be representative for all heath forests of Southeast Asia, Africa and South America it presents a novel contribution by being the first experiment of its kind in this forest formation, as previous fertilisation experiments have been conducted in lowland evergreen rain forest, montane forest or secondary forest (Wright et al. 2018). Furthermore, this study has produced a significant contribution by characterising the high sensitivity of this forest type to changes in soil N availability. This, along with the high amount of wet inorganic N deposition measured in our study site (Chapter 2), highlights the need to reduce atmospheric N input, at least in Sabah. If our results are confirmed by further N fertilisation experiments in other heath forests, it will be necessary to regulate the use of N fertiliser throughout tropical areas to preserve this spectacular and rare forest type.

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# 9 Supplementary informations:

*Supplementary Table 1: Soil chemical characteristics of the Kabili-Sepilok heath forest after our four experimental treatments. Soil chemical values reported here for each treatment at any time point are means of 16 samples, collected in four plot replicates.*

| Treatment | Date | Av.Ca | Av.Cu | Av.Fe | Av.K | Av.Mg | Av.Na | C | N | C:N |
|---|---|---|---|---|---|---|---|---|---|---|
| | | µg g$^{-1}$ | | | | | | % | % | |
| Control | Apr-16 | 69.23(±21.38) | 0.04(±0.01) | 19.67(±2.08) | 74.67(±10.42) | 83.14(±17.87) | 19.59(±3.76) | 5.2(±0.7) | 0.21(±0.03) | 25.3(±0.98) |
| Control | Feb-17 | 30.91(±5.98) | 0.05(±0.02) | 12.3(±1.43) | 26.05(±2.83) | 28.88(±4.15) | 12.47(±1.49) | 2.15(±0.23) | 0.07(±0.01) | 33.99(±2.99) |
| Control | Jul-17 | 12.15(±3.41) | 0.07(±0.02) | 11(±2.38) | 24.55(±3.26) | 19.1(±2.43) | 4.66(±1.19) | 2.04(±0.18) | 0.09(±0.01) | 25.96(±2.68) |
| CaCO3 | Apr-16 | 50.42(±15.72) | 0.06(±0.01) | 24.12(±3.43) | 57.3(±8.93) | 70.86(±19.48) | 21.62(±4.95) | 7.1(±1.38) | 0.73(±0.27) | 20.84(±2.42) |
| CaCO3 | Feb-17 | 204.95(±49.24) | 0.08(±0.03) | 15.53(±2.44) | 28.53(±5.97) | 34.32(±6.17) | 13.74(±2.4) | 2.53(±0.34) | 0.08(±0.01) | 34.18(±2.43) |
| CaCO3 | Jul-17 | 190.04(±33) | 0.08(±0.02) | 11.06(±1.77) | 19.4(±1.58) | 25.21(±3.81) | 9.01(±2.57) | 1.62(±0.11) | 0.08(±0.01) | 21.05(±1.25) |
| N | Apr-16 | 31.95(±12.72) | 0.06(±0.01) | 27.69(±4.97) | 69.97(±8.67) | 82.68(±24.34) | 19.79(±5.92) | 7.54(±1.16) | 0.32(±0.05) | 23.88(±1.15) |
| N | Feb-17 | 48.67(±4.27) | 0.13(±0.02) | 14.64(±1.9) | 33.4(±5.53) | 46.24(±8.47) | 18.11(±1.91) | 2.93(±0.34) | 0.11(±0.01) | 29.03(±1.85) |
| N | Jul-17 | 26.57(±6.41) | 0.04(±0.01) | 13.09(±1.36) | 27.1(±3.02) | 31.69(±4.83) | 8.33(±1.91) | 2.84(±0.34) | 0.13(±0.02) | 22.77(±1.2) |
| N+CaCO3 | Apr-16 | 67.08(±19.77) | 0.05(±0.01) | 35.03(±3.53) | 62.54(±5.46) | 83.51(±13.59) | 18.1(±4.85) | 6.46(±0.61) | 0.48(±0.2) | 21.8(±1.75) |
| N+CaCO3 | Feb-17 | 220.92(±36.68) | 0.04(±0.01) | 12.33(±1.25) | 21.74(±2.54) | 31.56(±4.69) | 10.56(±1.66) | 2.13(±0.23) | 0.07(±0.01) | 36.89(±5.47) |
| N+CaCO3 | Jul-17 | 294.21(±44.58) | 0.03(±0.01) | 11.09(±0.91) | 26.07(±5.76) | 29.54(±3.3) | 8.88(±1.87) | 2.02(±0.19) | 0.09(±0.01) | 21.92(±1.44) |

*Supplementary Table 1 continued*

| Treatment | Date | CEC | Exc.Acidity | Exc.Al | H:Al | Tot.Ca | Tot.Cu | Tot.Fe | Tot.K |
|---|---|---|---|---|---|---|---|---|---|
| | | cmol$_c$ kg$^{-1}$ | cmol$_c$ kg$^{-1}$ | cmol$_c$ kg$^{-1}$ | | μg g$^{-1}$ | | | |
| Control | Apr-16 | 1.67(±0.24) | 0.98(±0.13) | 0.38(±0.07) | 6.03(±0.79) | 72.85(±10.57) | 0.32(±0.05) | 68.55(±9.08) | 25.31(±3.14) |
| Control | Feb-17 | 0.61(±0.07) | 0.7(±0.08) | 0.1(±0.02) | 7.47(±0.79) | 93.89(±11.7) | 0.89(±0.16) | 55.3(±9.9) | 19.73(±3.17) |
| Control | Jul-17 | 0.4(±0.06) | 0.77(±0.06) | 0.1(±0.02) | 9.84(±1.59) | 56.47(±6.69) | 0.98(±0.13) | 49.91(±9.8) | 25.87(±3.26) |
| CaCO3 | Apr-16 | 1.6(±0.29) | 1.27(±0.18) | 0.52(±0.07) | 4.46(±0.52) | 59.21(±6.69) | 0.38(±0.08) | 91.33(±13.26) | 26.64(±3.67) |
| CaCO3 | Feb-17 | 1.54(±0.28) | 0.45(±0.08) | 0.09(±0.02) | 6.77(±1.25) | 235.94(±49.39) | 0.9(±0.16) | 86.03(±16.07) | 22.46(±3.2) |
| CaCO3 | Jul-17 | 1.29(±0.18) | 0.37(±0.04) | 0.04(±0.01) | 22.55(±5.99) | 185.38(±24.81) | 0.62(±0.08) | 53.16(±7.9) | 20.06(±2.7) |
| N | Apr-16 | 1.53(±0.29) | 1.34(±0.23) | 0.48(±0.07) | 4.57(±0.3) | 82.97(±12.47) | 0.38(±0.07) | 96.59(±14.82) | 31.41(±4.33) |
| N | Feb-17 | 0.95(±0.12) | 0.92(±0.11) | 0.16(±0.03) | 6.55(±0.79) | 106.97(±8.47) | 1.17(±0.11) | 66.63(±9.33) | 34.71(±5.1) |
| N | Jul-17 | 0.67(±0.11) | 0.94(±0.11) | 0.17(±0.04) | 5.98(±0.53) | 44.74(±8.64) | 0.73(±0.17) | 61.16(±13.7) | 25.48(±3.91) |
| N+CaCO3 | Apr-16 | 1.91(±0.23) | 1.33(±0.12) | 0.68(±0.09) | 3.47(±0.4) | 74.81(±9.3) | 0.37(±0.03) | 132.63(±17.16) | 27.97(±2.88) |
| N+CaCO3 | Feb-17 | 1.52(±0.23) | 0.39(±0.04) | 0.05(±0.02) | 21.33(±8.2) | 309.74(±50.88) | 1.04(±0.17) | 63.18(±7.55) | 26.59(±3.79) |
| N+CaCO3 | Jul-17 | 1.85(±0.24) | 0.36(±0.04) | 0.02(±0.01) | 538.83(±503.95) | 268.19(±36.86) | 0.85(±0.12) | 57.29(±4.45) | 21.63(±2.04) |

*Supplementary Table 1 continued*

| Treatment | Date | Tot.Mg | Tot.Mn | Tot.Na | Tot.Al | Tot.Ni | Tot.P | Av.P | Tot.S |
|---|---|---|---|---|---|---|---|---|---|
| | | µg g$^{-1}$ | | | | | | | |
| Control | Apr-16 | 34.93(±6.67) | 1.28(±0.47) | 11.43(±1.2) | 92.58(±11.88) | 0.2(±0.04) | 24.53(±3.47) | 13.95(±2.94) | 82.35(±11.55) |
| Control | Feb-17 | 33.54(±2.78) | 0.53(±0.07) | 21.96(±2.22) | 184.92(±14.37) | 0.16(±0.02) | 24.66(±1.84) | 16.39(±1.75) | 81.24(±7.68) |
| Control | Jul-17 | 21.83(±2.26) | 0.38(±0.05) | 11.1(±1.93) | 210.75(±12.87) | 0.22(±0.03) | 24.43(±1.96) | 13.82(±1.47) | 78.83(±8.16) |
| CaCO3 | Apr-16 | 41.55(±9.81) | 0.74(±0.11) | 10.77(±2.52) | 137.63(±27.93) | 0.33(±0.12) | 23.92(±2.51) | 13.27(±1.53) | 101.42(±14.67) |
| CaCO3 | Feb-17 | 40.98(±6.74) | 0.51(±0.09) | 18.57(±3.08) | 169.66(±19.55) | 0.69(±0.46) | 24.31(±2.4) | 12.01(±1.24) | 92.69(±9.15) |
| CaCO3 | Jul-17 | 26.29(±2.93) | 0.32(±0.04) | 14.91(±3.53) | 204.03(±16.36) | 0.17(±0.04) | 17.7(±1.32) | 11.75(±0.97) | 60.45(±2.68) |
| N | Apr-16 | 48.18(±10.53) | 1.27(±0.35) | 13.14(±2.89) | 112.81(±15.16) | 0.24(±0.05) | 29.14(±3.38) | 14.88(±2.25) | 111.9(±14.87) |
| N | Feb-17 | 42.28(±5.25) | 0.67(±0.14) | 17.61(±1.9) | 155.18(±14.98) | 0.2(±0.03) | 28.98(±2.58) | 11.48(±1.88) | 117.82(±11.7) |
| N | Jul-17 | 26.48(±3.9) | 0.42(±0.08) | 11.78(±2.2) | 192.71(±22.12) | 0.18(±0.04) | 26.1(±2.25) | 7.32(±1.02) | 93.61(±9.88) |
| N+CaCO3 | Apr-16 | 42.06(±5.64) | 1.1(±0.28) | 17.07(±2.46) | 152.59(±14.99) | 0.26(±0.03) | 27.3(±2.65) | 14.16(±1.9) | 99.9(±8.53) |
| N+CaCO3 | Feb-17 | 44.52(±6.45) | 0.59(±0.11) | 19.85(±2.71) | 182.79(±15.85) | 0.26(±0.05) | 24.86(±3.03) | 17.98(±1.69) | 93.33(±9.1) |
| N+CaCO3 | Jul-17 | 30.06(±2.69) | 0.43(±0.06) | 13.92(±2.66) | 163.68(±17.16) | 0.27(±0.05) | 20.32(±2.04) | 15.67(±1.39) | 70.65(±4.45) |

*Supplementary Table 1 continued*

| Treatment | Month | $NH_4^+$ | $NO_3^-$ | pH |
|---|---|---|---|---|
| | | μg $g^{-1}$ | μg $g^{-1}$ | |
| Control | Apr-16 | 6.57(±1.74) | 0.26(±0.16) | 3.82(±0.08) |
| Control | Feb-17 | 5.98(±0.53) | 0.17(±0.03) | 4.74(±0.06) |
| Control | Jul-17 | 5.75(±0.66) | 0.18(±0.05) | 4.01(±0.05) |
| Control | Dec-17 | 3.59(±0.49) | 0.31(±0.04) | 4.08(±0.04) |
| Control | Jun-18 | | | 4.11(±0.04) |
| CaCO3 | Apr-16 | 8.14(±0.79) | 0.39(±0.17) | 3.68(±0.06) |
| CaCO3 | Feb-17 | 5.37(±0.8) | 0.1(±0.07) | 5.04(±0.12) |
| CaCO3 | Jul-17 | 6.41(±2.05) | 0.22(±0.11) | 4.75(±0.1) |
| CaCO3 | Dec-17 | 2.84(±0.91) | 0.66(±0.17) | 5.46(±0.22) |
| CaCO3 | Jun-18 | | | 4.81(±0.1) |
| N | Apr-16 | 8.06(±2.23) | 1.05(±0.36) | 3.66(±0.05) |
| N | Feb-17 | 7.66(±1.26) | 0.24(±0.11) | 4.62(±0.06) |
| N | Jul-17 | 4.47(±0.56) | 0.11(±0.04) | 4.03(±0.04) |
| N | Dec-17 | 3.92(±1.53) | 0.66(±0.33) | 3.92(±0.06) |
| N | Jun-18 | | | 4.00(±0.02) |
| N+CaCO3 | Apr-16 | 10.89(±3.4) | 0.66(±0.19) | 3.67(±0.05) |
| N+CaCO3 | Feb-17 | 7.55(±1.54) | 0.23(±0.09) | 5.12(±0.13) |
| N+CaCO3 | Jul-17 | 3.35(±1.19) | 0.13(±0.07) | 4.91(±0.14) |
| N+CaCO3 | Dec-17 | 1.64(±0.95) | 0.61(±0.27) | 5.51(±0.22) |

*Supplementary Table 2: Chemical characteristics of the leaf litterfall collected in the Kabili-Sepilok heath forest after our four experimental treatments throughout one year. Values are means (± SE) of our four replicate plots for each treatment.*

| Treatment | Date | P | Ca | K | Mg | Na | N | C | C:N |
|---|---|---|---|---|---|---|---|---|---|
| | | mg $g^{-1}$ | | | | | % | % | |
| Control | Sep-16 | 0.18(±0.01) | 5.31(±0.52) | 1.88(±0.2) | 2.26(±0.51) | 0.14(±0.09) | 0.87(±0.05) | 47.31(±0.26) | 54.93(±3.52) |
| Control | Oct-16 | 0.2(±0.02) | 5.05(±0.52) | 1.79(±0.26) | 1.93(±0.36) | 0.15(±0.09) | 0.85(±0.04) | 47.22(±0.15) | 56.14(±3.21) |
| Control | Nov-16 | 0.18(±0.04) | 5.91(±0.24) | 1.11(±0.08) | 2.69(±0.67) | 0.2(±0.1) | 0.74(±0.09) | 48.76(±0.33) | 68.42(±7.23) |
| Control | Aug-16 | 0.18(±0.01) | 5.06(±0.3) | 1.76(±0.2) | 1.97(±0.41) | 0.14(±0.1) | 0.79(±0.04) | 47.68(±0.31) | 60.93(±3.73) |
| Control | Dec-16 | 0.16(±0.01) | 5.59(±0.98) | 1.2(±0.06) | 2.22(±0.34) | 0.2(±0.04) | 0.76(±0.06) | 49.51(±0.51) | 66.4(±5.07) |
| Control | Jan-17 | 0.18(±0.02) | 5.45(±0.4) | 0.99(±0.15) | 1.65(±0.21) | 0.14(±0.05) | 0.8(±0.04) | 49.56(±0.44) | 62.53(±3.75) |
| Control | Feb-17 | 0.2(±0.02) | 5.23(±0.49) | 1.26(±0.22) | 1.71(±0.28) | 0.13(±0.02) | 0.8(±0.04) | 49.86(±0.41) | 63.13(±3.23) |
| Control | Mar-17 | 0.19(±0.02) | 5.14(±0.33) | 1.71(±0.13) | 2.05(±0.28) | 0.14(±0.01) | 0.76(±0.05) | 49.11(±0.27) | 65.35(±4.72) |
| Control | Apr-17 | 0.19(±0.03) | 5.17(±0.33) | 1.8(±0.15) | 2.22(±0.36) | 0.11(±0.02) | 0.86(±0.07) | 48.76(±0.39) | 57.56(±4.1) |
| Control | May-17 | 0.16(±0.02) | 5.2(±0.26) | 1.33(±0.12) | 1.83(±0.26) | 0.1(±0.02) | 0.72(±0.03) | 49.83(±0.32) | 69.56(±2.43) |
| Control | Jun-17 | 0.17(±0.01) | 5.94(±0.57) | 1.76(±0.08) | 2.23(±0.41) | 0.11(±0.02) | 0.75(±0.04) | 49.68(±0.21) | 66.64(±3.7) |
| Control | Jul-17 | 0.17(±0.01) | 5.31(±0.58) | 1.5(±0.12) | 2.03(±0.34) | 0.17(±0.07) | 0.82(±0.03) | 49.48(±0.38) | 60.31(±2.08) |
| Control | Aug-17 | 0.19(±0.01) | 6.21(±0.62) | 1.41(±0.16) | 2.34(±0.27) | 0.11(±0.02) | 0.85(±0.04) | 50.02(±0.37) | 58.94(±2.33) |
| CaCO3 | Sep-16 | 0.18(±0.02) | 4.54(±0.57) | 1.58(±0.22) | 1.76(±0.17) | 0.09(±0.06) | 0.85(±0.1) | 46.94(±0.5) | 57.84(±6.75) |
| CaCO3 | Oct-16 | 0.17(±0.03) | 4.95(±0.64) | 1.35(±0.2) | 2.22(±0.14) | 0.35(±0.16) | 0.86(±0.12) | 47.19(±0.57) | 58.61(±9.11) |
| CaCO3 | Nov-16 | 0.18(±0.02) | 5.28(±0.84) | 1.18(±0.13) | 2.26(±0.27) | 0.23(±0.02) | 0.72(±0.07) | 48.77(±0.69) | 69.48(±7.31) |
| CaCO3 | Aug-16 | 0.15(±0.02) | 4.46(±0.69) | 1.38(±0.1) | 1.83(±0.12) | 0.26(±0.13) | 0.8(±0.11) | 47.39(±0.64) | 63.1(±8.34) |
| CaCO3 | Dec-16 | 0.17(±0.02) | 5.76(±0.5) | 1.28(±0.19) | 2.15(±0.38) | 0.19(±0.07) | 0.71(±0.09) | 48.45(±0.65) | 71.77(±9.1) |
| CaCO3 | Jan-17 | 0.15(±0.02) | 5.62(±0.89) | 0.78(±0.1) | 1.8(±0.25) | 0.22(±0.03) | 0.8(±0.05) | 48.92(±0.8) | 62.22(±4.02) |

*Supplementary Table 2 continued*

| Treatment | Date | P | Ca | K | Mg | Na | N | C | C:N |
|---|---|---|---|---|---|---|---|---|---|
| | | | | mg g$^{-1}$ | | | | % | |
| CaCO3 | Feb-17 | 0.18(±0.01) | 7.31(±0.4) | 0.96(±0.12) | 1.99(±0.19) | 0.22(±0.04) | 0.75(±0.07) | 48.7(±0.91) | 66.64(±6.23) |
| CaCO3 | Mar-17 | 0.13(±0.02) | 5.48(±0.82) | 1.17(±0.16) | 1.88(±0.1) | 0.23(±0.08) | 0.73(±0.08) | 48.29(±0.66) | 68.51(±7.37) |
| CaCO3 | Apr-17 | 0.15(±0.01) | 5.87(±0.66) | 1.2(±0.15) | 2.36(±0.16) | 0.31(±0.11) | 0.8(±0.09) | 48.12(±0.64) | 62.29(±6.44) |
| CaCO3 | May-17 | 0.16(±0) | 6.73(±0.32) | 0.94(±0.06) | 2.55(±0.32) | 0.24(±0.05) | 0.73(±0.06) | 48.71(±0.73) | 68.34(±5.71) |
| CaCO3 | Jun-17 | 0.15(±0.01) | 6.48(±0.65) | 1.09(±0.08) | 2.46(±0.25) | 0.36(±0.06) | 0.78(±0.08) | 48.27(±0.89) | 63.68(±6.7) |
| CaCO3 | Jul-17 | 0.18(±0.02) | 6.89(±0.71) | 1.33(±0.17) | 2.4(±0.28) | 0.22(±0.06) | 0.84(±0.09) | 48.12(±0.8) | 58.9(±6.19) |
| CaCO3 | Aug-17 | 0.17(±0.01) | 7.58(±0.73) | 0.98(±0.11) | 2.21(±0.2) | 0.14(±0.03) | 0.81(±0.07) | 48.34(±0.98) | 61.02(±5.48) |
| N | Sep-16 | 0.19(±0.01) | 6.17(±0.19) | 1.61(±0.1) | 2.52(±0.38) | 0.23(±0.13) | 0.83(±0.06) | 47.22(±0.24) | 57.48(±4.16) |
| N | Oct-16 | 0.18(±0.01) | 5.98(±0.66) | 1.62(±0.24) | 2.13(±0.35) | 0.2(±0.08) | 0.8(±0.04) | 47.24(±0.56) | 59.7(±3.55) |
| N | Nov-16 | 0.18(±0.01) | 6.16(±0.52) | 1.53(±0.2) | 2.53(±0.47) | 0.33(±0.16) | 0.73(±0.02) | 49.78(±0.77) | 68.41(±1.88) |
| N | Aug-16 | 0.2(±0.02) | 5.78(±0.47) | 1.87(±0.16) | 2.14(±0.24) | 0.04(±0.04) | 0.79(±0.05) | 47.84(±0.5) | 60.98(±4.16) |
| N | Dec-16 | 0.18(±0.02) | 6.41(±0.33) | 1.33(±0.07) | 2.33(±0.44) | 0.2(±0.06) | 0.72(±0.05) | 49.66(±0.3) | 69.99(±4.35) |
| N | Jan-17 | 0.17(±0.01) | 5.92(±0.35) | 1.12(±0.16) | 1.67(±0.22) | 0.21(±0.03) | 0.79(±0.04) | 50.28(±0.51) | 64.46(±3.3) |
| N | Feb-17 | 0.21(±0.01) | 5.93(±0.29) | 1.2(±0.06) | 1.88(±0.21) | 0.15(±0.03) | 0.75(±0.04) | 49.91(±0.58) | 67.15(±3.84) |
| N | Mar-17 | 0.19(±0.01) | 5.8(±0.57) | 1.93(±0.12) | 2.24(±0.37) | 0.32(±0.16) | 0.74(±0.02) | 48.73(±0.33) | 66.15(±1.8) |
| N | Apr-17 | 0.17(±0.02) | 5.98(±0.49) | 1.64(±0.16) | 2.31(±0.36) | 0.15(±0.04) | 0.78(±0.06) | 48.88(±0.21) | 63.5(±4.51) |
| N | May-17 | 0.18(±0.04) | 6.14(±0.5) | 1.41(±0.25) | 2.25(±0.35) | 0.12(±0.04) | 0.77(±0.07) | 49.84(±0.21) | 66.59(±5.61) |
| N | Jun-17 | 0.18(±0.01) | 6.21(±0.43) | 1.58(±0.15) | 2.39(±0.5) | 0.14(±0.06) | 0.76(±0.03) | 49.86(±0.18) | 66.21(±2.56) |
| N | Jul-17 | 0.17(±0.01) | 6.04(±0.27) | 1.44(±0.16) | 2.24(±0.35) | 0.16(±0.07) | 0.78(±0.03) | 49.49(±0.36) | 63.94(±2.89) |
| N | Aug-17 | 0.15(±0) | 6.28(±0.31) | 0.93(±0.08) | 2.35(±0.3) | 0.16(±0.05) | 0.87(±0.02) | 50.12(±0.49) | 57.52(±1.82) |

*Supplementary Table 2 continued*

| Treatment | Date | P | Ca | K | Mg | Na | N | C | C:N |
|---|---|---|---|---|---|---|---|---|---|
| | | mg g$^{-1}$ | | | | | % | | |
| N+CaCO3 | Sep-16 | 0.16(±0.01) | 4.75(±0.27) | 1.53(±0.17) | 2(±0.33) | 0.27(±0.11) | 0.82(±0.12) | 47.13(±0.67) | 61.52(±8.83) |
| N+CaCO3 | Oct-16 | 0.17(±0.01) | 4.89(±0.4) | 1.68(±0.14) | 2.12(±0.38) | 0.28(±0.09) | 0.75(±0.1) | 47.17(±0.45) | 66.64(±9.06) |
| N+CaCO3 | Nov-16 | 0.16(±0.01) | 6.13(±0.28) | 1.06(±0.02) | 2.06(±0.36) | 0.22(±0.05) | 0.75(±0.1) | 48.53(±0.86) | 69.34(±10.37) |
| N+CaCO3 | Aug-16 | 0.15(±0.01) | 4.74(±0.4) | 1.8(±0.17) | 1.87(±0.25) | 0.35(±0.12) | 0.73(±0.07) | 47.57(±0.5) | 66.77(±5.79) |
| N+CaCO3 | Dec-16 | 0.15(±0.02) | 5.86(±0.46) | 1.36(±0.17) | 2.44(±0.56) | 0.25(±0.1) | 0.66(±0.07) | 48.68(±0.38) | 76.97(±10) |
| N+CaCO3 | Jan-17 | 0.19(±0.02) | 6.45(±0.59) | 1.06(±0.06) | 1.71(±0.23) | 0.23(±0.03) | 0.79(±0.08) | 48.64(±0.44) | 63.57(±5.94) |
| N+CaCO3 | Feb-17 | 0.17(±0.03) | 6.24(±0.62) | 1.23(±0.16) | 1.8(±0.19) | 0.28(±0.06) | 0.78(±0.1) | 48.68(±0.82) | 65.82(±9.54) |
| N+CaCO3 | Mar-17 | 0.16(±0.01) | 5.68(±0.08) | 1.56(±0.18) | 2.07(±0.25) | 0.31(±0.08) | 0.74(±0.09) | 48.61(±0.61) | 69.32(±9.68) |
| N+CaCO3 | Apr-17 | 0.14(±0.01) | 5.42(±0.17) | 1.37(±0.07) | 2.07(±0.29) | 0.27(±0.14) | 0.77(±0.09) | 48.33(±0.62) | 65.56(±8.81) |
| N+CaCO3 | May-17 | 0.14(±0.01) | 6.35(±0.5) | 1.03(±0.13) | 2.14(±0.4) | 0.22(±0.07) | 0.72(±0.09) | 48.4(±0.97) | 69.87(±8.54) |
| N+CaCO3 | Jun-17 | 0.14(±0.01) | 6.44(±0.22) | 1.17(±0.18) | 2.39(±0.36) | 0.36(±0.1) | 0.72(±0.08) | 48.49(±0.83) | 70.15(±8.78) |
| N+CaCO3 | Jul-17 | 0.14(±0.01) | 7.01(±0.71) | 1.02(±0.04) | 2.21(±0.38) | 0.32(±0.09) | 0.75(±0.08) | 48.26(±0.95) | 66.48(±7.6) |
| N+CaCO3 | Aug-17 | 0.15(±0.01) | 9.52(±1.08) | 0.85(±0.14) | 2.22(±0.23) | 0.15(±0.03) | 0.82(±0.1) | 48.13(±1.25) | 61.16(±7.46) |

| Treatment | Date | S | Mn | Al | Fe | Ni | Cu | Zn |
|---|---|---|---|---|---|---|---|---|
| | | mg g$^{-1}$ | | | µg g$^{-1}$ | | | |
| Control | Aug-16 | 1.04(±0.08) | 0.24(±0.05) | 0.22(±0.11) | 33.197(±2.744) | 0.79(±0.538) | 4.807(±0.452) | 26.881(±3.959) |
| Control | Sep-16 | 1.02(±0.08) | 0.23(±0.05) | 0.17(±0.04) | 35.861(±0.59) | 1.681(±1.021) | 4.116(±0.287) | 30.148(±0.923) |
| Control | Oct-16 | 0.94(±0.11) | 0.25(±0.06) | 0.28(±0.08) | 32.953(±1.619) | 1.87(±1.482) | 4.327(±0.294) | 30.585(±2.246) |
| Control | Nov-16 | 1.01(±0.09) | 0.23(±0.06) | 0.11(±0.03) | 34.708(±4.23) | 1.761(±0.234) | 4.276(±0.762) | 36.167(±6.765) |
| Control | Dec-16 | 1.02(±0.07) | 0.28(±0.09) | 0.21(±0.12) | 37.527(±4.077) | 1.943(±0.357) | 3.623(±0.975) | 28.166(±3.782) |
| Control | Jan-17 | 0.93(±0.12) | 0.26(±0.06) | 0.18(±0.06) | 45.707(±4.462) | 1.749(±0.175) | 4.744(±0.976) | 33.972(±9.736) |
| Control | Feb-17 | 0.86(±0.03) | 0.31(±0.07) | 0.17(±0.04) | 32.103(±0.832) | 1.229(±0.046) | 4.247(±0.983) | 28.936(±3.984) |
| Control | Mar-17 | 1.04(±0.1) | 0.25(±0.07) | 0.16(±0.05) | 37.244(±4.043) | 1.887(±0.145) | 4.169(±0.367) | 29.309(±2.949) |
| Control | Apr-17 | 1.1(±0.13) | 0.22(±0.05) | 0.14(±0.06) | 33.782(±3.461) | 1.922(±0.306) | 3.825(±0.641) | 26.715(±4.276) |
| Control | May-17 | 0.9(±0.07) | 0.29(±0.05) | 0.06(±0.01) | 34.011(±0.925) | 1.823(±0.199) | 5.038(±0.544) | 26.475(±3.096) |
| Control | Jun-17 | 1.05(±0.18) | 0.31(±0.06) | 0.16(±0.07) | 31.491(±4.155) | 1.533(±0.276) | 4.559(±0.526) | 26.743(±1.329) |
| Control | Jul-17 | 0.89(±0.09) | 0.27(±0.07) | 0.09(±0.05) | 28.869(±2.606) | 1.503(±0.185) | 4.184(±0.31) | 27.713(±8.534) |
| Control | Aug-17 | 1.02(±0.09) | 0.34(±0.09) | 0.19(±0.1) | 33.051(±2.41) | 1.623(±0.213) | 4.868(±0.43) | 28.252(±6.426) |
| CaCO3 | Aug-16 | 0.96(±0.06) | 0.15(±0.03) | 0.1(±0.04) | 39.002(±4.687) | 0.304(±0.304) | 4.7(±0.79) | 21.087(±1.698) |
| CaCO3 | Sep-16 | 0.99(±0.1) | 0.14(±0.04) | 0.16(±0.11) | 40.953(±2.534) | 0.531(±0.483) | 4.156(±0.666) | 24.928(±0.881) |
| CaCO3 | Oct-16 | 0.95(±0.1) | 0.17(±0.03) | 0.2(±0.06) | 36.136(±3.156) | 2.731(±1.595) | 4.409(±0.335) | 29.09(±4.411) |
| CaCO3 | Nov-16 | 0.97(±0.12) | 0.14(±0.03) | 0.14(±0.03) | 35.411(±4.271) | 1.596(±0.276) | 3.766(±1.079) | 38.745(±4.108) |
| CaCO3 | Dec-16 | 1.02(±0.16) | 0.19(±0.02) | 0.2(±0.05) | 34.653(±3.804) | 1.859(±0.228) | 4.467(±1.199) | 31.606(±3.912) |
| CaCO3 | Jan-17 | 0.88(±0.11) | 0.17(±0.04) | 0.11(±0.06) | 49.614(±7.751) | 1.774(±0.284) | 4.982(±0.338) | 49.203(±3.908) |
| CaCO3 | Feb-17 | 1(±0.14) | 0.17(±0.04) | 0.12(±0.02) | 62.202(±14.496) | 2.367(±0.69) | 5.216(±1.712) | 26.709(±2.997) |

*Supplementary Table 2 continued*

| Treatment | Date | S | Mn | Al | Fe | Ni | Cu | Zn |
|---|---|---|---|---|---|---|---|---|
| | | | mg $g^{-1}$ | | | µg $g^{-1}$ | | |
| CaCO3 | Mar-17 | 0.84(±0.11) | 0.18(±0.04) | 0.09(±0.03) | 34.522(±6.636) | 1.353(±0.103) | 3.452(±0.38) | 27.551(±3.01) |
| CaCO3 | Apr-17 | 0.92(±0.05) | 0.18(±0.04) | 0.07(±0.03) | 47.68(±11.222) | 1.741(±0.093) | 3.238(±0.941) | 26.265(±4.668) |
| CaCO3 | May-17 | 0.96(±0.1) | 0.2(±0.03) | 0.11(±0.03) | 72.579(±20.403) | 2.139(±0.248) | 5.121(±1.001) | 30.414(±3.025) |
| CaCO3 | Jun-17 | 0.94(±0.12) | 0.18(±0.03) | 0.1(±0.03) | 41.585(±5.441) | 1.414(±0.134) | 3.866(±0.555) | 19.906(±1.745) |
| CaCO3 | Jul-17 | 0.9(±0.12) | 0.19(±0.04) | 0.06(±0.04) | 38.779(±4.313) | 1.551(±0.088) | 4.196(±0.516) | 23.995(±5.981) |
| CaCO3 | Aug-17 | 0.82(±0.06) | 0.19(±0.04) | 0.02(±0.01) | 51.128(±5.079) | 1.797(±0.158) | 4.123(±0.558) | 24.292(±3.453) |
| N | Aug-16 | 1.08(±0.08) | 0.17(±0.02) | 0.06(±0.02) | 34.68(±1.892) | 0.665(±0.665) | 4.615(±0.419) | 22.796(±3.6) |
| N | Sep-16 | 1.03(±0.07) | 0.17(±0.02) | 0.04(±0.01) | 36.164(±2.267) | 6.513(±4.627) | 4.064(±0.221) | 23.431(±5.908) |
| N | Oct-16 | 0.97(±0.09) | 0.2(±0.04) | 0.11(±0.02) | 33.157(±1.167) | 3.505(±1.377) | 3.914(±0.358) | 29.398(±4.548) |
| N | Nov-16 | 0.99(±0.07) | 0.16(±0.02) | 0.08(±0.04) | 37.49(±4.793) | 1.918(±0.208) | 4.699(±0.229) | 21.946(±5.937) |
| N | Dec-16 | 0.98(±0.07) | 0.22(±0.02) | 0.20(±0.1) | 28.718(±0.843) | 1.259(±0.15) | 2.325(±0.943) | 28.416(±4.401) |
| N | Jan-17 | 0.92(±0.06) | 0.25(±0.04) | 0.09(±0.01) | 49.971(±4.252) | 1.333(±0.185) | 5.832(±0.573) | 41.51(±4.193) |
| N | Feb-17 | 0.99(±0.08) | 0.23(±0.03) | 0.11(±0.03) | 39.343(±3.681) | 1.371(±0.035) | 5.359(±0.474) | 32.161(±3.931) |
| N | Mar-17 | 0.96(±0.1) | 0.18(±0.02) | 0.09(±0.01) | 37.018(±5.997) | 1.443(±0.26) | 4.417(±0.63) | 25.529(±1.317) |
| N | Apr-17 | 0.95(±0.06) | 0.18(±0.01) | 0.04(±0.02) | 31.425(±2.808) | 1.801(±0.177) | 4.12(±0.697) | 20.422(±2.093) |
| N | May-17 | 0.98(±0.09) | 0.22(±0.03) | 0.06(±0.02) | 35.807(±4.279) | 2.025(±0.054) | 5.003(±0.895) | 27.539(±4.087) |
| N | Jun-17 | 1.04(±0.07) | 0.2(±0.02) | 0.08(±0.01) | 33.47(±1.789) | 1.308(±0.08) | 4.08(±0.582) | 20.282(±4.5) |
| N | Jul-17 | 0.88(±0.06) | 0.18(±0.02) | 0.04(±0.03) | 26.857(±1.746) | 1.201(±0.214) | 4.523(±0.445) | 14.661(±3.655) |
| N | Aug-17 | 0.86(±0.05) | 0.22(±0.02) | 0.03(±0.01) | 29.035(±2.917) | 1.265(±0.233) | 4.571(±0.451) | 22.894(±3.552) |
| N+CaCO3 | Aug-16 | 1.00(±0.12) | 0.15(±0.03) | 0.25(±0.14) | 34.04(±1.1) | 3.841(±2.372) | 3.816(±0.413) | 27.837(±2.392) |

*Supplementary Table 2 continued*

| Treatment | Date | S | Mn | Al | Fe | Ni | Cu | Zn |
|---|---|---|---|---|---|---|---|---|
| | | mg g$^{-1}$ | | | µg g$^{-1}$ | | | |
| N+CaCO3 | Sep-16 | 0.96(±0.15) | 0.17(±0.02) | 0.07(±0.03) | 35.413(±2.774) | 0.336(±0.336) | 3.888(±0.516) | 21.124(±4.363) |
| N+CaCO3 | Oct-16 | 0.99(±0.16) | 0.19(±0.03) | 0.13(±0.03) | 35.657(±3.587) | 1.318(±0.544) | 3.734(±0.504) | 27.66(±2.37) |
| N+CaCO3 | Nov-16 | 0.9(±0.1) | 0.18(±0.02) | 0.06(±0.01) | 47.393(±6.277) | 1.943(±0.242) | 3.215(±1.127) | 35.967(±3.052) |
| N+CaCO3 | Dec-16 | 0.98(±0.18) | 0.18(±0.04) | 0.1(±0.02) | 29.703(±4.425) | 1.592(±0.211) | 2.149(±1.56) | 25.851(±2.46) |
| N+CaCO3 | Jan-17 | 1.02(±0.14) | 0.21(±0.02) | 0.13(±0.01) | 75.952(±6.598) | 2.105(±0.258) | 6.451(±1.041) | 43.327(±5.77) |
| N+CaCO3 | Feb-17 | 0.97(±0.15) | 0.2(±0.02) | 0.14(±0.03) | 54.64(±12.017) | 2.423(±0.407) | 6.29(±0.716) | 32.929(±3.894) |
| N+CaCO3 | Mar-17 | 0.97(±0.09) | 0.2(±0.04) | 0.24(±0.05) | 42.298(±7.912) | 1.715(±0.192) | 4.67(±0.596) | 26.935(±1.749) |
| N+CaCO3 | Apr-17 | 0.86(±0.13) | 0.18(±0.03) | 0.11(±0.08) | 37.391(±6.861) | 1.545(±0.199) | 3.439(±0.686) | 22.183(±2.877) |
| N+CaCO3 | May-17 | 0.85(±0.07) | 0.2(±0.05) | 0.13(±0.03) | 51.808(±12.515) | 2.108(±0.4) | 4.435(±0.753) | 20.991(±0.978) |
| N+CaCO3 | Jun-17 | 0.92(±0.12) | 0.19(±0.04) | 0.21(±0.08) | 39.34(±4.209) | 1.587(±0.055) | 3.32(±0.26) | 23.582(±3.405) |
| N+CaCO3 | Jul-17 | 0.84(±0.11) | 0.17(±0.03) | 0.08(±0.04) | 35.618(±6.118) | 1.675(±0.29) | 3.732(±0.535) | 17.713(±1.972) |
| N+CaCO3 | Aug-17 | 0.92(±0.15) | 0.2(±0.05) | 0.12(±0.05) | 62.563(±5.873) | 2.478(±0.265) | 5.066(±0.663) | 22.936(±3.379) |

# 10 Appendix.

## 10.1 Differences in soil chemistry among contrasting soil types in northern Borneo.

After: Differences in soil chemistry among contrasting soil types in northern Borneo. By Giacomo Sellan, Francis Q. Brearley, Reuben Nilus, Jupiri Titin & Noreen Majalap-Lee. In preparation for Geoderma Local.

Data was collected by Reuben Nilus, Jupiri Titin & Noreen Majalap-Lee, whereas Giacomo Sellan and Francis Q. Brearley prepared the manuscript.

**Abstract:** Soil diversity in the tropics is very high, and often regarded as a selective force able to shape forest tree communities. Here we investigate the differences among three soil types in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia, across a landscape encompassing Alluvial, Sandstone and Heath (“Kerangas”) forest. We found that, despite a clear difference in forest stand structure, soil texture and topography, Alluvial and Sandstone forest soil chemistry differs only for total- and mineral-nitrogen concentrations, base saturation and exchangeable calcium. The Heath forest soil was always significantly less fertile than the former two soils. Heath soil fertility, furthermore, was associated mainly with exchangeable aluminium, whereas Alluvial soil fertility correlated with clay content and Sandstone fertility with organic carbon. There was a general decline in nutrient concentrations in deeper horizons with the exception of exchangeable sodium and aluminium that remained constant through Alluvial and Sandstone soil profiles whereas they were concentrated in the Heath forest topsoil. We thus confirm the general consensus of a decreasing fertility trend from Alluvial to Heath forest soil, but soil fertility appears to be influenced by different variables among the three forest-soil associations. The inherent diversity of these forest-soil associations has clear implications for influencing plant performance and hence species distributions and may lead to differential responses to environmental changes.

### 10.1.1 Introduction:

Tropical soils are often considered together as highly acidic and poor in nutrients but, in reality, pedodiversity in tropical regions is high (Hartemink 2002; Richter and Babbar 1991; Sanchez et al. 1992; Townsend et al. 2008), and includes all the major soil types with a greater range of soil weathering and ages than temperate regions (Palm 2007). Currently, many lines of research hinge on tropical pedodiversity. Soil scientists have discussed how different soils can develop in sharp transition either from different parent materials (Bravard and Righi 1991; Lundstrom et al. 2000; Fujii et al. 2011) or through weathering and soil transformation (Dubroeucq and Volkoff 1998). For example, Dubroeucq and Volkoff (1998) considered that clay-rich Ferralsols could transform, over time, to spodosols through kaolinite dissolution. This variation in soil properties is important as soil is the main medium through which plants obtain mineral nutrients and thus can influence species performance and, hence, distributions. Ecologists have identified soil heterogeneity as an important selective force for tree species evolution and as a driver for the high species coexistence in tropical regions through soil-mediated habitat specialisation (Allié et al. 2015; Baldeck et al. 2012; Giles et al. 2004; John et al. 2007) in particular when considering nutrient poor regions such as the Colombian Guyana Shield (Duivenvoorden 1995) or north-western Borneo (Potts et al. 2002). Tropical spodosols are an interesting case in point and have been known to host a unique tree flora (known as Kerangas forest in Borneo) for many years (Beccari 1902; Richards 1941). In these cases, species richness, distribution and composition is influenced by edaphic variables, among which the most important are cation availability and exchange capacity, Al concentration and soil texture (Baker et al. 2003; Paoli et al. 2006; Slik et al. 2009).

Among tropical regions, the island of Borneo has a uniform lowland ever-wet climate yet hosts one of the most diverse lowland forests in the world (Kier et al. 2005). Although much of the island is covered by 'typical' lowland tropical Acrisols underlain by sedimentary rocks laid down during the Miocene and Pliocene, the influence of topography, parent materials, elevation and the degree of waterlogging are the key determinants of soil variation on the island, with major floristic associations related to soil typologies (e.g. forests over limestone, heath forests, montane forests and ultramafic forests: MacKinnon et al. 1996; Whitmore 1984). This extremely diverse soil and vegetation cover make the island of Borneo an important test field for a wide array of disciplines. Furthermore, the close proximity of these different environments allows researchers to test species coexistence theories at local scales (<100 km2) whilst standardising the locations for bio-climatic variables.

Many studies across Borneo have analysed soil nutrients at a range of sites (e.g. Brearley et al. 2004; van der Ent et al. 2015; Fujii et al. 2011; Kitayama and Aiba 2002; Moran et al. 2000; Pendry and Proctor 1996; Proctor et al. 1983a; Vernimmen et al. 2013) but the majority of them only focused on surface layers (to around 10 cm depth). Given that many nutrient-absorbing plant fine roots will occur deeper than this, it is also of value to determine nutrient concentration changes through soil depths; this will additionally provide insights on nutrient leaching processes. Nutrients are vertically stratified through soil by four processes: weathering, atmospheric deposition, leaching and biological cycling. The latter of these processes has been proposed to have a major role on nutrient distribution through soil depth (Jobbagy and Jackson 2001). The most important nutrients for plants are taken up by roots and returned the upper layers of the soil through rapid biological cycling, whereas the least important nutrients remain and leach through the soil profile. So, analysing nutrients by soil depth shows the leaching of certain nutrients which can thus be ascribed, for instance, to their importance for plants, to the physical features of a soil, to a lack of plant/microbial uptake or to an interaction of these (Binkley 1994; Jobbagy and Jackson 2001). This eventually sheds light on how soil composition and plant communities reciprocally influence one another (Bauters et al. 2016; Binkley 1994; Hobbie et al. 2007; Mueller et al. 2012).

In order to provide opportunities for insights into plant and soil associations as well as changes in soil chemistry along a soil fertility gradient we performed a detailed comparison of soil chemical and physical characteristics through depths at Kabili-Sepilok Forest Reserve (KSFR), in eastern Sabah, northern Malaysian Borneo. The reserve hosts three different forest-soil associations, namely Alluvial, Sandstone and Heath forest that typically develop on a soil gradient from Acrisols to Spodosol. Many studies have described and explored the different tree and liana communities among the three forest types (Baltzer et al. 2005; Born et al. 2014; DeWalt et al. 2006; Nilus 2003), nutrient cycling and limitation (Dent et al. 2006; Nilus et al. 2011), and above-ground carbon stocks (Coomes et al. 2017) though the majority of studies lack extensive details of soil structure and chemistry. The aim of this paper is thus to: 1) describe the differences in chemical composition, texture and nutrient leaching among the three soil types found in KSFR and 2) understand how soil fertility is influenced by soil texture, organic matter content and acidity in these three soil types.

### 10.1.2 Methods:

The Kabili-Sepilok Forest Reserve is situated around 5° 51' N and 117° 56' E in the state of Sabah, Malaysian Borneo. The climate is perhumid equatorial (Köppen Af) has a mean annual precipitation of 2975 mm (Dent et al., 2006). Nearly half of the annual precipitation falls between November to February; all months have more than 100 mm precipitation excepting a short dry season in April with an average of 55 mm (Fox 1973). The reserve soils originate from three bedrock types i.e. mudstone, sandstone and some siltstone whose age is upper Miocene or younger. Sandstone rises up to ~170 m a.s.l. forming the prominent scarps and ridges that characterise the reserve whereas mudstone generally gives rise to smaller hills. Siltstone is found in smaller amounts, intermixed with the former two bedrocks. The reserve hosts three soil associations, mapped locally as Silabukan, Lokan and Maliau (Acres & Folland, 1975). The first (Silabukan) consists of a juxtaposition of Acrisols, Fluvisols and Plinthosols (Figure 10.1a) (Ultisols, Fluvents and Plinthaquoxes in the USDA soil taxonomy). These soils are comprised of alluvium derived from the erosion of mudstone and sandstone hills. The topography is generally flat with small mudstone hills and hosts the “Alluvial” forest which is very species diverse with an upper canopy height of 45-60 m, trees that can reach a diameter of 2.4 m or larger and a low understorey density (Nilus 2003). On the ridges of the hills, the interbedding of sandstone and mudstone leads to the development of Haplic Cambisols and Plinthic Acrisols (Figure 10.1b) (both Ultisols in the USDA soil taxonomy) mapped together as the Lokan association. It is mainly composed of loamy sand and supports the “Sandstone” forest formation characterised by a lower canopy height (c. 30-40 m), a mean tree diameter intermediate between Alluvial and Heath forest and a high understorey density (Nilus 2003). The gentle slopes on the side of the hills host the Maliau soil association which is composed of Haplic Acrisols (Figure 10.1c) (also Ultisols in the USDA soil taxonomy) with some podzolised areas characterised by the presence of bleached sand, often with an indurated hardpan. This soil formation gives rise to the “Kerangas” or Heath forest, which has a very high understorey stem density, a regular canopy of 25-30 m in height with small tree crowns and low species diversity (Fox 1973; Nilus 2003). In the southern part of the reserve, the flat alluvial soil hosts a mangrove forest formation, which will not be considered further in this study.

#### **10.1.2.1 Soil sampling:**

In each of the three forest-soil associations, three 4-ha forest plots were installed in 2000 for a total of nine square plots. Every plot was divided into 20 m x 20 m blocks and, in 2002, we undertook a soil survey that sampled 20 % of the randomly selected blocks in each plot. In total, 20 blocks from each plot were sampled totalling 180 blocks. In each block, we collected five soil samples at three depths (0-5 cm, 5-20 cm, 20-35 cm, which roughly covers soil horizons A and B) and subsequently bulked the five samples from each depth together. In total, 540 samples were analysed. In addition, we excavated one soil pit per forest-soil association to determine the major soil type in the plots. From these soil pits we sampled each soil horizon for chemical analysis.

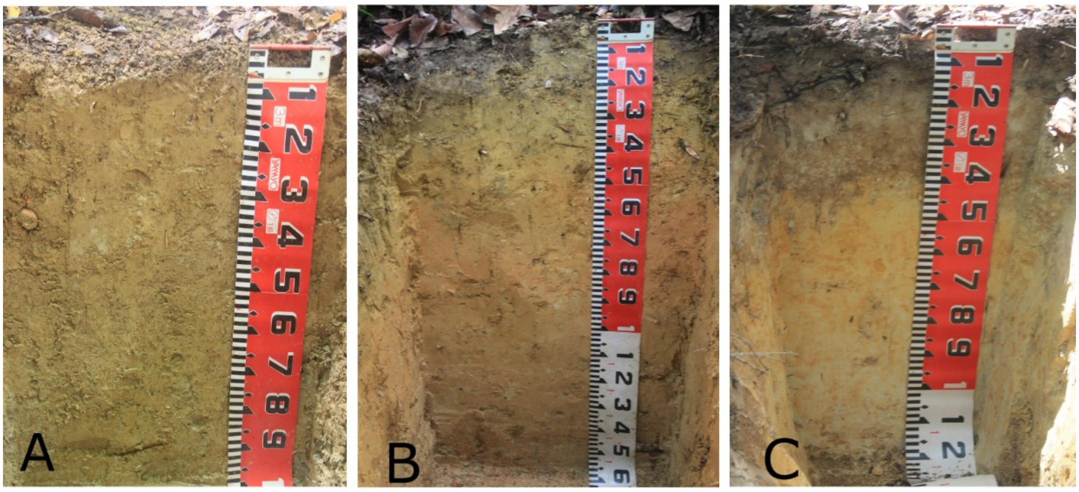

*Figure 10.1 Soil pits excavated in the three main soil types in Kabili-Sepilok Forest Reserve, Sabah, Malaysia. A) Alluvial forest soil (Haplic Fluvisol); B) Sandstone forest soil (Haplic Cambisol); C) Heath forest soil (Haplic Acrisol).*

### 10.1.2.2 Chemical analysis:

Subsamples were taken in duplicate from each fresh sample and extracted for mineral-N with 1.5 N KCl at a ratio of 1:14 w:v (adapted from Rowell 1994). The remaining samples were air-dried to constant mass, then ground and sieved through a 2-mm sieve and homogenised thoroughly before analysis. Moisture content was determined gravimetrically by drying the soil at 105° C until constant weight on sub-samples and used to convert the results to oven-dry mass. For total C and N, a sub-sample was ground further to pass through a 100-mesh sieve (212 µm) and then quantified by dry combustion with a CN analyzer (Elementar Vario Max). Soil texture was analysed following Day (1965) through soil digestion with H2O2, fine earth dispersion with NaOH, and separation of sand, clay and silt with a pipette apparatus. pH was measured with a pH-meter (Sartorius, Göttingen, Germany) and a combination glass-calomel electrode in a 1:2.5 suspension in water. Organic C was determined using the Walkley-Black method (Anderson and Ingram 1993). Extraction of soil available P followed the "Bray 2" method from Bray and Kurtz (1945) and colorimetric determination described in Anderson and Ingram (1993). Ammonium acetate (1 M; 1:10 w:v) extracts (Gillman et al. 1983; Thomas 1982) were measured for exchangeable Ca, Mg, Na and K on an atomic absorption spectrophotometer (GBC Scientific Equipment, Danderong, Victoria, Australia) while extracts in 1 M KCl (10 g soil in 150 ml KCl) were titrated with 0.1 N NaOH and then back-titrated with 0.1 N HCl to determine exchangeable acidity and Al respectively (Anderson & Ingram 1993). Cation exchange capacity was calculated as the sum of exchangeable base cations and exchangeable acidity (i.e. effective exchangeable acidity or ECEC) and base saturation was calculated as the percentage of ECEC occupied by the exchangeable bases.

#### 10.1.2.3 Statistical analysis:

As a first investigation of the data, we assessed whether soil type, soil depth or an interaction of the two explained more of the nutrient and texture variation. To this aim, we compared the F-statistic of a linear mixed effect model (lme) which had the interaction of soil type with depth (soil*depth) as a fixed effect and plot as a random effect. We then used the same model to test the differences in soil nutrients among soil types. P-values were obtained by likelihood ratio tests of the full model with the "soil type" effect against the model without the effect in question. We then performed a Tukey HSD test for the variables with $P \leq 0.05$. All the variables with non-normal distributions (tested for normality with Shapiro-Wilk's test) were log-transformed. To graphically highlight the differences in soil chemistry and texture among the three soil types, we performed a principal components analysis. To account for the variation in soil fertility (response variable) with soil texture, pH, exchangeable acidity, Al, C and moisture content (predictors) we performed an AIC stepwise regression on the log-transformed values of the 0-5 cm depth samples and with the overall 0-35 cm depth values. We considered soil fertility as effective cation exchange capacity (ECEC), base saturation (BS), available phosphorus (Av P), ammonium ($NH_4^+$), nitrate ($NO_3^-$), exchangeable potassium and magnesium (Exc K, Exc Mg). Soil texture was accounted for by clay, silt and sand content, whereas soil acidity comprised three variables: pH, exchangeable acidity (Exc Ac) and exchangeable Al (Exc Al). Furthermore, we added soil C and moisture content as proxies for soil organic matter that plays a fundamental role in regulating soil fertility

(Tiessen et al. 1994; Zaman and Chang 2004). All the analysis were conducted using R 3.3.2 (R Development Core Team 2009).

### 10.1.3 Results:

#### 10.1.3.1 Chemo-textural differences among the three soil-forest associations:

Representative soil pits are shown in Figure 10.1 with their descriptions and soil chemo-textural characteristics provided in the supplementary material. The soil*depth interaction was significant for all the soil chemical and textural variables, followed by the soil depth variable alone (that was the least significant factor for exchangeable Al, acidity and $NO_3^-$) and the soil type alone (which was the least significant factor for pH, organic C, exchangeable Mg and base saturation; Table 10.1). All the chemical and physical characteristics analysed with the soil*depth model showed clear variation among the three soil types except, surprisingly, pH (that had a p-value of 0.059; Table 10.1 and 8.2). The greatest variation was recorded for available P, which ranged from 0.38 µg $g^{-1}$ to 51.29 µg $g^{-1}$ in an Alluvial and a Heath forest soil sample, respectively. The Heath forest soil had the lowest $NH_4^+$ and $NO_3^-$ concentrations in addition to the lowest exchangeable acidity, exchangeable Al, Mg, K, Na and ECEC (Table 10.2). Nonetheless, the Heath forest soil had the highest available P and the lowest exchangeable Ca concentration. Base saturation was statistically indistinguishable among the Alluvial and Heath soil and lowest in Sandstone soil (Table 10.2). The difference between Alluvial and Sandstone soil was clear only for base saturation, exchangeable Ca, $NO_3^-$ (all greater in Alluvial) and $NH_4^+$ (greater in Sandstone) (Table 10.2).

Generally, nutrient concentrations declined from the 0-5 cm horizon to the 5-20 cm horizon by around 50 % with a further decrease of around 30 % to the 20-35 cm horizon - except for Al, which increased, and Na, which was relatively stable, except in the Heath forest soil where it declined sharply (Table 10.2).

*Table 10.1 Results of linear mixed effect models (Soil*Depth interaction) to evaluate model F-statistic significance for each of the soil chemical and physical characteristics found in three soil associations in Kabili-Sepilok Forest Reserve, Sabah, Malaysia.*

| | | | Soil*Depth | | |
|---|---|---|---|---|---|
| | | | Soil | Depth | Soil:Depth |
| pH | | F | 3.0 | 202.0 | 47.2 |
| Moisture content | | F | 72.2 | 135.7 | 48.3 |
| Organic C | | F | 15.3 | 935.8 | 3.3 |
| Total N | | F | 23.6 | 588.6 | 3.0 |
| $NO_3^-$ | | F | 16.9 | 9.9 | 12.1 |
| $NH_4^+$ | | F | 83.7 | 170.4 | 7.6 |
| Available P | | F | 34.4 | 720.4 | 0.7 |
| Exchangeable | acidity | F | 71.6 | 12.0 | 41.2 |
| | Al | F | 80.9 | 2.3 | 15.6 |
| | Ca | F | 30.5 | 318.7 | 24.6 |
| | Mg | F | 6.0 | 238.6 | 19.0 |
| | K | F | 24.5 | 438.3 | 30.4 |
| | Na | F | 109.8 | 117.9 | 69.3 |
| ECEC | | F | 61.5 | 128.6 | 58.4 |
| Base saturation | | F | 12.6 | 405.7 | 8.9 |
| Clay | | F | 66.6 | 68.7 | 1.8 |
| Silt | | F | 21.8 | 4.8 | 0.8 |
| Sand | | F | 38.2 | 52.2 | 2.6 |

*Table 10.2 Soil chemical and physical characteristics (mean ± standard errors) for soil at three depths beneath three forest/soil associations at Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Mean values sharing the same superscript letter within a column are not significantly different at $P < 0.05$ according to Tukey's HSD tests.*

| Soil type | Soil depth (cm) | pH | Moisture Content | Organic C | Total N | $NO_3^-$ | $NH_4^+$ | Available P | Exchangeable Acidity |
|---|---|---|---|---|---|---|---|---|---|
| | | | | % | | µg $g^{-1}$ | | µg $g^{-1}$ | cmolc kg-1 |
| | 0-5 | 4.48±0.04$^{b}$ | 3.41±0.16$^{a}$ | 1.48±0.07$^{b}$ | 0.14±0.008$^{a}$ | 8.44±0.80$^{a}$ | 8.04±0.75$^{b}$ | 6.73±0.38$^{b}$ | 4.01±0.2$^{a}$ |
| Alluvial | 5-20 | 4.56±0.04 | 3.14±0.19 | 0.73±0.02 | 0.08±0.003 | 4.32±0.30 | 4.47±0.40 | 2.91±0.10 | 4.86±0.3 |
| | 20-35 | 4.75±0.04 | 3.28±0.21 | 0.47±0.03 | 0.06±0.003 | 2.21±0.22 | 3.42±0.29 | 1.66±0.14 | 5.37±0.38 |
| | 0-5 | 4.53±0.03$^{a}$ | 3.60±0.14$^{a}$ | 1.47±0.05$^{b}$ | 0.12±0.006$^{b}$ | 3.05±0.48$^{b}$ | 10.6±0.71$^{a}$ | 5.71±0.28$^{b}$ | 4.19±0.18$^{a}$ |
| Sandstone | 5-20 | 4.68±0.02 | 2.98±0.12 | 0.74±0.02 | 0.07±0.003 | 1.87±0.23 | 7.28±0.79 | 2.87±0.12 | 4.52±0.23 |
| | 20-35 | 4.80±0.02 | 3.01±0.15 | 0.39±0.02 | 0.05±0.003 | 1.45±0.24 | 5.51±0.76 | 1.60±0.13 | 4.92±0.28 |
| | 0-5 | 4.08±0.03$^{b}$ | 2.54±0.15$^{b}$ | 1.9±0.09$^{a}$ | 0.09±0.005$^{c}$ | 0.9±0.13$^{c}$ | 3.74±0.35$^{c}$ | 9.22±0.82$^{a}$ | 2.96±0.17$^{b}$ |
| Heath | 5-20 | 4.73±0.03 | 1.08±0.08 | 0.9±0.04 | 0.05±0.002 | 1.17±0.12 | 1.58±0.11 | 4.04±0.17 | 1.59±0.13 |
| | 20-35 | 5.02±0.04 | 1.21±0.07 | 0.6±0.03 | 0.03±0.002 | 1.07 ±0.23 | 1.07±0.08 | 2.44±0.22 | 1.58±0.10 |

*Table 8.2. Continued*

| Soil type | Soil depth (cm) | Exchangeable Al | Ca | Mg | K | Na | ECEC |
|---|---|---|---|---|---|---|---|
|  |  | cmolc kg-1 |  |  |  |  |  |
|  | 0-5 | 3.46±0.20$^{a}$ | 1.16±0.20$^{a}$ | 1.08±0.10$^{a}$ | 0.23±0.01$^{a}$ | 0.07±0.004$^{a}$ | 6.56 ±0.40$^{a}$ |
| Alluvial | 5-20 | 4.38±0.30 | 0.26±0.06 | 0.71±0.10 | 0.14±0.01 | 0.05±0.003 | 6.04±0.42 |
|  | 20-35 | 4.89±0.36 | 0.15±0.02 | 0.89±0.14 | 0.12±0.01 | 0.06±0.003 | 6.60±0.51 |
|  | 0-5 | 3.48±0.16$^{a}$ | 0.48±0.14$^{b}$ | 0.92±0.17$^{a}$ | 0.22±0.01$^{a}$ | 0.07±0.002$^{a}$ | 5.90±0.32$^{a}$ |
| Sandstone | 5-20 | 3.85±0.22 | 0.15±0.07 | 0.49±0.10 | 0.11±0.01 | 0.05±0.003 | 5.34±0.32 |
|  | 20-35 | 4.27±0.27 | 0.11±0.05 | 0.52±0.11 | 0.08±0.01 | 0.05±0.003 | 5.70±0.39 |
|  | 0-5 | 1.63±0.13$^{b}$ | 0.22±0.01$^{c}$ | 0.75±0.08$^{b}$ | 0.22±0.02$^{b}$ | 0.07±0.006$^{b}$ | 4.24±0.25$^{b}$ |
| Heath | 5-20 | 1.15±0.11 | 0.09±0.003 | 0.12±0.01 | 0.06±0.005 | 0.02±0.003 | 1.90±0.13 |
|  | 20-35 | 1.22±0.08 | 0.08±0.01 | 0.05±0.01 | 0.03±0.004 | 0.01±0.001 | 1.76±0.11 |

*Table 8.2 Continued*

| Soil type | Soil depth (cm) | Saturation | Clay | Silt | Sand |
|---|---|---|---|---|---|
| | | | % | | |
| | 0-5 | 31.1±2.8$^{a}$ | | | |
| Alluvial | 5-20 | 16.0±1.3 | 29.1±1.3$^{a}$ | 20.8±1.2$^{a}$ | 50.2±2.4$^{c}$ |
| | 20-35 | 14.7±1.29 | 31.6±1.6 | 21.4±1.1 | 47.0±2.5 |
| | 0-5 | 22.5±2.69$^{b}$ | | | |
| Sandstone | 5-20 | 12.0±1.57 | 25.4±1.06$^{b}$ | 16.6±1.05$^{b}$ | 58.0±1.9$^{b}$ |
| | 20-35 | 9.99±1.47 | 28.0±1.1 | 17.6±0.9 | 54.4±1.9 |
| | 0-5 | 29.5±1.45$^{a}$ | | | |
| Heath | 5-20 | 19.2±1.2 | 14.4±0.5$^{c}$ | 10.1±0.4$^{c}$ | 75.4±0.7$^{a}$ |
| | 20-35 | 11.6±1.07 | 16.4±0.6 | 11.2±0.4 | 72.5±0.8 |

It is interesting to note that exchangeable Mg, K and Na concentrations did not show significant differences among soil types if considering only the upper 0-5 cm depth (Table 10.2). This indicates that these elements are homogeneously partitioned among soil types for the first 5 cm, but their vertical distribution varies widely among soil types.

Organic C increased and total N decreased from the Alluvial to the Heath forest soil leading to an increased C:N ratio, whereas both elements decreased through the soil profile (Table 10.2). The C:N ratio, considering all the three depths together was 9.6 ± 0.34, 10.8 ± 0.29 and 20.0 ± 0.38 for the Alluvial, Sandstone and Heath forest soil, respectively; individual depths reflect the same C:N pattern.

Soil texture, too, showed a significant difference for all the three size fractions among the three soil types. The sand fraction had the greatest variation among soils and was predominant in the Heath forest soil. Clay and silt both decreased through the Alluvial>Sandstone>Heath forest soil sequence (Table 10.2).

#### 10.1.3.2 Correlation of soil fertility with acidity, texture and organic matter:

The PCA showed a clear positive correlation between clay and silt with exchangeable acidity and Al, whereas sand correlated negatively with them (Figure 10.2). pH appears to be negatively correlated with exchangeable cations, available P, organic C and total N. The data clusters in three horizons (different sized symbols in the legend of Figure 10.2), with the 0-5 cm horizon showing the greatest variation and the soils becoming more similar with depth. Notably, soil texture, exchangeable acidity and exchangeable Al vary between soil types (different colours) but not among soil depths (different sized symbols). All the remaining parameters, instead, seem to vary greatly among soil depths. The dispersion of the Alluvial soil data coincides with, and is slightly wider than, the Sandstone soil data. On the other hand, the Heath forest soil data are concentrated together, highlighting a unique distribution of the data points.

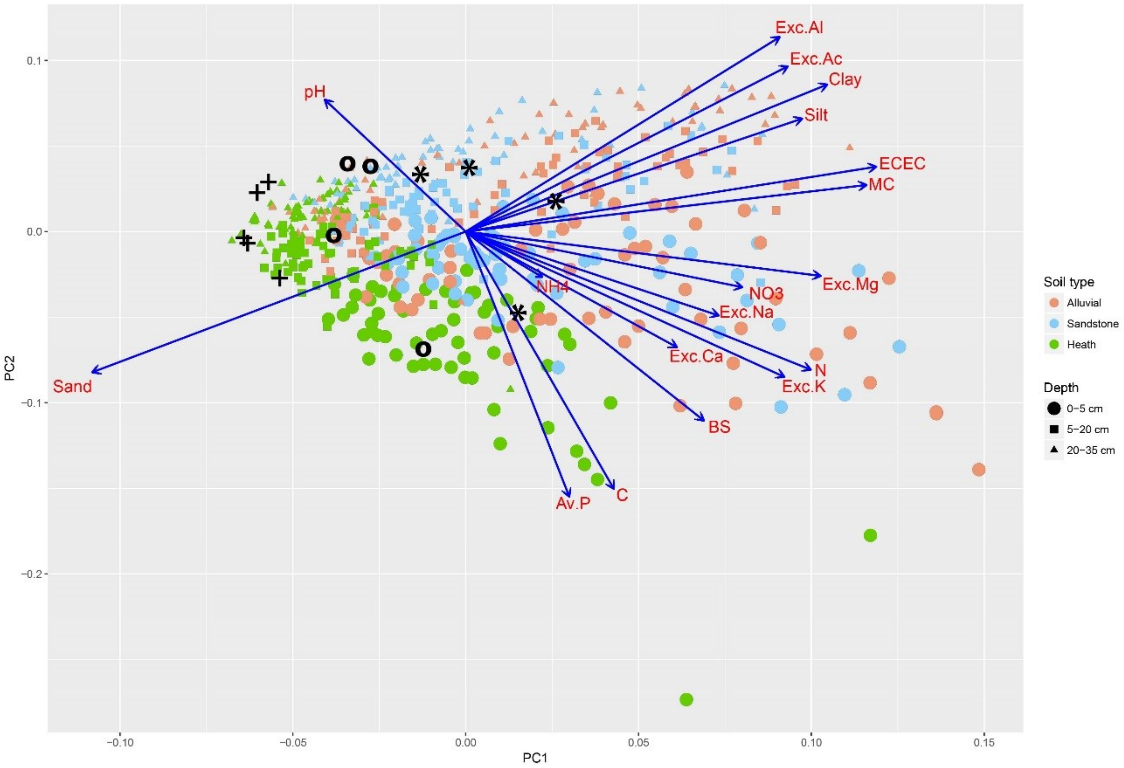

*Figure 10.2 Principal component analysis biplot of soil variables in three soil types in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Abbreviations are as follows: total N (N), organic C (C), available P (Av. P), exchangeable Al (Exc. Al), exchangeable acidity (Exc. Ac), exchangeable Mg (Exc. Mg), exchangeable Na (Exc. Na), exchangeable Ca (Exc. Ca), exchangeable K (Exc. K), ammonium (NH4), nitrate (NO3), effective cation exchange capacity (ECEC), base saturation (BS) and moisture content (MC). Also plotted are the samples taken from the three soil pits at four (Alluvial and Sandstone) and five (Heath) depths (see supplementary material). Symbols are "+" for Heath, "o" for Sandstone and "*" for Alluvial samples.*

*Table 10.3 (Next page) AIC stepwise regression to account for the variation among chemical and physical variables of three soil types in Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Abbreviations used: organic carbon (C), moisture content (MC), exchangeable acidity (Exc Ac), exchangeable Al (Exc Al), effective cation exchange capacity (ECEC), base saturation (BS), available phosphorus (Av P), ammonium (NH4+), nitrate (NO3-), exchangeable potassium (Exc K) and exchangeable magnesium (Exc Mg). Significance for the retained predictor variables were P < 0.001 (***), P < 0.05 (**), P < 0.1 (*) and P > 0.1 (non-significant, ns).*

| Log Response Variable | Soil | Depth (cm) | $R^2$ adj | P | Log Significant predictors |
|---|---|---|---|---|---|
| ECEC | Alluvial | 0-5 | 0.9 | < 2.2e-16 | Clay***, MC***, Exc Al*, pH$^{\cdot}$ |
| | | 0-35 | 0.91 | < 2.2e-16 | Clay***, Exc Ac***, MC***, pH**, Silt$^{\cdot}$ |
| | Sandstone | 0-5 | 0.91 | < 2.2e-16 | Clay***, MC***, Silt***, Exc Al*, pH* |
| | | 0-35 | 0.91 | < 2.2e-16 | Clay***, MC***, Silt***, Exc Ac*, pH* |
| | Heath | 0-5 | 0.93 | < 2.2e-16 | Exc Ac***, Exc Al***, MC*** |
| | | 0-35 | 0.98 | < 2.2e-16 | Exc Ac***, Exc Al***, MC***, pH*** |
| BS | Alluvial | 0-5 | 0.72 | < 0.001 | Exc Ac***, MC***, Clay*, Silt$^{ns}$ |
| | | 0-35 | 0.62 | < 2.2e-16 | Exc Ac***, MC***, Clay*, Silt*, pH*, C$^{\cdot}$ |
| | Sandstone | 0-5 | 0.66 | < 0.001 | Sand***, MC**, Exc Ac*, C$^{\cdot}$, Exc Al$^{ns}$ |
| | | 0-35 | 0.62 | < 2.2e-16 | C***, Exc Ac***, Exc Al***, MC***, Sand*** |
| | Heath | 0-5 | 0.61 | < 0.001 | Exc Al***, pH**, MC$^{\cdot}$ |
| | | 0-35 | 0.78 | < 2.2e-16 | Exc Ac***, Exc Al***, MC***, pH*** |
| Av P | Alluvial | 0-5 | 0.44 | < 0.001 | Exc Ac***, Sand***, Silt***, C**, Clay**, pH** |
| | | 0-35 | 0.73 | < 2.2e-16 | Clay***, C***, pH***, Sand***, Silt***,Exc Ac* |
| | Sandstone | 0-5 | 0.13 | 0.0021 | Sand** |
| | | 0-35 | 0.63 | < 2.2e-16 | C***, Exc Ac**, pH*, Sand$^{ns}$ |
| | Heath | 0-5 | 0.48 | < 0.001 | Exc Al***, MC**, Exc Ac*, Sand* |
| | | 0-35 | 0.65 | < 2.2e-16 | C***, Clay***, Exc Ac***, Exc Al***, pH$^{\cdot}$ |
| $NO_{3-}$ | Alluvial | 0-5 | 0.32 | < 0.001 | Clay***, Exc Al$^{\cdot}$, pH$^{\cdot}$, |
| | | 0-35 | 0.24 | < 0.001 | Clay***, C*, Exc Al*, Silt*, pH$^{\cdot}$, Sand$^{\cdot}$ |
| | Sandstone | 0-5 | 0.14 | 0.00759 | Sand**, Exc Ac$^{ns}$, Exc Al$^{ns}$ |
| | | 0-35 | 0.14 | < 0.001 | Sand***, pH**, Exc Ac*, Exc Al* |
| | Heath | 0-5 | 0.02 | 0.1749 | Exc Al$^{\cdot}$, MC$^{ns}$ |
| | | 0-35 | 0.04 | 0.01545 | C*, Exc Ac*, Exc Al*, Sand* |
| $NH_{4+}$ | Alluvial | 0-5 | 0.34 | < 0.001 | Clay***, Sand$^{\cdot}$ |
| | | 0-35 | 0.32 | < 0.001 | C***, Clay***, Silt$^{\cdot}$ |
| | Sandstone | 0-5 | 0.21 | 0.0026 | C*, Silt*, Clay$^{\cdot}$, Exc Ac$^{ns}$, Exc Al$^{ns}$ |
| | | 0-35 | 0.24 | < 0.001 | C***, MC*, Clay$^{\cdot}$, Exc Ac$^{\cdot}$, Exc Al$^{\cdot}$, Silt$^{\cdot}$ |
| | Heath | 0-5 | 0.4 | < 0.001 | Exc Al**, pH**, Sand**, MC$^{\cdot}$, Exc Ac$^{ns}$ |
| | | 0-35 | 0.47 | < 2.2e-16 | C***, Exc Al***, Sand**, MC*, pH* |

*Table 8.3 Continued*

| Log Response Variable | Soil | Depth (cm) | $R^2$ adj | P | Log Significant predictors |
|---|---|---|---|---|---|
| Exc K | Alluvial | 0-5 | 0.65 | < 0.001 | MC***, Clay**, Exc Ac**, pH* |
| | | 0-35 | 0.74 | < 2.2e-16 | C***, MC***, pH***, Clay**, Sand*, Silt$^{\cdot}$ |
| | Sandstone | 0-5 | 0.69 | < 0.001 | MC***, Sand***, Exc Ac$^{\cdot}$, Exc Al$^{\cdot}$, |
| | | 0-35 | 0.72 | < 2.2e-16 | C***, MC***, Sand*, Exc Ac$^{\cdot}$, Exc Al$^{ns}$ |
| | Heath | 0-5 | 0.56 | < 0.001 | Exc.Al***, Exc Ac**, C*, Silt$^{ns}$ |
| | | 0-35 | 0.76 | < 2.2e-16 | C***, Exc Ac***, Exc Al***, pH** |
| Exc Mg | Alluvial | 0-5 | 0.68 | < 0.001 | Clay**, Exc Ac**, MC**, Silt$^{ns}$ |
| | | 0-35 | 0.71 | < 2.2e-16 | MC***, pH* |
| | Sandstone | 0-5 | 0.69 | < 0.001 | Sand***, Exc Al**, MC$^{\cdot}$ |
| | | 0-35 | 0.68 | < 2.2e-16 | MC***, Sand***, C*, Exc Ac* |
| | Heath | 0-5 | 0.7 | < 0.001 | Exc Al***, Exc Ac**, pH**, MC$^{\cdot}$ |
| | | 0-35 | 0.84 | < 2.2e-16 | C***, Exc Ac***, Exc Al***, pH** |

Generally, the stepwise regression shows ECEC to have the highest correlation with the predictor variables, whereas nitrate had the lowest (Table 10.3). For every soil type, the inclusion of the deepest samples in the analysis resulted in an greater correlation coefficient and increased significance of soil fertility with soil chemo-physical features. The most powerful predictor for nutrient availability in Alluvial forest soil was clay, followed by pH, moisture content and organic C. Clay here correlated positively with all the nutrients, except NH4+ and P. In Heath forest soil, instead, the most important predictor was exchangeable Al followed by exchangeable acidity and organic C. Texture in the Heath forest soil had a strong significant correlation only with soil P, where a sandier soil contains more available P. This is in agreement with the process of P complexation by Al, which derives from clay weathering. Furthermore, texture has only a weak correlation with $NH_4^+$ and $NO_3^-$; the former increase and latter decrease with more clay. The Sandstone soil lies in the middle of the two other soil-forest associations, with organic C being the most explanatory predictor for fertility, followed by moisture content and exchangeable acidity.

### 10.1.4 Discussion:

With the present work we confirm the fertility gradient already formulated by others for this area (Alluvial>Sandstone>Heath forest) (Dent et al. 2006; Nilus 2003) and also shown for other similar studies on the island of Borneo (Metali et al. 2015; Proctor et al. 1983a; Vernimmen et al. 2013). Nonetheless, the stepwise regression uncovered different roles of soil Al, exchangeable acidity, pH, organic matter and texture in determining soil fertility between the different soil types.

The three soils developed from the interaction and weathering of different parent materials underlying the plots and this, along with topography and erosion, drives the differences among them. The in situ weathering of a mixture of sandstone and mudstone leads to soils under Sandstone and Heath forest, which likely differ among themselves in the amount of mudstone-derived clay. Alluvial soil, eventually, might receive a steady amount of clay from neighbouring mudstone hills, and its flat topography is likely to reduce the effect of weathering and erosion. In other studies elsewhere, Heath forests show a podsolized soil profile with a gray-white sandy A-B horizon with weathered clay and eluviated Fe as well as Al underlain by an indurated hardpan (Andriesse 1968; Bravard and Righi 1989; Dubroeucq and Volkoff 1998; Luizao 1996; Tanaka et al. 2013). However, our soil pits showed Heath forest soil to be Haplic Acrisols without a hardpan, although we did find spodosols elsewhere – notably where forest biomass was lower (chapter 3).

Andriesse (1968) shows that spodosols usually develop on slopes less than 15 % fitting with difference between Sandstone (>20 %) and Heath forest (10-20 %) slopes in this study and suggests the podsolization process requires around 5000 years to be accomplished. Thus KSFR Heath forest soil might still be in an incipient podsolization stage.

Our analysis revealed the most acidic soils (Heath forest) to have least Al despite the general consensus of a positive correlation of Al with soil acidity. To this regard, several researchers reported spodosols to be poorer in Al when compared to Acrisols (Vernimmen et al. 2013) as Al in tropical soils derives mainly from the weathering of clay minerals which precipitates and binds to Fe (Lundstrom et al. 2000). In our Heath forest soil, the low concentration of Al is likely due to a low clay content, and thus a small "reserve" of Al, which is corroborated by the correlation among clay and exchangeable Al in the PCA. Proctor (1999) and Kidd and Proctor (2001) proposed this lack of Al in spodosols to be the reason for their unique acidity with Al buffering the effect of $H^+$ ions on pH and Heath forest soil acidity dominated by $H^+$, rather than Al, ions. Aluminium, furthermore, seems to leach through Alluvial and Sandstone soil profiles, whereas its concentration is less and remains quite constant through the Heath soil profile, probably due to its association with soil organic matter, which is more evenly distributed through the Heath forest soil profile. This would imply that our Heath forest soil underwent a strong clay weathering where Al leached and eventually was lost or never had clay, due to the scarcity of mudstone in those areas.

With regard to other nutrients, Heath forest soil shows the strongest ongoing leaching process among the three soils with Mg, K and Na more concentrated in the topsoil and presenting a clear decrease with depth. Greater nutrient concentrations in topsoil is likely driven by the fast cycling among litterfall and root/mycorrhizal components (Jobbagy and Jackson, 2001), whereas the decrease with depth is probably due to the stronger leaching in the Heath forest soil due to its sandy nature. Aluminium also seems to determine the differences in available P concentrations among the three soils with Heath forest soils having the greatest P concentration; this is likely due to its low Al content, which binds and immobilises P in the Alluvial and Sandstone soils. On the other hand, the high available P concentrations in Heath forest soil might be, at least partly, an artefact of the weak acid extraction method used and not directly represent what is available to plants.

In our soils, ammonium is the dominant form of mineral nitrogen and its ratio with nitrate changes among soil formations with Alluvial soil having a 1:1 ratio and Sandstone and Heath forest soils having a ratio c. 1:4. This difference might be due to the effect of leaf litter quality, soil moisture and soil acidity. Alluvial forest litter usually has the lowest C:N ratio (Dent et al. 2006) and a high moisture content as well as the least acidic pH, which together favour the activity of nitrifiers (Sahrawat 2008; Stark and Firestone 1995; Zaman and Chang 2004).

Effective CEC, as expected, decreased from Alluvial to Heath forest soil, whereas base saturation was higher in the Heath forest soil rather than in the Sandstone soil. This could lead to the conclusion that the former is more fertile, but this is not the case. The difference in base saturation between the two soils in fact is driven by the Heath forest soil's low extractable Al and exchangeable acidity, which increase the relative base saturation. Proctor et al. (1984) highlight a constant high concentration of Mg throughout heath forest soils in comparison with dipterocarp-dominated forests, but this is not the case in our sites likely due to geological differences between them. Furthermore, Mg seems to leach through the Alluvial soil, whereas in the Heath forest soil it is concentrated in the upper horizon suggesting a tighter cycle and thus maybe a limitation. Moran (2000) showed a Brunei Heath forest soil to be high in Ca in contrast to our Heath forest soil, but it can be seen how Ca leaches more through Heath forests soils rather than Alluvial and Sandstone soils.

The Carbon:Nitrogen ratio is high in Heath forest and low in Alluvial soil and this pattern seems to be ubiquitous among Mixed and Heath forests soil gradients (Kartawinata 1980; Luizao 1994; Luizao et al. 2007; Wood and Beckett 1961). The high C:N ratio of Heath soils depicts poorly decomposing organic matter probably due to the sclerophyllous and high-phenolic nature of Heath forest leaves, which increase soil acidity and slow down decomposition.

From the stepwise regression we see that soil fertility is explained by different variables among the three soil types, but organic C plays a role in all of them. In the Alluvial forest soil, surprisingly, pH correlated negatively with nutrient availability. This might be due to the greater organic matter content at low pH. Moisture content is always positively correlated with fertility variables, except for $NH_{4+}$, which decreases with increasing moisture. This is likely due to the action of autotrophic nitrifiers, which are more active in wet soil and quickly consume the available $NH_{4+}$. In the Sandstone forest soil, the importance of organic C is followed by soil moisture content and exchangeable acidity. These last two share equal significance, the former enhancing nutrient availability, the latter decreasing available P (as Sandstone soil exchangeable acidity is still dominated by Al ions) and $NH_4^+$, as acidity hampers N mineralization. From an overall point of view, Heath forest soil fertility is positively related to exchangeable Al and acidity, and secondarily to soil organic C content. As highlighted before, Al reduces soil P availability, and also has a negative effect on $NO_3^-$ and base saturation. On the other hand, it correlates positively with exchangeable K, Mg and ECEC.

### 10.1.5 Conclusions:

The three forest-soil associations found at Kabili-Sepilok Forest Reserve in northern Malaysian Borneo seem to be of a young age. In particular, the Heath forest soil, contrary to our expectations, is just at an incipient stage of podzolisation. Surprisingly, Alluvial and Sandstone soils seems similar with regard to element concentration and texture. Also the correlation between fertility, acidity and texture, which is partly a reflection of the wide variation in the individual soil types, follows similar patterns among Alluvial and Sandstone soils. We might expect the Sandstone and Heath forest soils to be more similar given their bedrock geological similarity but the differences are probably due to the podzolization process ongoing in Heath forest soil. Aluminium seems to be retaining P in the least acidic and more clay-rich soils, whereas in the Al-poor Heath forest soil, P is more available, whereas its uptake by roots might be hampered by $H^+$ ion toxicity. We suggest that in this toposequence, the most fertile soils' nutrient supply comes from soil organic matter decomposition and, secondarily, from weathering of clay, whereas the clay-poor Heath forest soils have developed a more acidic soils that slows decomposition of soil organic matter to act as a slow-releasing nutrient supply.

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