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Foliar chemistry and standing folivory of early and late successional species in a Bornean rainforest

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Running headline: Leaf traits and herbivory in a rainforest

ABSTRACT

Background: Few studies have investigated the chemical, morphological and physiological foliar traits and the intensity of standing folivory in a representative set of species of tropical rainforests including species of different successional stages.

Aims : (i) To quantify leaf elemental composition, leaf phenolics and tannin concentrations, physical leaf traits and the intensity of standing folivory in a representative set of species of different successional stages in a Bornean tropical rainforest, and (ii) to investigate the relationships among leaf traits and between leaf traits and accumulated standing folivory.

Methods: Analyses of leaf elemental concentrations, phenolics (Ph) and tannin (Tan) concentrations, leaf mass area (LMA), C assimilation rate and accumulated standing folivory in 88 common rainforest species of Borneo.

Results and Conclusions: Accumulated standing folivory was correlated with the scores of the first axis of the elemental concentrations PCA (mainly loaded by K and C:K and N:K ratios) with lower accumulated standing folivory at high leaf K concentrations ($R = -0.33$, $P = 0.0016$). The results show that consistent with growth rate hypothesis, fast-growing pioneer species have lower leaf N:P ratios than late successional species, that species with higher leaf N concentration have lower LMA according with 'leaf economics spectrum' hypothesis, and that species with lower leaf nutrient concentration allocate more C to leaf phenolics. This study also shows that species with different ecological role have different biogeochemical 'niche' assessed as foliar elemental composition.

Keywords: biogeochemical niche; ecological stoichiometry; foliar elemental concentration; growth rate hypothesis; herbivory; LMA; N:P; phenolics; rainforest; tannins; successional stages; trace elements.

Introduction

The ‘biogeochemical niche’ hypothesis proposes that plants competing in the same community tend to use the nutrients in different amount and proportion, which should diminish the competition for resources among them (Peñuelas et al. 2008; Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010). This has been observed when comparing leaf elemental composition in plants growing in different climatic conditions (Peñuelas et al. 2008) and when comparing native and coexisting alien species (Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010). Thus, the ‘biogeochemical niche’ hypothesis, by considering organisms’ elemental chemical composition, provides a new tool to study the suitability of niche partitioning among coexisting species. This implies the use of elements in different proportions and consequently different plant elemental composition among different species (Peñuelas et al. 2008; Peñuelas Sardans, Llusia, Owen, Carnicer et al. 2010). Element concentrations and their ratios constitute the final phenotypical expression of the different biogeochemical niches. Different biological functioning results in different proportional contents of different molecules and structures built from different proportions of elements such as carbon (C), nitrogen (N), phosphorus (P) or sulphur (S). Moreover, several physiological mechanisms such as those involved in water conservation strategies are directly related to some elements, such as K or Ca. Competitive exclusion is determined by nutrient availability and by the degree of different nutrient requirements of species, such as observed in aquatic (Tilman

1986; Tilman and Wedin 1991) and terrestrial (Mamolos et al. 1995; Gusewell and Bollens 2003; Everard et al. 2010; Venterink and Gusewell 2010; Harpole and Suding 2011) ecosystems.

Tropical forest tree diversity has been observed to be correlated with soil nutrient contents in many studies (Laurance et al. 2010; Long et al. 2012; Sahu et al. 2012) and soil nutrient distribution has been correlated with tree species distribution (John 2007). Thus the differences in leaf nutrient concentrations and stoichiometry of species should reflect and be correlated with species diversity in rainforests. Competition among species can diminish when they take up different elements in different proportion and/or take advantage of micro-scale soil differences. In addition, plant species of different successional stages can have different nutrient requirements and consequently different foliar elemental composition. An and Shanguan (2010) have observed different foliar elemental stoichiometry in different successional communities on the Loess Plateau of China.

These differences in the foliar elemental concentrations can influence herbivore behaviour and anti-herbivore defence strategies (Kusar and Coley 1991; Crone and Jones 1999; Munding et al. 2009). Different foliar elemental composition can be directly related to leaf palatability, for example leaves that have higher nutrient concentrations and lower C to nutrients ratio can be more palatable and experience extensive folivory (Yamasaki and Kikuzawa 2003; Kurokawa and Nakashizuka 2008). Leaf elemental concentration can also affect leaf palatability indirectly, e.g. the synthesis of secondary metabolites linked to anti-herbivory defence can be related to leaf nutrient concentrations and stoichiometry and especially with N concentration since phenolics and protein synthesis compete for their main common synthesis precursors, phenylalanine (Jones and Hartley 1999; Peñuelas and Estiarte 1998). Given the variety

of plant defences against herbivores and that their effectiveness appears to depend on the environment and the composition of the herbivore community, it is plausible that plant defence traits lie along a spectrum of niche axes that can foster the coexistence of many species. It is optimal for each herbivore to consume leaves with the most similar stoichiometry to itself to optimize its metabolic efficiency.

Although various kinds of plant defences are known to be effective against herbivory, less is known about which defence strategies are most effective in specific environments and especially regarding those linked directly or indirectly to leaf elemental composition and different molecular composition. Under low nutrient availability, plant species have also relatively higher leaf mass area (LMA) and leaf morphological traits that are associated with C-rich structural compounds, and these altogether can act as deterrent to herbivores (Kursar and Coley 2003). Plants that have low C to nutrient ratios, high photosynthetic capacity, and low LMA will invest relatively less in chemical defences (Bryant et al. 1983; Herms and Mattson 1992; Kursar and Coley 2003; Eichhorn et al. 2007). Several studies have suggested that investment in physical leaf defences, such as high LMA, which is associated with the allocation of C to C-structural molecules, e.g., lignin or cellulose, might compete with the demands for investment in phenolics and tannins (Fincher et al. 2008). In this context, 'leaf economics spectrum' (LES) predicts an inverse relationship between leaf production capacity (nutrient content and photosynthetic rates) and the investment in leaf structure (Wright et al. 2004). Moreover, phenolic synthesis can compete with protein synthesis for N and P sources (Jones and Hartley 1999). Phenolics and tannins are secondary metabolites that act as defensive compounds (Reed 1995). Phenolics are present in high concentrations in leaf tissues (typically between 5-40% dry weight) (Meyer and Karasov 1989; Adams et al. 2009; Peñuelas, Sardans, Llusia, Owen, Silva

et al. 2010). They are effective against a broad range of herbivores (Coley et al. 1985; Kouki and Manetas 2002; Novotny et al. 2002). The effect of phenolics depends on their tissue concentrations (Feeny 1992; Nomura and Itioka 2002) since they act by reducing digestibility to herbivores, rather than directly through toxicity (Eichhorn et al. 2007).

Few studies have investigated the intensity of accumulated standing folivory in relation to the leaf nutrient concentrations and stoichiometry, and the leaf chemical defenses in a representative set of species of tropical rainforests (Wu et al. 2007). Such studies are especially uncommon in the rainforests of Asia (Wu et al. 2007). A few studies have investigated specific defensive leaf compounds such as tannins (Eck et al. 2001; Kurokawa et al. 2004), LMA (Turner et al. 2000), and leaf morphological properties such as toughness (Fincher et al. 2008), in the most common tree species in the Bornean rainforest. These studies have observed considerable levels of tannin contents in some dominant tree species (Kurokawa et al. 2004), some relationships between leaf tannin concentrations and protection against herbivory in species of the genus *Macaranga* (Eck et al. 2001) and a relationships between LMA and leaf N concentration (Turner et al. 2000) and apparently no relationships between leaf toughness and herbivore attack (Fincher et al. 2008). Kurokawa and Nakashizuka (2008) examined the relationships between some leaf traits and herbivory rates in 40 woody species in the rainforest of the Malacca Peninsula and found that some leaf traits such as N concentration, C:N ratio, and leaf physical traits accounted for a small amount of the variance in accumulated standing folivory when phylogenetic relationships were included in the analyses. Collectively, those studies indicated that many defensive mechanisms beyond C:N ratios and specific leaf morphologies are used by woody species in tropical Asian rainforests. As far as we know, no study has investigated the

relationships among nutrient and trace element concentrations and stoichiometry, leaf phenolic and tannin concentrations, and accumulated standing folivory in a large number of the most common woody species in a primary rainforest in Borneo including species of different successional stages.

In Borneo, many soils are N- and P-limited (Nomura and Kikuzawa 2003; Paoli et al. 2005; Paoli 2006); e.g., typically, soil (NH₄OAc/HOAc)-extractable concentrations are <1 µg P g⁻¹ (Brearley et al. 2007). In nutrient-limited tropical ecosystems, plant defences against leaf herbivores can be adaptations to avoid the loss of nutrients. Borneo rainforests have high tree diversity (Wills et al. 2006), which makes them adequate to study the effects of environmental and phylogenetic factors on plant traits. In addition, insect diversity is very high in Borneo (Stork 1991; Dial et al. 2006) and highly diverse plant-insect interactions are assumed to exist there.

We hypothesised that in this highly diverse tropical forest the different use of nutrients as final expression of different defensive, successional and nutrient-use strategies should be related to different foliar elemental concentrations and stoichiometry among the different species. We thus linked elemental stoichiometry, including N:P ratios, with leaf traits related to production capacity, such as LMA, leaf N concentration and photosynthetic rates.

We analysed 88 woody species occupying various stages of ecological succession in the rainforest in the Danum Valley, Sabah, Malaysia with the following aims: (i) to quantify their foliar chemical traits, (ii) to investigate the relationships among their leaf elemental concentrations and stoichiometries, leaf phenolic and tannin concentrations, LMA, and the accumulated standing folivory.

Methods

Study site

The study site was within the 438-km² Danum Valley Conservation Area (a Class I protected rainforest) (117° 48.75' E, 5° 01' N), Borneo Island. The field station is on the periphery of the conservation area, which is within the Ulu Segama Forest Reserve, a portion of the ~10,000-km² Yayasan Sabah Forestry Concession. The Danum Valley conservation area is the largest parcel of undisturbed lowland dipterocarp forest in Sabah. Dipterocarp trees predominate in the forest within the field station and, in spots, the canopy is >70 m high. Ninety percent of the area is lowland dipterocarp forest and 10% is low-canopy, sub-montane forest, mostly at Mt. Danum, in the centre of the Conservation Area. The climate is equatorial and the mean annual temperature is 26.8 °C. Temperatures >34 °C are rare and occur during prolonged dry periods, only. Minimum temperatures below 19 °C are rare. Mean relative humidity at 08:00 h and 14:00 h are 95% and 78%, respectively. Mean annual rainfall (1985-2006) is 2,825 mm. Typically, rainfall is lowest in March and April, which are the most drought-prone months during ENSO events, and in August and September, when the south-westerly monsoon is at its height.

Plant species

Eighty-eight common woody species were studied (Figure 1). Species nomenclature followed the local floras (Whitmore 1972; Soepadmo et al. 2004). The successional position (early-, mid-, late-), life form, and heights (Table S1 Supporting information) of species were based on Cockburn (1976, 1980) and Köhler et al. (2000). The study included 19 early-, 44 mid-, and 25 late-successional species.

Plant sampling

Plant sampling was conducted in medium and large forest gaps (10-100 m diameter). Well-developed, mature but non-senescent, sun-oriented leaves located at the tips of branches (between 2 and 10 m height) were collected from at least three randomly selected mature trees of each species, at least 100 m apart. Generally at least 20 leaves (average \pm SE = 20.2 ± 0.7 leaves, $n = 264$ plants) were collected from each plant, although fewer leaves were collected from large-leafed species that have a small number of large leaves; e.g., *Artocarpus anisophyllus*, *Helicia artocarpoides*, and *Macaranga gigantea*. In parallel, twigs for gas-exchange measurements were collected between 08:00 h and 12:00 h. After the twigs were cut under water, they were placed in water in plastic bags, which stopped transpiration while the samples were transported to the laboratory. In the lab, the twigs were cut again under water and allowed to stabilise at room temperature (25-28 °C) in dim light. To maximise stomatal openness and obtain stable maximum values of photosynthetic capacity (A_{mass}), measurements were made the following day (Niinemets et al. 2005; Niinemets et al. 2009).

Leaf physiological and morphological analyses

The photosynthetic capacity (A_{mass}) of the leaves ($\mu\text{mol g}^{-1} \text{s}^{-1}$) was measured using an ADC pro (LCpro+ Portable Photosynthesis System, ADC BioScientific Ltd. Hoddesdon, Herts) gas exchange system at a quantum flux density of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, a leaf temperature of 25 °C, and an ambient CO_2 concentration of $385 \mu\text{mol mol}^{-1}$.

The leaves collected for the folivory analyses were sealed in plastic bags that contained wet filter paper and immediately transported to the laboratory at the field station. In the laboratory, the fresh mass of each leaf was determined and, to calculate leaf area and accumulated standing folivory, they were pressed flat between a white board and a large transparent acrylic sheet before being photographed (following

Niinemets et al. 2003). The digital photographs were taken using a Nikon Coolpix 990 camera (Nikon Corporation, Tokyo, Japan) from a distance (1.4-2.0 m) that depended on the size of the leaf.

After the dimensions and the standing folivory of the leaves were measured, they were dried in an oven at 70 °C for at least 48 h before the dry mass of each leaf was determined. Those measurements were used to calculate the leaf dry mass per unit area (LMA, g m⁻²) and the leaf dry mass to fresh mass ratio. Eight of the species examined had compound leaves (*Caesalpinia major*, *Cassia alata*, *Clausena excavata*, *Duabanga moluccana*, *Fordia splendidissima*, *Leea indica*, *Reinwardtioidendron humile* and *Sindora irpicina*) and, in those species, leaflets were considered functional analogues of simple leaves and all structural and chemical traits refer to leaflets.

Leaf chemical analyses

Dried leaves were ground in a CYCLOTEC 1093 sample homogeniser (Foss Tecator, Höganäs, Sweden). To measure the concentrations of C and N, 1-2 mg of the pulverised dried sample was mixed with 2 mg of V₂O₅ (an oxidant). C and N concentrations were determined by combustion coupled to gas chromatography using a Thermo Electron Gas Chromatograph model NA 2100 (C.E. instruments-Thermo Electron, Milan, Italy). For the determination of other elements, dried ground samples were digested, using concentrated HNO₃ and H₂O₂ (30%, p/v) in a microwave oven. To assess the accuracy of the digestions and the analytical procedures, a certified standard (NIST 1573a, tomato leaf, NIST, Gaithersburg, MD) was used as a reference. The concentrations of As, Cd, Cr, Cu, Mo, Ni, Pb, V, and Zn were determined using Inductively Coupled Plasma Mass Spectrometry, and the concentrations of Ca, Fe, K, Mg, Mn, Na, and P were measured using Inductively Coupled Plasma Optic Emission Spectrometry. For As

determination we used the hydride generation method. Briefly, As (V) was reduced to As (III) using a mixture of HCl (30% v/w), KI (1% w/v), and ascorbic acid (0.2% w/v) added to a digestion solution. The solution was pumped into a gas-liquid separator, where it reacted with NaBH₄ (1.3% w/v solution in 0.1 M NaOH) to form arsenic hydrides, which were analyzed using ICP-MS.

The phenolics (Ph) concentrations of leaves were measured by using an improved Folin-Ciocalteu Assay (Singleton and Rossi 1965; Marigo 1973) which used a blank of polyvinylpyrrolidone (PVPP). An Helios Alpha spectrophotometer (Thermo Spectronic, Cambridge, UK) was used to the determination the absorbances of the samples A and B (at 760 nm), with gallic acid as the standard for calibration.

Total soluble tannins (Tan) were extracted from 20 mg of leaf powder with 12 ml of 70% acetone. After centrifugation, the extract was assayed with the butanol/HCl method (Porter et al. 1986), modified as in (Makkar and Goodchild 1996). The absorbance was measured at 550 nm by spectrophotometer Helios Alpha (Thermo Spectronic, Cambridge, UK). Non-heated replicate tubes for each extract were used as anthocyanin blank and their absorbance values subtracted from the absorbance of the heated tubes (Porter et al. 1986). The Tta content on a dry weight basis was estimated by using a 1-cm-wide cuvette (Porter et al. 1986, Makkar and Goodchild 1996). Tan analyses were conducted in triplicate. For additional details on the analytical procedures, see Peñuelas, Sardans, Llusia, Owen, Carnicer et al. (2010).

Determination of accumulated standing leaf folivory

To quantify the extent of the damage caused to leaves by herbivores (we discarded other types of damage, such as necrosis from pathogens/fungi/bacteria), the digital images were processed to fill in all of the portions of each leaf that were removed by

herbivores, and the area of each of the leaves were measured again by using the UTHSCSA Imagetool software to give a leaf area estimate, $S_{A,T}$. The proportion of each leaf that had been removed by herbivores, F_R , was calculated as follows:

$$F_R = 1 - \frac{S_A}{S_{A,T}}.$$

where S_A is the measured leaf area. Three indices were used to quantify the extent of the damage caused by herbivores. The average F_R of all of the leaves collected characterises the total accumulated standing herbivory damage (folivory). The coefficient of variation (standard deviation per sample mean) of F_R characterises the variation in the extent of accumulated standing folivory. The average of the three highest estimates of F_R provided an estimate of the potential vulnerability of a species to folivory.

Statistical analyses

All the leaf elemental concentrations and nutrient ratios were subjected to PCA and discriminant analyses. Thereafter, we correlated the scores of the species on Axis 1 of the PCA that represented their 'biogeochemical niche' (Peñuelas et al. 2008; Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010) and the accumulated standing folivory of each species. Those analyses were performed using Statview 5.0.1 (SAS Institute Inc., Cary, NC, USA) and Statistica 6.0 (StatSoft, Inc. Tule, Oklahoma, USA).

Species-specific averages were calculated for leaf structure, foliage concentrations of elements, phenolics, and tannins, and accumulated standing folivory. The program Phylomatic (Webb and Donoghue 2005) was used to create a phylogenetic tree that included the 88 woody species (Figure S1; for details, see Peñuelas, Sardans, Llusia, Owen, Carnicer et al. (2010), Peñuelas et al. (2011) and section of Methods in the Supporting Information accompanying file). We correlated leaf nutrient

concentrations and ratios with leaf LMA and A_{mass} , the concentrations of phenolics and tannins, and accumulated standing folivory by using standardised major-axis regression. We also tested the possible effects of different successional stages on the leaf variables and on the accumulated standing folivory. When assessing multiple correlations, false discovery rate corrections were included in the analyses. Moreover, when simple regressions had a triangular form, a variance covariate was included in the model to take into account the side-effect.

Results

The different leaf concentrations of the 20 elements analysed, concentrations of phenolics and tannins, and the values of A_{mass} and of the morphological traits are shown in Tables S2, S3 and S4 (supporting information).

Differences in foliar elemental composition and accumulated standing folivory among species of different successional stages

The PCA conducted with the leaf concentrations of the 20 elements analysed, and the C:N, C:P, C:K, N:P, N:K, and P:K ratios resulted in a PC1 explaining 17.7% of the total variance and significantly correlated with the extent of accumulated standing folivory ($R = -0.24$, $P = 0.025$, $n = 88$) (Figure 2). The PC2 (explaining 14.2% of the total variance) was significantly correlated with the leaf phenolics concentration ($R = 0.28$, $P = 0.006$, $n = 88$). PC2 scores separated species of different successional stages (Figure 2).

The extent of accumulated standing folivory was inversely correlated with leaf K content per leaf area unit, K_{area} ($R = -0.33$, $P = 0.0016$, $n = 88$; $R = 0.27$ for K concentration, $P < 0.05$) (Figure 3). The maximum amount of accumulated standing

folivory (the proportion of a leaf consumed among the 10% most consumed leaves) and the coefficient of variation (CV) of the proportion of the leaf consumed were also negatively correlated with K_{area} ($R = -0.25$, $P = 0.02$, $n = 88$ and $R = -0.29$, $P = 0.006$, $n = 88$ respectively). The extent of accumulated standing folivory was not significantly correlated with any of the other variables analysed (Table S5 and S6, supporting information).

Early successional species had higher leaf P concentrations and lower N:P ratios (Figure 4). Among leaf morphological traits, leaves were more elongated in late successional species than in the early successional species ($F = 4.0$, $P = 0.021$, $n = 88$). No significant differences among successional stages were observed in other foliar traits, including accumulated standing folivory (Table S6 and S7, supporting information). Leaf N:P ratio was not correlated with accumulated standing folivory (Table S5, supporting information).

Leaf N concentrations scaled at approximately 1/3 (0.31) of leaf P concentrations ($N = 4.04P^{0.31}$, $P < 0.001$), and nitrogen concentration per leaf area N_{area} scaled at approximately 2/3 (0.62) of P concentrations per leaf area P_{area} ($N_{\text{area}} = 7.46P_{\text{area}}^{0.62}$, $P < 0.001$).

Elemental, phenolic and tannin concentrations, A_{mass} and LMA relationships

All the leaf nutrient concentrations per mass tended to be positively correlated with each other, but no strong correlations existed between the concentrations of nutrients and trace elements, or among the trace elements (data not shown). N, P, and K concentrations per leaf area were positively correlated with each other: N and P ($R = 0.8$, $P < 0.001$, $n = 88$), N and K ($R = 0.66$, $P < 0.001$, $n = 88$), and P and K ($R = 0.8$, $P < 0.001$, $n = 88$).

Leaf N concentrations were positively correlated with A_{mass} ($R = 0.41$, $P = 0.014$, $n = 35$) and negatively with LMA ($R = -0.33$, $P = 0.001$, $n = 88$) (Figure 5) and also with total leaf phenolics (TPh) ($R = -0.24$, $P = 0.027$, $n = 88$) (Figure 6).

The extent of accumulated standing folivory was not correlated with leaf Ph or Tan (Table S6, supporting information). Discriminant analyses that included leaf compactness and leaf K_{area} ($F = 5.17$, $P = 0.0076$, $n = 88$) discriminated between species that had low or high accumulated standing folivory.

Leaf N concentrations were negatively correlated with Tan ($R = -0.34$, $P < 0.001$, $n = 88$) (Figure 5). Leaf C:N ratios were positively correlated with Ph ($R = 0.27$, $P < 0.01$, $n = 88$) and Tan ($R = 0.35$, $P < 0.001$, $n = 88$). Ph was positively correlated with LMA ($R = 0.23$, $P = 0.032$, $n = 88$) and with leaf dry: fresh weight (Table S7, supporting information); i.e. Ph were highest in the leaves that had the lowest water content ($R = 0.30$, $P = 0.005$, $n = 88$).

Discussion

Main findings

In addition to providing a survey of the foliar elemental composition and stoichiometry of a large set of tropical tree species (see supporting information), this study identified significant relationships of leaf elemental concentrations and stoichiometry with ecological variables such as the extent of standing accumulated folivory or the successional stage.

The scores of the PC1 of elemental concentrations, that was mainly loaded by leaf K concentrations and P:K ratios, were negatively correlated with accumulated standing folivory, highlighting the role of K in plant-herbivore relationships, in agreement with some previous studies (Baskaran et al. 1985; Dale 1988). These results

indicate that there is a relationship between the extent of folivory experienced by a species and its 'biogeochemical niche' (Peñuelas et al. 2008; Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010).

Early successional species, mostly fast-growing species, had higher leaf P concentrations and lower leaf N:P ratios than did mid- and late- successional species, which is consistent with the 'growth rate hypothesis' (Elser et al. 2000). Foliar N concentrations were positively correlated with A_{mass} and negatively correlated with LMA, which is consistent with the leaf 'economic spectrum paradigm' (Wright et al. 2004; Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010). Thus, the results are consistent with the ecological stoichiometry paradigms showing that the high diversity of this ecosystem is related to the different elemental composition of the different species and that this elemental composition is related to different ecological properties. The results suggest that a differentiation in the use of nutrients can be underlying niche fragmentation and the coexistence of species of different successional stages. Different use of nutrients should diminish the competition intensity among different species. Moreover, leaves that had the lowest nutrient concentrations (low production capacity) allocated more C to the production of carbon-based secondary compounds such as phenolics and tannins. However, leaves with relatively high concentrations of phenolics and tannins, and high LMA did not present reduced accumulated standing folivory. Nevertheless, these results on folivory should be taken with caution because leaves with higher C to nutrient ratios live longer and may thus accumulate more leaf damage, leaves completely eaten are missed, and sun leaves do not represent the overall leaf biomass. Other mechanisms than those based on chemicals could be underlying plant defense in this ecosystem such as the susceptibility of herbivores to predator and parasitoid attack (Havill and Raffa 2000; Heil et al. 2001). All in all, the observed range

of accumulated standing folivory, 0.09-21%, is slightly under the range observed in previous studies in sets of tropical plant species in Australia, 3.3-41% (Lowman 1992) and in south China, 3-16% (Schuldt et al. 2010).

Foliar elemental concentrations, successional stage and folivory

Significant differences in the leaf concentrations of the 20 different elements and the stoichiometry of the most important ones (C, N, P, K), which represented the ‘biogeochemical niche’ (Peñuelas et al. 2008; Peñuelas, Sardans, Llusia, Owen, Carnicer et al. 2010) were found in species of different successional stage. Changes in plant N:P ratio (An and Shangguan 2010) and in plant nutrient use strategies (Yan et al. 2006) have been observed in some previous studies, but this is the first time, as far as we know, that a shift in the concentration of a set of 20 elements has been observed in the leaves of species of different successional stage of the same community. Species of early successional stages frequently have higher growth rates (Llambi et al. 2003), that should suppose a different use of nutrients and consequently different elemental and stoichiometric composition.

Other studies have described strong relationships between leaf elemental composition and the types of soil (Duvigneaud and Denaeyer-DeSmet 1968), but our study reports the relationships between element concentrations and stoichiometry in co-existing plant species and trophic relationships. In the highly diverse tropical forest ecosystem studied, different nutrient requirements composition among the different species could reduce competition among them and favour species niche differentiation. Taking into account that nutrients are frequently limiting in tropical rainforests (Tanner et al. 1998; Reich and Oleksyn 2004; Wright et al. 2011; Baribault et al. 2012; Santiago et al. 2012) this could be a factor that partly accounts for the great tree diversity

observed in tropical rainforests (Paoli et al. 2006; Siddique et al. 2010; Long et al. 2012). In fact, soil heterogeneity affects early succession of plant communities (Collins and Wein 1998) and soil niche partitioning has been suggested by Paoli et al. (2006) in a study conducted in a Bornean rain forest.

Accumulated standing folivory was negatively correlated with leaf K concentrations and contents and positively correlated with leaf C:K and N:K ratios. These results are in accordance with previous ones also reporting negative correlations between leaf K concentrations and herbivore attack (Baskaran et al. 1985; Dale 1988). The negative effect of high leaf K concentrations on insects acts through a reduction in the accumulation of soluble carbohydrates and amino acids in leaves (Baskaran et al. 1985) and an increase in leaf sclerophylly (Dale 1988). High K concentrations can have adverse effects on the growth of lepidopterans (Denke et al. 2000) and aphids (Havlickova and Smetankova 1998). In this regard, leaf K concentrations have been observed to be correlated with some secondary metabolite concentrations, such as phenolics, quinic acid and tartaric acid, and altogether probably related to mechanisms of water use efficiency (Rivas-Ubach et al. 2012). These results reinforce the need of considering K in ecological stoichiometry studies (Sardans, Peñuelas et al. 2012; Rivas-Ubach et al. 2012).

Leaf P concentrations were higher and leaf N:P ratios lower in early-successional species, which in most cases are fast-growing species, than in mid- and late-successional species, which is consistent with the Growth Rate Hypothesis (GRH) of Elser et al. (2000). The differences in foliar N:P ratios among plants can have an evolutionary component driven by a long-term evolution towards a determined style of life (Willby et al. 2001; Sardans, Rivas-Ubach et al. 2012). On average, N leaf concentrations scale with a coefficient between 0.66 and 0.75 of P leaf concentrations

(Niklas et al. 2005; Reich et al. 2010). The coefficient found here is smaller (0.33) but in any case, our results give further evidence that leaf P concentration increases more than leaf N concentration when both N and P leaf concentrations increase. This result fits well with the GRH because species with higher production capacity (higher N and P concentrations) have lower N:P ratio, thus coinciding higher plant growth rate capacity with lower leaf N:P ratio both favouring fast growth rates. A complementary explanation of the increase in foliar N:P concentrations across the successional gradient could come from a transition from N to P limitation. Some studies have suggested that after a disturbance, recovering tropical forests may be N limited (due to N losses from the disturbance) favouring species adapted to N limitation (and possibly with lower N:P ratios), and thereafter, during the succession, present a transition back to P limitation once returned to mature forest status (Vitousek and Howarth 1991; Davidson et al. 2007).

In other tropical rainforests, woody plants had leaf N:P ratios in the range of those observed in this study suggesting a frequent limiting role of P in tropical forest as observed in several previous studies (Tanner et al. 1998; Reich and Oleksyn 2004; Wright et al. 2011; Baribault et al. 2012; Santiago et al. 2012). For example, leaf N:P ratios were 11.7-17.6 in an Australian rainforest (Asner et al. 2009), 17.2-26.1 in Central and South American rainforests (Townsend et al. 2007), and 21.4 ± 1.0 in tropical forests in Oahu, Hawaii (Peñuelas, Sardans, Llusia, Owen, Carnicer et al 2010).

Relationships among concentrations of elements, phenolics and tannins, LMA, and A_{mass}

The observed relationships among leaf C:N, LMA and A_{mass} are in agreement with the leaf 'economic spectrum' paradigm (Wright et al. 2004). Leaves with low nutrient concentrations allocated more C to the production of carbon-based secondary

compounds such as phenolics and tannins, which is consistent with the “Excess Carbon Hypothesis” of Peñuelas and Estiarte (1998). A recent meta-analysis has demonstrated that plant traits other than secondary metabolites, such as for example morphological (e.g., number of branches, plant size) and physical resistance (e.g., latex, trichomes) more strongly predicted a species’ susceptibility to herbivores (Carmona et al. 2010). Abiotic factors such as air temperature, drought, ozone levels and radiation might cause changes in total leaf phenolics and tannin concentrations because they are involved in mechanisms that protect against abiotic (Peñuelas and Estiarte 1998; Peñuelas et al. 1999) and biotic (Kurokawa and Nakashizuka 2008) stressors. However, the considerable variation among these compounds, and differences in the importance of specific phenolics and tannins in plant defenses, warrants further research to determine whether phenolics and tannins are important in the defense against folivory in these humid tropical forests.

There was an absence of apparent effects of total leaf phenolics and tannin concentrations on accumulated standing folivory. Some studies have observed a negative relationships between leaf phenolics concentrations and herbivore attack (Dudt and Shure 1994; Eichhorn et al. 2007), however, other studies have observed that leaf phenolic concentration is only marginally correlated with levels of herbivore attack (Schuldt et al. 2012). Leaf phenolics synthesis can be induced by herbivore attack as observed in some plant species (Boege 2004). At this regard, the synthesis of phenolics in leaves with more accumulated standing folivory can prevent the observation of negative correlations between leaf phenolics and accumulated standing folivory. Leaf traits not measured in our study, e.g., concentrations of alkaloids, morphological traits, such as toughness, might have had a significant effect on the inter-specific variation in the extent of herbivory, but it is likely that there is a highly diverse range of defensive

strategies among these very highly species-diverse forests. In this regard, it is important to consider that plants can counteract insect attack by mechanisms other than accumulating chemical defenses, e.g. by increasing the susceptibility of herbivores to predator and parasitoid attack (Havill and Raffa 2000; Heil et al. 2001).

Leaf elemental concentrations

Most leaf elemental concentrations of the 88 woody plant species in this study were similar to those in the leaves of rainforest tree species in other studies (Table S9, supporting information). Most of the leaf concentrations of some potentially toxic elements such as As, Cu, Zn, V, Cr, Ni, Mo, Cd, and Pb were within the range of concentrations observed in non-polluted areas throughout the world and considerably lower than the concentrations required to cause leaf damage (Sardans and Peñuelas 2007). The leaf concentrations of As, Cd, Cu, Sr, Mo, Pb, Mo, and Zn were lower, and concentrations of Cr, Fe, Mn, and Ni were higher than those observed in Hawaiian and Australian tropical forests (Table S9, supporting information).

Summarising, the results show a great heterogeneity in leaf composition in this tropical forest as observed in other studies (Townsend et al. 2008). Importantly, the results highlight that the leaf elemental concentrations and stoichiometry in this tropical forest are linked with different ecological strategies, including the adaptation to different successional stages and plant-herbivore relationships. Thus, as we hypothesized, the use of elements in different quantities and proportions can be underlying the great biodiversity of the tropical rainforest. Leaf elemental composition and stoichiometry are related with tree successional stage, leaf molecular composition, and leaf accumulated standing folivory. Moreover early successional species, mostly fast-growing species, had low leaf N:P concentration ratio as expected by the GRH.

Furthermore, the leaf variables relationships fit well with the predictions of the ‘leaf economic spectrum’ and the relations between leaf N concentrations and total phenolics and total tannins fit with ‘carbon excess’ hypotheses. The results also show the importance considering K in stoichiometry ecological studies. Altogether, these results suggest that the different use of nutrients is a cause and/or an effect of the processes underlying in the niche fragmentation and high diversity of this ecosystem.

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Notes on contributions

Josep Peñuelas is a professor, working on a range of issues related to plant ecology: plant ecophysiology, ecosystem functioning, plant-atmosphere and plant-herbivore interactions, ecological stoichiometry and ecometabolomics, and global ecology.

Jordi Sardans is a senior researcher, whose main research lines are the nutrient cycling, ecological stoichiometry and ecometabolomic studies in the frame of ecosystems structure and function and their responses to global change.

Joan Llusia is a senior researcher, whose main research lines are the plant-atmosphere relationships. He has focused his main studies on the research of the terpene content-emission relationships with abiotic and biotic plant relationships,

Jorge Silva is a technician, specialised in the research linked to secondary organic metabolites and chemical ecology in general

Susan M. Owen is a research scientist, whose main research lines are VOCs in, all their biological and environmental aspects, and plant nutrient ecology.

B. Bala-Ola is a botanist who is interested in all the botanical aspects of the tropical forest flora.

Alona C Linatoc is a Ph.D. student. She is interested in all aspects of chemical ecology of tropical forest flora.

M. Noh Dalimin is a professor, interested in all aspects of global change ecology and in the chemical ecology of the tropical forests of south-east Asia.

Ülo Niinemets is a professor, interested in plant stress ecophysiology, physical-chemical-physiological traits of plant species, volatile isoprenoids, community ecology, remote sensing, and global change ecology.

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Figure Captions

Figure 1. Location of the Danum Valley field site in Borneo, Malaysia, and the phylogenetic tree for the 88 woody rain forest species studied. Acronyms of the species used in the other figures are indicated by two letters in bold type face after each species' name..

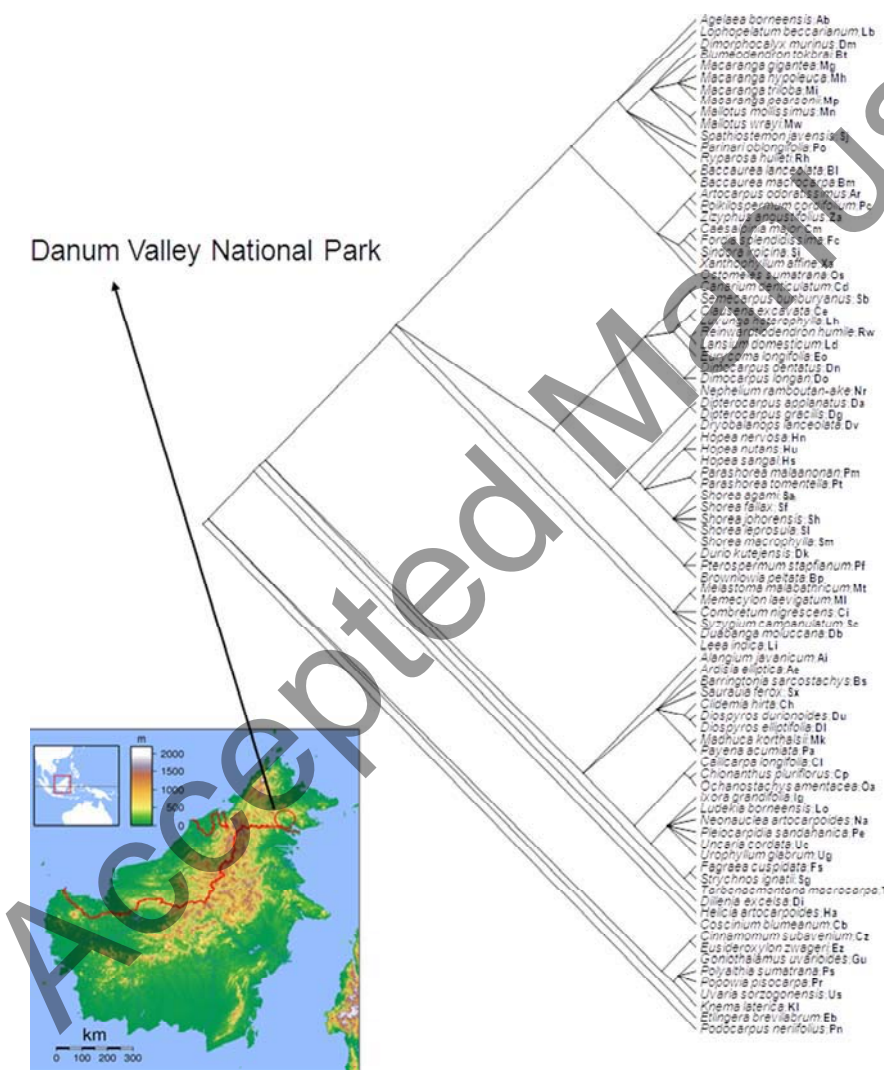


Figure 2. ‘Biogeochemical niche’, successional stages and folivory. (a) Principal component analysis of the leaf concentrations of the 20 elements analysed, and leaf N:P, N:K, and P:K ratios of different 88 woody species. (b) Relationship between accumulated standing folivory and PC1 scores for each species (indication of their Biogeochemical niche). (c) PC2 scores in different successional stages. Different letter indicates statistically significant differences ($P < 0.05$). (Species acronyms defined in Figure 1).

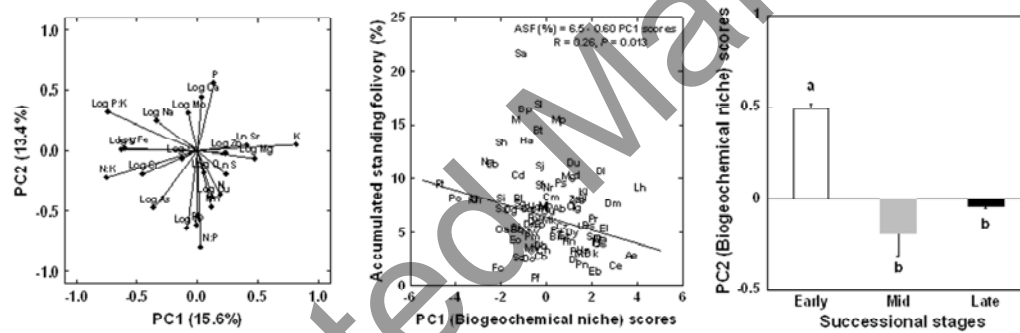


Figure 3. Relationship between accumulated standing folivory and leaf $[K]_{area}$ among 88 woody species in the Bornean rainforest studied. (Species acronyms defined in Figure 1).

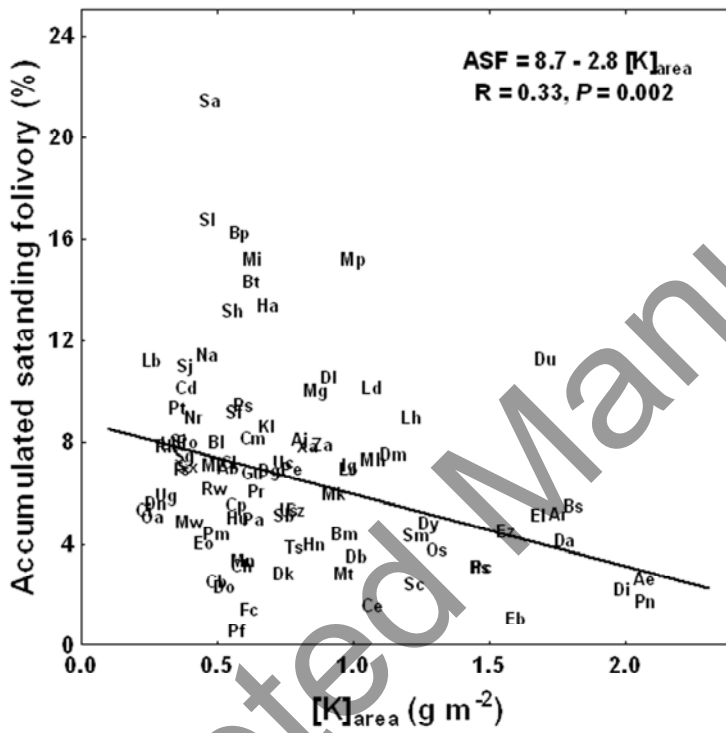


Figure 4. Leaf P concentrations and N:P ratio (means + S.E.) in the species of different successional stages. Different letters indicate significant differences (ANOVA, $P < 0.05$).

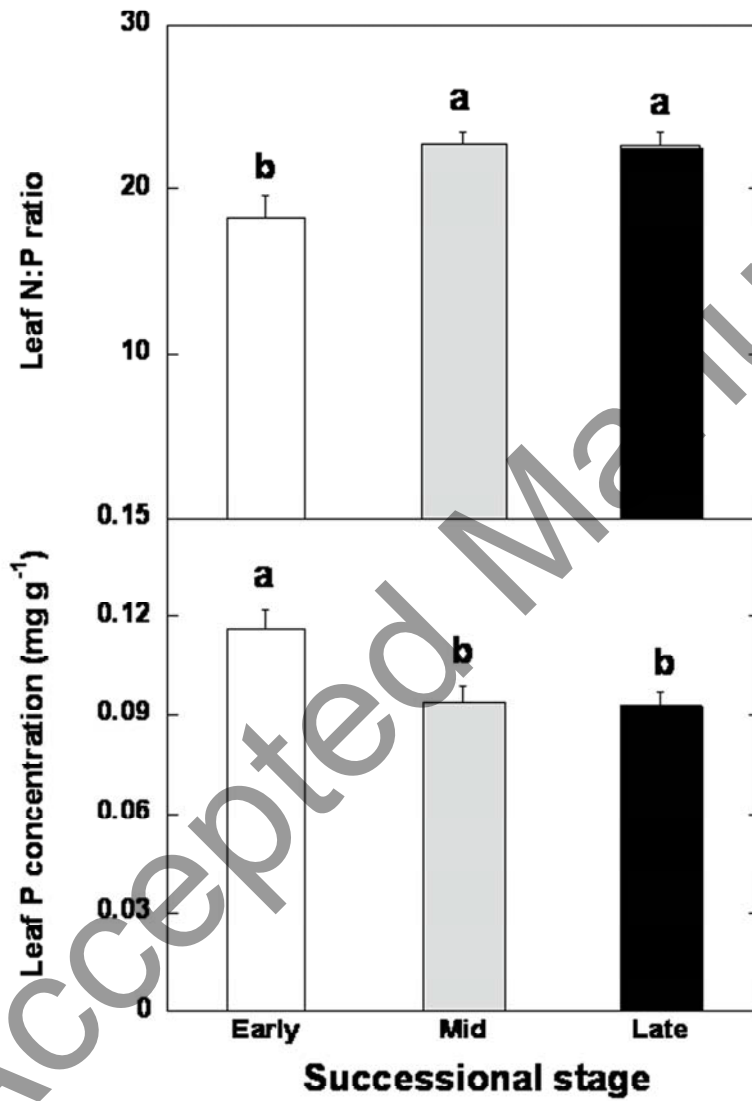


Figure 5. Relationships of LMA and A_{mass} (leaf photosynthetic capacity per unit of leaf weight) with foliar N concentrations (% dry weight) among 88 woody rain forest species in the Danum Valley, Borneo. (Species acronyms defined in Figure 1).

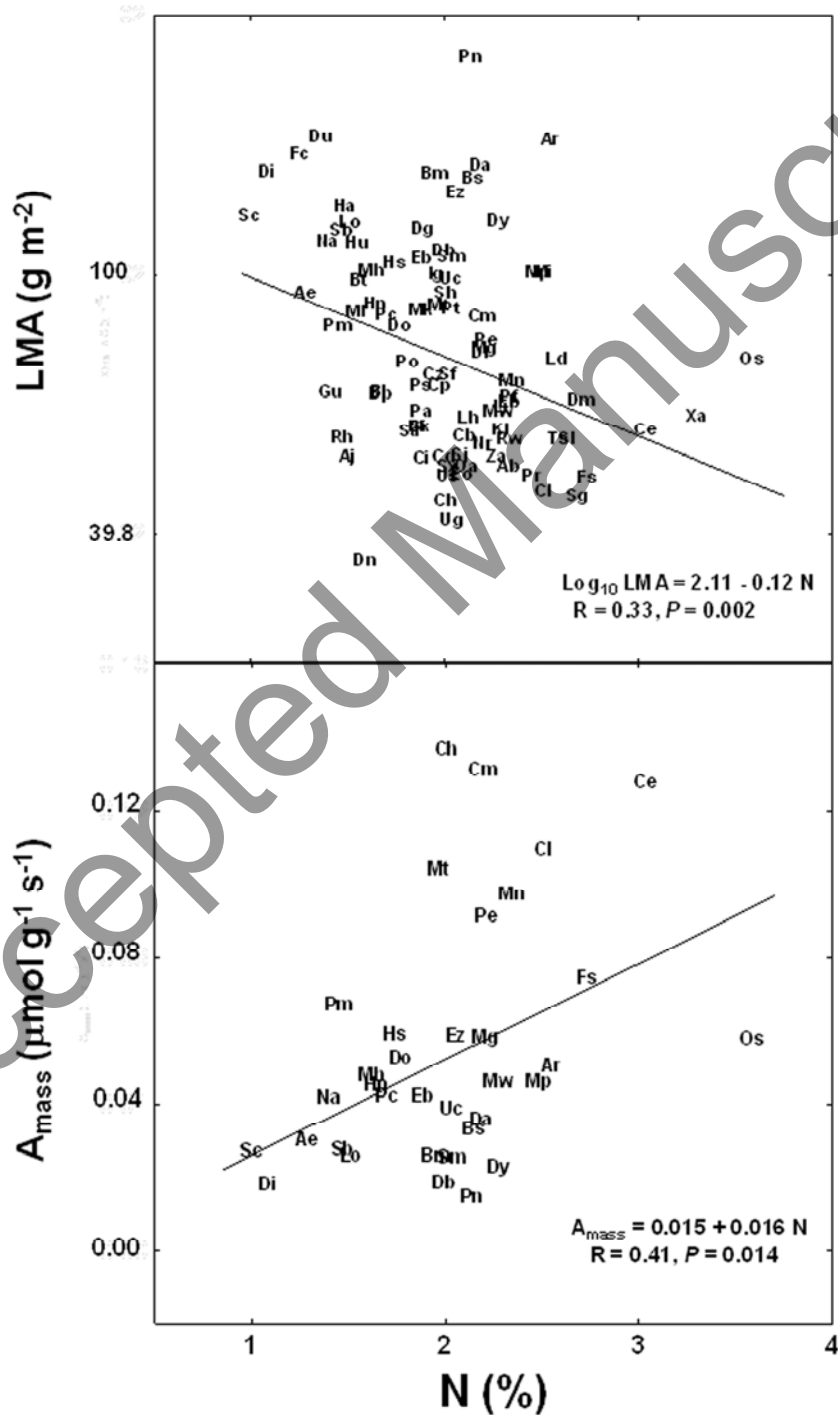
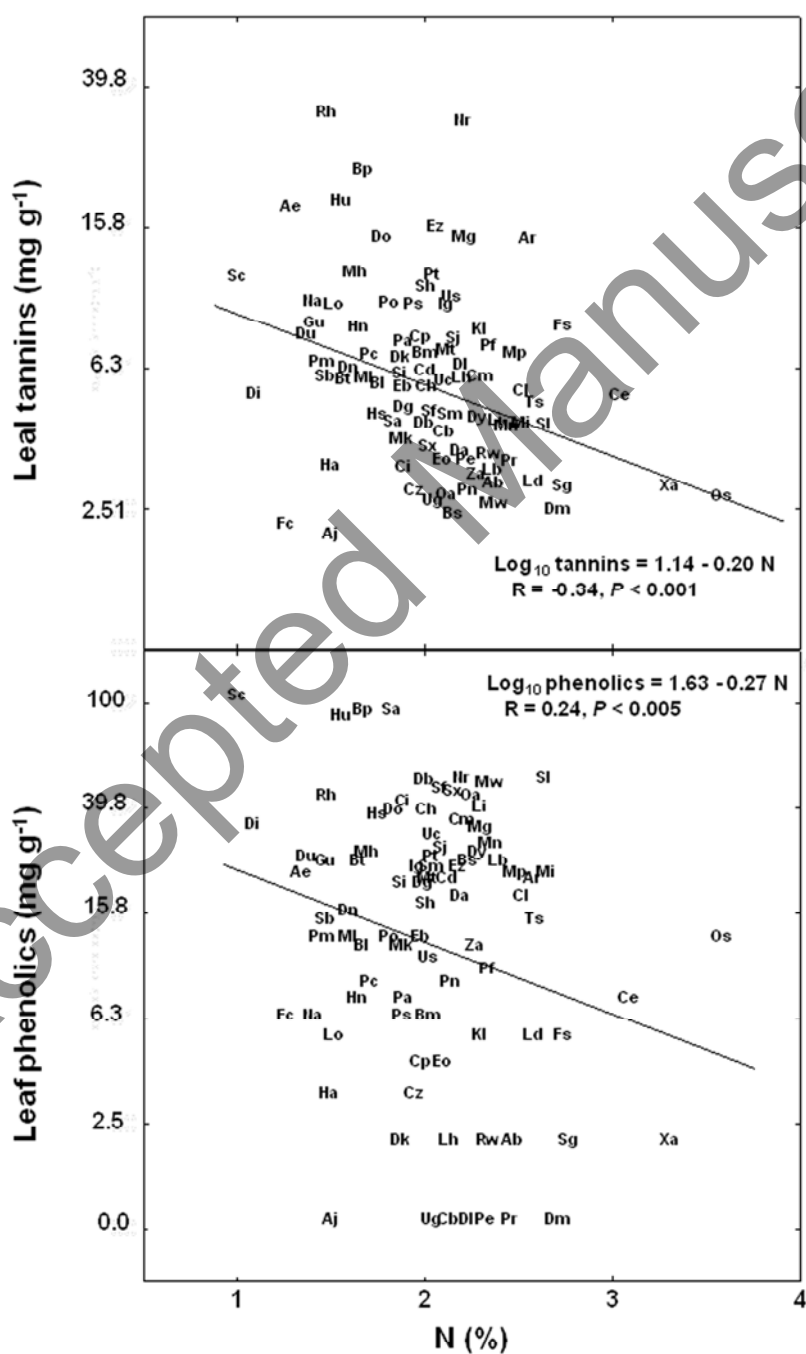


Figure 6. Relationships of concentrations of total leaf phenolics and leaf tannins with foliar N concentrations (% dry weight) of 88 woody species woody rain forest species in the Danum Valley, Borneo. (Species acronyms defined in Figure 1).



Supporting information

Methods

PHYLOGENETIC ANALYSES.- Species-specific averages were calculated for leaf structure, foliage concentrations of elements, phenolics, and tannins, and accumulated standing folivory. The program Phylomatic (Webb and Donoghue 2005) was used to create a phylogenetic tree that included the 88 woody species (Figure S1). Phylomatic assembles a phylogeny for the species of interest using a backbone plant megatree that is based on a variety of sources, primarily, DNA analyses. In our study, the phylogenetic hypothesis was based on a conservative megatree in which unresolved nodes were included as soft polytomies; i.e., multi-branches in the phylogeny that occurred because of insufficient phylogenetic information. To transform the phylogenetic tree into a matrix of phylogenetic distances, we used the Phenotype Diversity Analysis Program (PDAP) (Garland et al. 1993). Significant phylogenetic signals in the traits, i.e., the tendency of closely related species to resemble each other through a shared ancestry, were identified using the randomization procedure in the Matlab PHYSIG module developed by Blomberg et al. (2003), which compares the variance in independent phylogenetic contrasts in the real dataset against a null distribution derived from the phenotypic data after randomizing across the tips of the phylogeny, which breaks any pattern of phylogenetic resemblance between relatives). A phylogenetic signal was significant if the variance in the contrasts in the real dataset was lower than the variance in 95% of the permuted datasets. To make comparisons across traits, we used the k statistic, which indicates how much phylogenetic signal is in the phenotypic data relative to the expectation based on a random walk model of phenotypic evolution (Blomberg et al. 2003). If $k = 1$, then the phenotypic trait has

exactly the amount of signal expected from the phylogenetic tree and it follows a random walk model (Brownian motion). If $k > 1$, the phylogenetic resemblance is greater than expected, and if $k < 1$, it less than expected. Those analyses determined whether phylogenetic correction was required in subsequent regression analyses. Generalized linear models (GLM) were used to identify the “significant” relationships among leaf elemental composition, C:N:P:K stoichiometry, leaf morphological traits, physical and chemical defences, and accumulated standing folivory. When the dependent variable did not exhibit a significant phylogenetic signal, we used ordinary least square regressions (OLS); otherwise, phylogenetic generalized least square regressions (PGLS) were used. PGLS controls for phylogenetic relatedness by adjusting the expected variance/covariance of the regression residuals using the matrix of phylogenetic distances (which is mathematically equivalent to analyzing the data using phylogenetically independent contrasts). Those analyses were performed using the RegressionV2 module in Matlab 7.6.0 (Lavin et al. 2008).

Table S1. Family, life form, height at maturity, and successional stage of 88 woody species in the Danum Valley (Borneo). The acronym used for each species in the figures is shown in the first column together with the species name.

Species	Family	Life form	Mature height (m)	Successional position
<i>Agelaea borneensis</i> (Hook. f.) Merr. Ab	Connaraceae	liana/shrub		mid
<i>Alangium javanicum</i> (Bl.) Wang Ai	Alangiaceae	Tree	30	mid
<i>Ardisia elliptica</i> Thunb. Ae	Myrsinaceae	Tree	6	mid
<i>Artocarpus anisophyllus</i> Ar	Moraceae	tree	25	mid
<i>Baccaurea lanceolata</i> (Miq.) Muell. Arg. Bi	Euphorbiaceae	tree	27	mid
<i>Baccaurea macrocarpa</i> (Miq.) Muell. Arg. Bm	Euphorbiaceae	tree	24	mid
<i>Barringtonia sarcostachys</i> (Bl.) Miq. Bs	Lecythidaceae	tree	24	mid
<i>Blumeodendron tokbrai</i> (Bl.) Kurz Bt	Euphorbiaceae	tree	24	mid
<i>Brownlowia peltata</i> Benth. Bp	Tiliaceae	tree	20	mid
<i>Caesalpinia major</i> (Medik.) Dandy and Exell Cm	Leguminosae	shrub/vine	3	early
<i>Callicarpa longifolia</i> Lamk. Cl	Verbenaceae	shrub	5	early
<i>Canarium denticulatum</i> Bl. Cd	Burseraceae	tree	30	mid
<i>Chionanthus pluriflorus</i> (Knobl.) Kiew Cp	Oleaceae	tree	18	mid
<i>Cinnamomum subavenium</i> Miq. Cz	Lauraceae	tree	35	mid
<i>Clausena excavata</i> Burm. f. Ce	Rutaceae	tree	15	early
<i>Clidemia hirta</i> (L.) D. Don Ch	Melastomaceae	shrub	2	early
<i>Combretum nigrescens</i> King Ci	Combretaceae	liana		mid
<i>Coscinium blumeianum</i> Miers ex Hook. f. and Thomson Cb	Menispermaceae	liana		mid
<i>Dillenia excelsa</i> (Jack) Gilg. DI	Dilleniaceae	tree	35	mid
<i>Dimocarpus dentatus</i> Meijer ex Leenh. Dn	Sapindaceae	tree	15	mid
<i>Dimocarpus longan</i> Lour. subsp. <i>malesianus</i> Leenh. Do	Sapindaceae	tree	30	mid
<i>Dimorphocalyx murinus</i> Elm. Dm	Euphorbiaceae	tree	15	mid
<i>Diospyros durionoides</i> Bakh. Du	Ebenaceae	tree	25	late
<i>Diospyros elliptifolia</i> Merr. DI	Ebenaceae	tree	18	late
<i>Dipterocarpus applanatus</i> Shooten Da	Dipterocarpaceae	tree	50	late
<i>Dipterocarpus gracilis</i> Blume Dg	Dipterocarpaceae	tree	50	late
<i>Dryobalanops lanceolata</i> Burck Dv	Dipterocarpaceae	tree	80	late

<i>Duabanga moluccana</i> Blume Db	Lytraceae	tree	45	early
<i>Durio kutejensis</i> (Hassk.) Becc. Dk	Malvaceae	tree	24	mid
<i>Etilingera brevilabrum</i> (Val.) R.M. Smith Eb	Zingiberaceae	herb	5	early
<i>Eurycoma longifolia</i> Jack Eo	Simaroubaceae	tree/shrub	8	late
<i>Eusideroxylon zwageri</i> Teijsm. and Binn. Ez	Lauraceae	tree	50	late
<i>Fagraea cuspidata</i> Blume Fs	Loganiaceae	tree	18	mid
<i>Fordia splendissima</i> (Blume ex Miq.) Buijsen Fc	Leguminosae	tree/shrub	5	mid
<i>Goniothalamus uvarioides</i> King Gu	Annonaceae	shrub/tree	15	late
<i>Helicia artocarpoides</i> Elmer Ha	Proteaceae	tree	25	mid
<i>Hopea nervosa</i> King Hn	Dipterocarpaceae	tree	30	late
<i>Hopea nutans</i> Ridl. Hu	Dipterocarpaceae	tree	40	late
<i>Hopea sangal</i> Korth. Hs	Dipterocarpaceae	tree	40	late
<i>Ixora grandifolia</i> Zoll. and Moll. Ig	Rubiaceae	shrub/tree	18	mid
<i>Knema latericia</i> Elmer Kl	Myristicaceae	shrub/tree	20	mid
<i>Lansium domesticum</i> Correa Ld	Meliaceae	tree	15	late
<i>Leea indica</i> (Burm. f.) Merr. Li	Leeaceae	shrub/tree	10	mid
<i>Lophopetalum beccarianum</i> Pierre Lb	Celastraceae	tree	36	late
<i>Ludekia borneensis</i> Ridsd. Lo	Rubiaceae	tree	25	early
<i>Luvunga heterophylla</i> Merr. Lh	Rutaceae	liana		mid
<i>Macaranga gigantea</i> (Reichb. f. and Zoll.) Muell. Arg. Mg	Euphorbiaceae	tree	21	early
<i>Macaranga hypoleuca</i> (Reichb. f. and Zoll.) Muell. Arg. Mh	Euphorbiaceae	tree	24	early
<i>Macaranga pearsonii</i> Merr. Mp	Euphorbiaceae	tree	22	early
<i>Macaranga triloba</i> (Thunb.) Mull. Mi	Euphorbiaceae	tree	20	early
<i>Madhuca korthalsii</i> (Pierre) Lam. Mk	Sapotaceae	tree	35	mid
<i>Mallotus mollissimus</i> (Geisel.) Airy Shaw Mn	Euphorbiaceae	tree	26	early
<i>Mallotus wrayi</i> King ex Hook. f. Mw	Euphorbiaceae	shrub/tree	12	mid
<i>Melastoma malabathricum</i> L. Mt	Melastomaceae	shrub	2	early
<i>Memecylon laevigatum</i> Blume Ml	Melastomaceae	shrub/tree	20	mid
<i>Neonauclea artocarpoides</i> Ridsd. Na	Rubiaceae	tree	20	early
<i>Nephelium ramboutan-ake</i> (Labill.) Leenh. Nr	Sapindaceae	tree	40	mid
<i>Ochanostachys amentacea</i> Mast. Oa	Olacaceae	tree	30	mid
<i>Octomeles sumatrana</i> Miq. Os	Datiscaceae	tree	70	early
<i>Parashorea malaanonan</i> (Blanco) Merr. Pm	Dipterocarpaceae	tree	60	late
<i>Parashorea tomentella</i> (Symingt.) Meijer Pt	Dipterocarpaceae	tree	65	late

<i>Parinari oblongifolia</i> Hk. f. Po	Chrysobalanaceae	tree	40	mid
<i>Payena acuminata</i> (Bl.) Pierre Pa	Sapotaceae	tree	30	mid
<i>Pleiocarpidia sandahanica</i> Brem. Pe	Rubiaceae	tree	15	early
<i>Podocarpus nerifolius</i> D. Don Pn	Podocarpaceae	tree	36	late
<i>Poikilospermum cordifolium</i> (Barg.-Petr.) Merrill Pc	Urticaceae	liana		mid
<i>Polyalthia sumatrana</i> (Miq.) Kurz Ps	Annonaceae	tree	15	mid
<i>Popowia pisocarpa</i> (Bl.) Endl. Pr	Annonaceae	shrub/tree	10	late
<i>Pterospermum stapfianum</i> Ridl. Pf	Malvaceae	tree	25	mid
<i>Reinwardtiodendron humile</i> (Hassk.) Mabb. Rw	Meliaceae	tree	27	mid
<i>Ryparosa hulletii</i> King. Rh	Flacourtiaceae	tree	15	mid
<i>Saurauia ferox</i> Korth. Sx	Actinidiaceae	tree	5	mid
<i>Semecarpus bunburyanus</i> Gibbs Sb	Anacardiaceae	tree	15	early
<i>Shorea agami</i> P. S. Ashton Sa	Dipterocarpaceae	tree	50	late
<i>Shorea fallax</i> Meijer Sf	Dipterocarpaceae	tree	50	late
<i>Shorea johorensis</i> Foxw. Sh	Dipterocarpaceae	tree	50	late
<i>Shorea leprosula</i> Miq. Sl	Dipterocarpaceae	tree	60	late
<i>Shorea macrophylla</i> (de Vriese) P. S. Ashton Sm	Dipterocarpaceae	tree	45	mid
<i>Sindora irpicina</i> de Wit Si	Leguminosae	tree	40	mid
<i>Spathiostemon javensis</i> Bl. Sj	Euphorbiaceae	tree	17	mid
<i>Strychnos ignatii</i> Bergius Sg	Loganiaceae	liana	35	mid
<i>Syzygium campanulatum</i> Korth. Sc	Myrtaceae	tree	30	early
<i>Tabernaemontana macrocarpa</i> Jack Ts	Apocynaceae	shrub/tree	30	mid
<i>Uncaria cordata</i> (Lour.) Merr. Uc	Rubiaceae	liana		early
<i>Urophyllum glabrum</i> Wall. sensu Ridl. Ug	Rubiaceae	shrub/tree	5	mid
<i>Uvaria sorzogonensis</i> C. Presl. Us	Annonaceae	liana		mid
<i>Xanthophyllum affine</i> Korth. Xa	Polygalaceae	tree	30	late
<i>Zizyphus angustifolius</i> (Miq.) Hatusima ex Steen Za	Rhamnaceae	tree	30	mid

Table S2. Foliar bioelement concentrations (mean; S.E. between brackets) in 88 woody plant species in the Bornean rainforest studied (n = 3 sets of 6-37 leaves each).

Species	C (%)	N (%)	Ca (%)	K (%)	Mg (%)	S (%)	P (%)	Fe (mg kg ⁻¹)
<i>Agelaea borneensis</i>	46.2 (0.5)	2.33 (0.08)	0.45 (0.18)	1.11 (0.09)	0.53 (0.07)	0.26 (0.01)	0.09 (0.006)	72.7 (13.4)
<i>Alangium javanicum</i>	48.7 (0.1)	1.50 (0.01)	0.44 (0.01)	1.60 (0.01)	0.18 (0.01)	0.19 (0.003)	0.12 (0.001)	44.0 (0.2)
<i>Ardisia elliptica</i>	47.0 (0.8)	1.29 (0.27)	1.27 (0.12)	2.30 (0.25)	0.63 (0.08)	0.11 (0.01)	0.08 (0.01)	39.7 (5.4)
<i>Artocarpus anisophyllus</i>	45.2 (0.4)	2.55 (0.05)	1.35 (0.17)	1.13 (0.11)	0.13 (0.07)	0.16 (0.00)	0.12 (0.003)	139 (13.3)
<i>Baccaurea lanceolata</i>	45.7 (4.5)	1.66 (0.20)	2.13 (0.79)	0.79 (0.14)	0.34 (0.04)	0.23 (0.06)	0.08 (0.005)	123 (44.0)
<i>Baccaurea macrocarpa</i>	46.8 (0.5)	1.96 (0.48)	1.80 (0.20)	0.71 (0.20)	0.59 (0.03)	0.13 (0.02)	0.08 (0.01)	53.0 (14.7)
<i>Barringtonia sarcostachys</i>	47.2 (0.8)	2.15 (0.13)	2.13 (0.49)	1.33 (0.09)	0.55 (0.23)	0.34 (0.03)	0.11 (0.004)	104 (26.7)
<i>Blumeodendron tokbrai</i>	47.2 (0.6)	1.56 (0.13)	2.08 (0.68)	0.66 (0.14)	0.27 (0.10)	0.28 (0.13)	0.08 (0.008)	80.0 (33.3)
<i>Brownlowia peltata</i>	51.1 (1.5)	1.67 (0.18)	0.76 (0.27)	0.93 (0.13)	0.18 (0.02)	0.19 (0.06)	0.10 (0.007)	87.7 (0.3)
<i>Caesalpinia major</i>	48.4 (0.8)	2.20 (0.20)	2.27 (0.62)	0.76 (0.12)	0.23 (0.03)	0.20 (0.02)	0.11 (0.003)	58.3 (5.2)
<i>Callicarpa longifolia</i>	48.8 (0.9)	2.51 (0.56)	1.14 (0.23)	1.22 (0.24)	0.23 (0.02)	0.17 (0.01)	0.12 (0.02)	74.0 (7.1)
<i>Canarium denticulatum</i>	47.6 (0.7)	2.00 (0.10)	0.91 (0.22)	0.77 (0.12)	0.22 (0.02)	0.15 (0.01)	0.10 (0.003)	80.0 (1.5)
<i>Chionanthus pluriflorus</i>	49.2 (0.6)	1.98 (0.34)	1.18 (0.17)	0.88 (0.22)	0.17 (0.03)	0.13 (0.03)	0.12 (0.01)	41.3 (3.8)
<i>Cinnamomum subavenium</i>	49.5 (0.5)	1.95 (0.19)	0.76 (0.20)	1.17 (0.03)	0.19 (0.003)	0.16 (0.12)	0.08 (0.01)	71.0 (22.0)
<i>Clausena excavata</i>	45.5 (1.1)	3.04 (0.06)	1.50 (0.00)	1.93 (0.13)	0.36 (0.01)	0.23 (0.02)	0.14 (0.00)	62.3 (7.4)
<i>Clidemia hirta</i>	47.9 (1.5)	2.01 (0.04)	0.61 (0.06)	1.37 (0.09)	0.34 (0.04)	0.15 (0.01)	0.10 (0.003)	159 (90)
<i>Combretum nigrescens</i>	44.7 (0.3)	1.88 (0.14)	1.16 (0.10)	0.46 (0.08)	0.29 (0.06)	0.12 (0.01)	0.10 (0.02)	1266 (808)
<i>Coscinium blumeanum</i>	49.6 (0.02)	2.11 (0.17)	0.49 (0.05)	0.92 (0.03)	0.14 (0.01)	0.17 (0.02)	0.08 (0.01)	64.5 (5.7)
<i>Dillenia excelsa</i>	46.5 (0.2)	1.09 (0.07)	0.85 (0.04)	1.43 (0.03)	0.22 (0.03)	0.23 (0.04)	0.08 (0.002)	57.7 (4.3)
<i>Dimocarpus dentatus</i>	45.0 (3.7)	1.59 (0.18)	1.06 (0.19)	0.80 (0.21)	0.28 (0.04)	0.16 (0.04)	0.11 (0.02)	59.3 (14.5)
<i>Dimorphocalyx murinus</i>	47.3 (0.5)	2.71 (0.07)	1.23 (0.19)	1.87 (0.20)	0.91 (0.23)	0.14 (0.003)	0.11 (0.02)	75.3 (24.4)
<i>Diospyros durionoides</i>	47.0 (1.5)	1.37 (0.54)	2.13 (0.26)	1.09 (0.12)	0.46 (0.25)	0.12 (0.02)	0.10 (0.003)	55.7 (11.9)
<i>Diospyros elliptifolia</i>	49.2 (0.1)	2.19 (0.07)	1.50 (0.13)	1.25 (0.03)	0.46 (0.01)	0.24 (0.03)	0.08 (0.00)	47.0 (3.3)
<i>Dipterocarpus applanatus</i>	49.2 (2.2)	2.19 (0.21)	1.50 (0.40)	1.25 (0.29)	0.46 (0.08)	0.24 (0.04)	0.08 (0.02)	47.0 (25.7)
<i>Dipterocarpus gracilis</i>	53.4 (2.4)	1.89 (0.05)	0.88 (0.03)	0.61 (0.05)	0.24 (0.06)	0.15 (0.02)	0.09 (0.01)	104 (39.4)
<i>Dryobalanops lanceolata</i>	53.6 (6.2)	2.28 (0.32)	0.90 (0.12)	1.10 (0.21)	0.58 (0.10)	0.20 (0.04)	0.09 (0.02)	81.3 (9.3)
<i>Duabanga moluccana</i>	47.4 (0.0)	2.00 (0.01)	1.20 (0.00)	0.97 (0.01)	0.30 (0.00)	0.12 (0.00)	0.13 (0.00)	66.0 (0.2)
<i>Durio kutejensis</i>	46.4 (0.6)	1.87 (0.16)	0.76 (0.14)	1.33 (0.15)	0.50 (0.08)	0.17 (0.01)	0.07 (0.01)	54.3 (3.8)

<i>Etlingera brevilabrum</i>	46.5	1.89	1.22	1.57	0.39	0.15	0.09	57.3
	(1.1)	(0.22)	(0.49)	(0.20)	(0.12)	(0.003)	(0.00)	(9.3)
<i>Euphoria malaiensis</i> =	51.4	1.41	0.77	1.13	0.25	0.15	0.10	47.3
<i>Dimocarpus longan</i>	(0.5)	(0.04)	(0.08)	(0.08)	(0.02)	(0.01)	(0.00)	(0.03)
<i>Eurycoma longifolia</i>	44.2	2.09	0.40	0.96	0.27	0.14	0.10	118
	(1.2)	(0.07)	(0.05)	(0.22)	(0.01)	(0.003)	(0.02)	(31.9)
<i>Eusideroxylon</i>	46.6	2.06	0.97	1.21	0.40	0.13	0.12	76.7
<i>zwageri</i>	(0.9)	(0.16)	(0.19)	(0.26)	(0.09)	(0.01)	(0.00)	(4.7)
<i>Fagraea cuspidata</i>	47.2	1.26	1.11	0.42	0.20	0.11	0.07	70.3
	(1.0)	(0.13)	(0.25)	(0.12)	(0.02)	(0.01)	(0.03)	(11.9)
<i>Fordia splendidissima</i>	49.9	2.74	0.23	0.80	0.17	0.17	0.09	61.3
	(0.2)	(0.17)	(0.04)	(0.06)	(0.04)	(0.01)	(0.01)	(4.9)
<i>Goniothalamus</i>	47.8	1.41	1.09	1.00	0.16	0.15	0.06	64.3
<i>uvarioides</i>	(1.7)	(0.20)	(0.56)	(0.31)	(0.04)	(0.05)	(0.004)	(14.2)
<i>Helicia artocarpoides</i>	45.5	1.49	0.51	0.56	0.39	0.13	0.04	53.7
	(0.9)	(0.05)	(0.07)	(0.02)	(0.02)	(0.02)	(0.00)	(6.4)
<i>Hopea nervosa</i>	48.1	1.65	1.41	0.99	0.38	0.17	0.10	75.5
	(1.5)	(0.09)	(0.53)	(0.27)	(0.19)	(0.03)	(0.01)	(13.7)
<i>Hopea nutans</i>	51.8	1.56	0.76	0.54	0.22	0.16	0.06	61.0
	(0.2)	(0.05)	(0.10)	(0.06)	(0.01)	(0.01)	(0.002)	(10.0)
<i>Hopea sangal</i>	49.1	1.75	0.82	1.47	0.39	0.18	0.11	84.7
	(1.8)	(0.14)	(0.24)	(0.33)	(0.13)	(0.03)	(0.02)	(15.3)
<i>Ixora grandifolia</i>	48.0	1.96	1.47	1.02	0.35	0.20	0.05	37.0
	(1.3)	(0.52)	(0.15)	(0.19)	(0.06)	(0.05)	(0.006)	(3.5)
<i>Knema latericia</i>	57.2	2.29	0.69	1.23	0.43	0.17	0.10	41.3
	(6.5)	(0.39)	(0.21)	(0.21)	(0.10)	(0.02)	(0.01)	(9.9)
<i>Lansium domesticum</i>	47.8	2.58	0.99	1.50	0.43	0.18	0.14	94.7
	(0.3)	(0.04)	(0.11)	(0.25)	(0.08)	(0.01)	(0.01)	(24.7)
<i>Leea indica</i>	50.6	2.29	0.48	0.53	0.24	0.12	0.08	108
	(0.9)	(0.76)	(0.02)	(0.09)	(0.03)	(0.02)	(0.01)	(44.1)
<i>Lophoetalum</i>	49.6	2.34	1.37	0.43	0.44	0.24	0.10	38.0
<i>beccarianum</i>	(0.3)	(0.51)	(0.12)	(0.03)	(0.07)	(0.03)	(0.01)	(3.6)
<i>Ludekia borneensis</i>	50.7	1.52	1.00	0.85	0.16	0.14	0.12	41.3
	(0.4)	(0.20)	(0.21)	(0.13)	(0.05)	(0.02)	(0.01)	(6.9)
<i>Luvunga heterophylla</i>	49.7	2.13	0.70	2.10	0.54	0.18	0.07	59.0
	(0.3)	(0.04)	(0.14)	(0.06)	(0.05)	(0.02)	(0.001)	(7.5)
<i>Macaranga gigantea</i>	46.6	2.21	1.35	1.17	0.55	0.21	0.13	82.7
	(2.9)	(0.20)	(0.28)	(0.15)	(0.15)	(0.02)	(0.00)	(9.3)
<i>Macaranga hypoleuca</i>	48.4	1.63	0.64	1.10	0.24	0.17	0.10	73.5
	(0.5)	(0.30)	(0.09)	(0.23)	(0.02)	(0.01)	(0.003)	(9.1)
<i>Macaranga triloba</i>	47.7	2.51	0.81	0.65	0.26	0.16	0.11	68.0
	(0.0)	(0.01)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.5)
<i>Macaranga pearsonii</i>	47.3	2.49	1.35	1.04	0.32	0.27	0.13	80.0
	(0.1)	(0.28)	(0.10)	(0.18)	(0.01)	(0.02)	(0.003)	(8.0)
<i>Madhuca korthalsii</i>	44.9	1.88	0.46	1.10	0.31	0.38	0.05	130
	(1.4)	(0.13)	(0.02)	(0.01)	(0.03)	(0.12)	(0.003)	(23.6)
<i>Mallotus mollissimus</i>	46.7	2.35	2.20	0.90	0.41	0.26	0.17	151
	(0.7)	(0.38)	(0.46)	(0.21)	(0.06)	(0.03)	(0.01)	(15.5)
<i>Mallotus wrayi</i>	45.7	2.28	0.76	0.68	0.20	0.30	0.09	77.7
	(0.4)	(0.04)	(0.17)	(0.05)	(0.01)	(0.003)	(0.00)	(12.8)
<i>Melastoma</i>	45.3	1.97	1.72	1.12	0.60	0.19	0.11	77.5
<i>malabathricum</i>	(1.9)	(0.35)	(0.36)	(0.31)	(0.09)	(0.06)	(0.01)	(21.8)
<i>Memecylon</i>	45.9	1.55	0.87	0.57	0.25	0.43	0.05	44.7
<i>laevigatum</i>	(0.6)	(0.11)	(0.20)	(0.09)	(0.01)	(0.15)	(0.004)	(1.3)
<i>Neonauclea</i>	47.6	1.40	1.60	0.43	0.43	0.16	0.08	127
<i>artocarpoides</i>	(0.5)	(0.19)	(0.25)	(0.01)	(0.03)	(0.01)	(0.02)	(15.6)
<i>Nephelium</i>	50.2	2.20	1.26	0.79	0.53	0.15	0.10	58.3
<i>ramboutan-ake</i>	(0.6)	(0.32)	(0.32)	(0.19)	(0.11)	(0.02)	(0.01)	(7.0)
<i>Ochanostachys</i>	50.9	2.12	0.14	0.54	0.12	0.15	0.08	55.0
<i>amentacea</i>	(0.5)	(0.09)	(0.02)	(0.04)	(0.02)	(0.01)	(0.001)	(4.0)

	49.4	3.59	0.93	1.83	0.38	0.17	0.16	102
<i>Octomeles sumatrana</i>	(0.6)	(0.02)	(0.04)	(0.12)	(0.09)	(0.01)	(0.01)	(26.8)
<i>Parashorea</i>	47.0	1.46	1.39	0.63	0.37	0.19	0.07	73.0
<i>malonaanan</i>	(0.6)	(0.44)	(0.42)	(0.14)	(0.11)	(0.01)	(0.03)	(4.6)
<i>Parashorea</i>	45.5	2.04	1.67	0.42	0.18	0.16	0.10	183
<i>tomentella</i>	(0.6)	(0.10)	(0.41)	(0.02)	(0.06)	(0.01)	(0.01)	(91.7)
	46.8	1.81	0.88	0.56	0.19	0.16	0.07	261
<i>Parinari oblongifolia</i>	(1.1)	(0.21)	(0.11)	(0.08)	(0.07)	(0.03)	(0.00)	(178)
	52.0	1.89	0.48	1.07	0.22	0.17	0.06	64.7
<i>Payena acuminata</i>	(0.7)	(0.06)	(0.09)	(0.09)	(0.02)	(0.01)	(0.003)	(11.8)
<i>Pleiocarpidia</i>	45.4	2.22	1.20	1.0	0.35	0.27	0.11	97.7
<i>sandahanica</i>	(0.5)	(0.17)	(0.10)	(0.08)	(0.04)	(0.07)	(0.01)	(31.7)
	47.2	2.14	1.53	0.99	0.44	0.22	0.10	46.7
<i>Podocarpus neriifolius</i>	(1.5)	(0.08)	(0.33)	(0.21)	(0.15)	(0.08)	(0.00)	(6.4)
<i>Poikilospermum</i>	39.9	1.71	5.33	1.77	0.54	0.22	0.15	182
<i>cordifolium</i>	(1.9)	(0.13)	(0.61)	(0.39)	(0.16)	(0.02)	(0.01)	(55.0)
	52.8	1.88	0.68	0.93	0.20	0.15	0.07	51.0
<i>Polyalthia sumatrana</i>	(0.5)	(0.01)	(0.10)	(0.09)	(0.00)	(0.01)	(0.004)	(2.6)
	47.4	2.46	0.52	1.37	0.43	0.26	0.08	61.0
<i>Popowia pisocarpa</i>	(0.03)	(0.10)	(0.09)	(0.12)	(0.04)	(0.01)	(0.004)	(3.6)
<i>Pterospermum</i>	47.3	2.34	2.03	0.92	0.23	0.20	0.18	73.3
<i>stapfianum</i>	(0.4)	(0.18)	(0.19)	(0.14)	(0.05)	(0.02)	(0.04)	(14.2)
<i>Reinwardtiodendron</i>	47.3	2.34	2.03	0.92	0.23	0.20	0.18	73.3
<i>humile</i>	(0.7)	(0.02)	(0.15)	(0.17)	(0.07)	(0.01)	(0.01)	(1)
	49.4	1.48	1.21	0.58	0.28	0.15	0.08	132
<i>Ryparosa hulletii</i>	(1.6)	(0.16)	(0.62)	(0.12)	(0.04)	(0.02)	(0.01)	(41.4)
	48.1	2.02	1.51	0.80	0.16	0.31	0.10	124
<i>Saurauia ferox</i>	(2.9)	(0.08)	(0.66)	(0.00)	(0.02)	(0.08)	(0.01)	(51.1)
<i>Semecarpus</i>	46.6	1.47	1.04	0.66	0.29	0.16	0.15	45.7
<i>bunburyanus</i>	(0.5)	(0.06)	(0.14)	(0.09)	(0.03)	(0.01)	(0.03)	(6.2)
	48.6	1.83	1.17	0.86	0.21	0.11	0.08	139
<i>Shorea agami</i>	(1.18)	(0.19)	(0.18)	(0.20)	(0.07)	(0.01)	(0.02)	(46.5)
	50.9	2.02	0.90	0.84	0.29	0.13	0.09	78.3
<i>Shorea fallax</i>	(0.8)	(0.23)	(0.36)	(0.25)	(0.02)	(0.01)	(0.01)	(41.1)
	50.5	2.01	1.08	0.62	0.31	0.18	0.10	138
<i>Shorea johorensis</i>	(0.2)	(0.15)	(0.25)	(0.07)	(0.06)	(0.02)	(0.004)	(41.1)
	51.4	2.64	0.86	0.87	0.22	0.15	0.12	60.0
<i>Shorea leprosula</i>	(0.1)	(0.06)	(0.07)	(0.05)	(0.05)	(0.01)	(0.003)	(4.0)
	47.0	2.04	1.80	1.20	0.63	0.29	0.16	50.0
<i>Shorea macrophylla</i>	(0.0)	(0.01)	(0.01)	(0.02)	(0.00)	(0.00)	(0.003)	(0.7)
	50.7	1.87	0.77	0.64	0.22	0.16	0.08	126
<i>Sindora irpicina</i>	(0.4)	(0.21)	(0.09)	(0.04)	(0.05)	(0.02)	(0.01)	(80.6)
<i>Spathiostemon</i>	48.2	2.08	1.39	0.75	0.30	0.23	0.09	71.3
<i>javensis</i>	(1.1)	(0.40)	(0.33)	(0.07)	(0.09)	(0.07)	(0.01)	(11.9)
	46.1	2.69	1.18	0.87	0.43	0.27	0.08	68.0
<i>Stychnos ignatii</i>	(0.6)	(0.22)	(0.40)	(0.13)	(0.11)	(0.07)	(0.001)	(9.1)
<i>Syzygium</i>	50.6	1.00	0.77	1.03	0.10	0.12	0.09	45.3
<i>campanulatum</i>	(0.5)	(0.05)	(0.12)	(0.17)	(0.05)	(0.02)	(0.03)	(10.6)
<i>Tarbernaemontana</i>	50.8	2.59	0.65	1.47	0.31	0.29	0.09	53.7
<i>macrocarpa</i>	(0.6)	(0.08)	(0.11)	(0.12)	(0.04)	(0.01)	(0.01)	(5.6)
	51.7	2.04	0.64	0.79	0.21	0.20	0.08	58.3
<i>Uncaria cordata</i>	(1.0)	(0.21)	(0.14)	(0.04)	(0.02)	(0.03)	(0.01)	(9.7)
	51.7	2.04	0.64	0.79	0.21	0.20	0.08	58.3
<i>Urophyllum glabrum</i>	(0.84)	(0.22)	(0.16)	(0.05)	(0.16)	(0.02)	(0.01)	(6.6)
	47.2	2.02	0.39	1.63	0.28	0.14	0.10	70.3
<i>Uvaria sorzogonensis</i>	(3.1)	(0.12)	(0.07)	(0.13)	(0.03)	(0.003)	(0.01)	(3.2)
	47.9	3.30	0.37	1.43	0.17	0.23	0.11	45.7
<i>Xanthophyllum affine</i>	(0.62)	(0.34)	(0.13)	(0.29)	(0.01)	(0.01)	(0.03)	(3.5)
	51.1	2.27	0.92	1.77	0.33	0.17	0.13	82.3
<i>Zizyphus angustifolius</i>	(2.3)	(0.60)	(0.33)	(0.17)	(0.06)	(0.01)	(0.02)	(30.6)

Table S3. Foliar trace element concentrations in 88 woody plant species (mean; S.E. between brackets) in the Bornean rainforest studied (n = 3 sets of 6-37 leaves each).

Species	Mn (mg kg ⁻¹)	V (mg kg ⁻¹)	Cr (mg kg ⁻¹)	Ni (mg kg ⁻¹)	Cu (mg kg ⁻¹)	Zn (mg kg ⁻¹)	As (mg kg ⁻¹)	Sr (mg kg ⁻¹)	Mo (mg kg ⁻¹)	Cd (mg kg ⁻¹)	Pb (mg kg ⁻¹)
<i>Agelaea borneensis</i>	1161 (141)	<0.200	4.5 (2.1)	22.7 (5.6)	18.3 (1.8)	19.8 (1.7)	0.103 (0.001)	27 (6.4)	<0.200	0.147 (0.042)	0.603 (0.399)
<i>Alangium javanicum</i>	199 (5)	0.222 (0.003)	0.6 (0.1)	2.5 (0.4)	6.7 (0.0)	13.0 (0.1)	0.084 (0.003)	32 (1)	<0.200	0.123 (0.004)	0.202 (0.006)
<i>Ardisia elliptica</i>	20 (0)	<0.200	0.4 (0.1)	1.1 (0.4)	3.1 (0.9)	9.2 (0.2)	0.111 (0.002)	53 (16)	0.209 (0.003)	0.154 (0.010)	0.210 (0.008)
<i>Artocarpus anisophyllus</i>	92 (7)	0.205 (0.003)	9.2 (0.5)	5.1 (0.1)	6.1 (0.3)	12.3 (3.1)	0.165 (0.002)	53 (4)	0.500 (0.067)	0.130 (0.002)	0.270 (0.047)
<i>Baccaurea lanceolata</i>	166 (28)	0.270 (0.070)	21.0 (8.9)	5.7 (2.0)	5.8 (1.2)	21.3 (6.8)	0.102 (0.009)	53 (22)	0.237 (0.037)	0.106 (0.011)	0.240 (0.040)
<i>Baccaurea macrocarpa</i>	364 (174)	<0.200	0.8 (0.3)	8.8 (2.1)	9.0 (2.0)	27.0 (10.0)	<0.090	118 (20)	0.255 (0.033)	0.165 (0.006)	0.360 (0.027)
<i>Barringtonia sarcostachys</i>	1020 (978)	0.207 (0.007)	1.0 (0.4)	2.6 (0.8)	9.7 (1.4)	54.7 (16.5)	0.123 (0.011)	69 (45)	0.221 (0.013)	0.121 (0.002)	0.373 (0.149)
<i>Blumeodendron tokbrai</i>	696 (244)	0.217 (0.017)	0.6 (0.2)	2.7 (1.6)	5.3 (1.1)	10.2 (3.6)	<0.090	118 (74)	0.290 (0.090)	0.110 (0.012)	0.266 (0.043)
<i>Brownlowia peltata</i>	187 (105)	0.223 (0.023)	3.2 (1.8)	1.6 (0.5)	4.6 (0.8)	15.0 (2.5)	0.150 (0.012)	22 (7)	0.211 (0.023)	<0.100	0.211 (0.032)
<i>Caesalpinia major</i>	1151 (345)	0.288 (0.026)	0.3 (0.1)	2.6 (0.2)	13.3 (0.9)	12.3 (1.3)	<0.090	123 (27)	0.276 (0.09)	<0.100	0.217 (0.017)
<i>Callicarpa longifolia</i>	1534 (918)	0.213 (0.022)	0.6 (0.4)	2.6 (1.0)	2.6 (2.1)	12.0 (13.1)	<0.090	51 (11)	0.207 (0.007)	0.103 (0.011)	<0.200
<i>Canarium denticulatum</i>	104 (54)	0.287 (0.033)	3.0 (0.1)	8.3 (3.2)	6.6 (0.6)	10.2 (0.4)	0.143 (0.005)	53 (19)	0.277 (0.077)	<0.100	0.503 (0.224)
<i>Chionanthus pluriflorus</i>	253 (214)	<0.200	0.5 (0.2)	2.6 (0.7)	8.3 (3.5)	10.7 (2.9)	0.121 (0.031)	52 (24)	<0.200	<0.100	0.223 (0.016)
<i>Cinnamomum subavenium</i>	696 (640)	<0.200	1.7 (0.9)	6.2 (0.6)	7.4 (1.3)	19.3 (3.1)	0.140 (0.009)	79 (29)	0.221 (0.024)	0.107 (0.012)	1.267 (1.068)
<i>Clausena excavata</i>	26 (0.3)	<0.200	0.3 (0.1)	3.7 (0.4)	6.1 (0.3)	32.3 (2.4)	<0.090	82 (3.6)	0.209 (0.004)	<0.100 (0.004)	0.213 (0.013)
<i>Clidemia hirta</i>	229 (185)	0.330 (0.130)	2.1 (1.4)	9.2 (1.9)	8.9 (0.6)	18.0 (4.9)	<0.090	98 (63)	0.217 (0.017)	0.320 (0.220)	0.430 (0.169)
<i>Combretum nigrescens</i>	114 (15)	4.603 (3.221)	4.7 (0.5)	2.9 (0.1)	10.2 (1.9)	11.0 (1.5)	0.203 (0.103)	52 (15)	<0.200 (0.028)	0.150 (0.028)	0.750 (0.339)
<i>Coscinium</i>	101	0.298	1.9	2.2	23.2	17.4	0.110	53	<0.200	<0.100	1.080

<i>blumeum</i>	(39)	(0.030)	(0.2)	(0.4)	(9.2)	(5.1)	(0.011)	(11)			(0.547)
<i>Dillenia excelsa</i>	20	0.300	1.9	2.4	6.0	15.0	0.103	37	0.283	<0.100	<0.200
	(1)	(0.002)	(0.7)	(0.5)	(0.2)	(1.2)	(0.009)	(8)	(0.060)		
<i>Dimocarpus</i>	494	0.210	1.0	2.0	5.2	8.5	0.099	25	0.237	0.125	0.205
<i>dentatus</i>	(475)	(0.019)	(0.4)	(0.5)	(1.5)	(1.8)	(0.008)	(4)	(0.037)	(0.011)	(0.036)
<i>Dimorphocalyx</i>	972	0.213	0.9	8.9	8.3	15.3	0.110	129	0.277	0.120	1.793
<i>murinus</i>	(108)	(0.013)	(0.3)	(0.5)	(0.9)	(0.9)	(0.028)	(29)	(0.077)	(0.007)	(1.105)
<i>Diospyros</i>	1187	<0.200	0.5	6.1	5.0	11.0	<0.090	90	0.206	<0.100	0.507
<i>durionoides</i>	(489)		(0.1)	(3.5)	(3.0)	(2.5)	()	(19)	(0.032)		(0.297)
<i>Diospyrus elliptifolia</i>	1156	<0.200	0.4	9.9	5.8	25.0	<0.090	107	<0.200	<0.100	0.203
	(27)		(0.1)	(0.7)	(0.1)	(8.7)		(7)			(0.037)
<i>Dipterocarpus</i>	1156	<0.200	0.4	9.9	5.8	25.0	0.133	107	<0.200	<0.100	0.232
<i>applanatus</i>	(48)		(0.9)	(1.4)	(1.1)	(4.1)	(0.009)	(95)			(1.466)
<i>Dipterocarpus</i>	1051	0.210	1.1	14.6	13.2	18.0	0.100	25	0.253	0.105	0.220
<i>gracilis</i>	(658)	(0.006)	(2.4)	(3.6)	(2.5)	(0.7)	(0.010)	(6)	(0.030)	(0.003)	(0.022)
<i>Dryobalanops</i>	269	<0.200	0.5	6.6	6.8	14.3	<0.090	57	0.250	<0.100	0.250
<i>lanceolata</i>	(96)		(0.1)	(0.3)	(1.7)	(1.2)		(10)	(0.013)		(0.026)
<i>Duabanga</i>	28	0.256	0.4	1.6	5.1	9.0	0.098	24	0.267	<0.100	<0.200
<i>moluccana</i>	(0.9)	(0.027)	(0.1)	(0.3)	(1.8)	(1.0)	(0.008)	(1)	(0.015)		
<i>Durio kutejensis</i>	146	0.298	0.3	6.4	7.2	7.0	0.111	65	<0.200	0.101	0.377
	(52)	(0.030)	(0.01)	(1.2)	(1.0)	(0.3)	(0.002)	(32)		(0.008)	(0.177)
<i>Etilingera</i>	1122	0.251	0.6	2.9	9.4	11.4	0.101	64	0.203	<0.100	0.228
<i>brevilabrum</i>	(243)	(0.031)	(0.3)	(2.1)	(0.5)	(1.8)	(0.007)	(39)	(0.003)		(0.005)
<i>Euphorbia</i>	1286	0.269	0.4	2.2	7.9	15.0	<0.090	73	0.277	0.108	0.222
<i>malaiensis</i>	(55)	(0.032)	(0.1)	(0.1)	(1.0)	(3.3)		(29)	(0.004)	(0.22)	(0.004)
<i>Dimocarpus longan</i>	388	<0.200	5.2	6.8	5.1	8.9	0.127	16	0.212	<0.100	0.423
	(188)		(2.6)	(1.1)	(0.7)	(1.8)	(0.0707)	(4)	(0.037)		(0.118)
<i>Eurycoma longifolia</i>	604	<0.200	1.4	6.5	7.4	35.3	0.132	94	<0.200	0.247	0.227
	(131)		(0.5)	(1.7)	(0.6)	(11.6)	(0.08)	(42)		(0.123)	(0.027)
<i>Eusideroxylon</i>	1085	0.209	1.1	1.7	6.4	23.7	<0.090	48	<0.200	0.393	0.243
<i>zugerii</i>	(419)	(0.029)	(0.1)	(0.8)	(0.8)	(3.4)		(23)		(0.212)	(0.043)
<i>Fagraea cuspidata</i>	140	<0.200	0.7	7.5	8.2	21.3	0.104	37	0.209	<0.100	0.457
	(38)		(0.1)	(0.9)	(0.4)	(1.5)	(0.021)	(14)	(0.055)		(0.091)
<i>Fordia</i>	1324	<0.200	1.8	2.2	4.6	9.3	0.121	39	0.201	<0.100	<0.200
<i>splendidissima</i>	(361)		(0.4)	(1.0)	(1.1)	(1.0)	(0.004)	(11)	(0.043)		
<i>Goniothalamus</i>	406	0.290	0.8	7.4	5.1	5.8	0.127	45	<0.200	<0.100	0.527
<i>uvaroides</i>	(48)	(0.034)	(0.1)	(1.3)	(0.47)	(0.65)	(0.022)	(12)			(0.164)
<i>Helicia</i>	1052	0.211	0.8	3.9	6.6	14.5	0.143	343	0.299	0.180	0.240
<i>artocarpoides</i>	(664)	(0.022)	(0.1)	(1.4)	(0.1)	(1.7)	(0.009)	(218)	(0.036)	(0.053)	(0.027)
<i>Hopea nervosa</i>	1347	0.276	0.6	3.0	3.4	12.8	0.132	32	0.232	0.105	0.325
	(32)	(0.033)	(0.03)	(0.5)	(0.1)	(2.1)	(0.007)	(1)	(0.034)	(0.003)	(0.083)

<i>Hopea sangal</i>	1116 (613)	0.234 (0.033)	1.1 (0.2)	3.0 (0.2)	9.3 (0.9)	16.7 (0.9)	<0.090	62 (40)	<0.200	0.110 (0.010)	0.230 (0.030)
<i>Ixora grandifolia</i>	63 (43)	0.244 (0.013)	3.7 (3.0)	1.8 (0.8)	11.4 (1.1)	9.8 (0.8)	0.133 (0.009)	81 (10)	0.283 (0.083)	<0.100 (0.120)	0.320 (0.120)
<i>Knema latericia</i>	231 (87)	<0.200	0.7 (0.3)	10.1 (3.1)	12.3 (5.0)	24.7 (7.3)	<0.090	49 (20)	0.240 (0.044)	0.143 (0.038)	0.207 (0.007)
<i>Lansium domesticum</i>	50 (10)	0.230 (0.030)	1.4 (0.4)	7.1 (2.6)	13.0 (5.1)	23.7 (3.3)	0.100 (0.009)	54 (22)	0.266 (0.060)	<0.100 (0.132)	0.457 (0.132)
<i>Leea indica</i>	269 (137)	0.280 (0.040)	1.1 (0.3)	5.3 (1.4)	4.6 (0.9)	9.1 (2.3)	0.100 (0.011)	11 (1)	<0.200	0.107 (0.007)	<0.200
<i>Lophoetalum beccarianum</i>	50 (7)	<0.200	1.2 (0.4)	38.3 (10.3)	3.4 (0.4)	5.4 (0.4)	<0.090	88 (23)	<0.200	<0.100	0.201 (0.012)
<i>Ludekia borneensis</i>	21 (0.7)	<0.200	1.4 (0.7)	3.2 (0.6)	6.8 (1.7)	9.8 (1.1)	<0.090	46 (31)	<0.200	0.104 (0.004)	0.217 (0.017)
<i>Luvunga heterophylla</i>	2022 (405)	0.220 (0.043)	0.5 (0.1)	7.4 (1.2)	7.4 (0.5)	21.0 (3.1)	0.102 (0.012)	161 (31)	0.206 (0.065)	0.187 (0.009)	0.222 (0.032)
<i>Macaranga gigantea</i>	681 (408)	0.200 (0.010)	1.3 (0.7)	6.5 (3.8)	14.8 (5.7)	16.7 (3.2)	0.143 (0.043)	149 (74)	0.232 (0.031)	0.109 (0.009)	0.597 (0.266)
<i>Macaranga hypoleuca</i>	312 (282)	<0.200	3.9 (2.0)	4.7 (1.9)	11.0 (0.3)	13.5 (1.5)	<0.090	34 (4)	<0.200	0.121 (0.008)	0.200 (0.017)
<i>Macaranga triloba</i>	2032 (222)	0.236 (0.011)	2.2 (1.1)	1.6 (0.4)	10.0 (0.6)	15.0 (0.9)	<0.090	46 (4)	<0.200	0.176 (0.005)	0.250 (0.020)
<i>Macaranga pearsonii</i>	2631 (253)	<0.200	1.6 (0.1)	3.3 (0.5)	8.9 (0.7)	17.0 (0.7)	<0.090	65 (21)	0.208 (0.020)	<0.100	0.335 (0.063)
<i>Madhuca korthalsii</i>	221 (132)	0.246 (0.011)	11.9 (5.2)	6.0 (2.5)	8.4 (0.7)	7.5 (0.2)	<0.090	40 (11)	0.233 (0.033)	0.154 (0.006)	0.450 (0.131)
<i>Mallotus mollissimus</i>	434 (335)	0.263 (0.054)	1.5 (0.2)	5.5 (0.8)	5.3 (0.7)	16.0 (1.7)	0.117 (0.028)	117 (28)	0.237 (0.037)	<0.100	0.205 (0.011)
<i>Mallotus wrayi</i>	2565 (53)	0.300 (0.031)	0.9 (0.2)	1.3 (0.2)	7.0 (1.0)	17.0 (1.5)	0.107 (0.027)	62 (5)	0.243 (0.031)	<0.100	0.207 (0.007)
<i>Melastoma malabathricum</i>	646 (275)	0.220 (0.029)	0.7 (0.3)	7.3 (3.6)	7.5 (2.1)	11.8 (3.6)	0.143 (0.023)	251 (43)	0.208 (0.021)	0.118 (0.008)	0.235 (0.040)
<i>Memecylon laevigatum</i>	55 (4)	0.263 (0.011)	1.3 (0.4)	2.9 (0.2)	5.2 (0.5)	6.9 (1.0)	<0.090	115 (18)	<0.200	0.109 (0.010)	<0.200
<i>Neonauclea artocarpoides</i>	73 (30)	0.250 (0.025)	1.9 (0.4)	6.9 (2.6)	6.0 (0.6)	13.0 (0.6)	0.153 (0.053)	65 (19)	<0.200	<0.100	0.430 (0.125)
<i>Nephelium ramboutan-ake</i>	62 (24)	<0.200	1.0 (0.2)	3.1 (0.8)	9.4 (2.1)	18.7 (3.0)	<0.090	57 (18)	0.244 (0.023)	<0.100 (0.033)	0.233 (0.033)
<i>Ochanostachys amentacea</i>	224 (26)	<0.200	0.4 (0.02)	1.3 (0.5)	7.8 (0.8)	10.8 (1.11)	<0.090	26 (3.5)	0.255 (0.005)	0.103 (0.020)	0.307 (0.107)
<i>Octomeles sumatrana</i>	1203 (386)	<0.200	0.3 (0.1)	3.7 (1.1)	6.0 (0.6)	17.7 (1.2)	0.123 (0.010)	110 (54)	0.243 (0.043)	0.103 (0.003)	<0.200

<i>Parashorea malonaana</i>	333	0.288	3.4	24.8	6.2	7.3	<0.090	201	0.290	0.102	0.205
	(189)	(0.065)	(1.9)	(14.5)	(2.1)	(2.0)		(97)	(0.060)	(0.037)	(0.012)
<i>Parashorea tomentella</i>	294	0.393	1.8	4.5	6.8	14.0	0.143	41	0.255	0.177	0.417
	(209)	(0.194)	(1.0)	(0.7)	(0.9)	(3.5)	(0.043)	(5)	(0.032)	(0.052)	(0.096)
<i>Parinari oblongifolia</i>	317	0.633	7.4	76.8	7.2	12.3	0.100	38	0.220	0.154	0.437
	(267)	(0.434)	(5.3)	(35.5)	(0.3)	(3.9)	(0.012)	(9)	(0.020)	(0.017)	(0.185)
<i>Payena acuminata</i>	45	<0.200	0.9	3.4	2.4	10.2	<0.090	44	0.200	<0.100	1.333
	(12)		(0.4)	(0.8)	(1.0)	(0.4)		(15)	(0.006)		(0.988)
<i>Pleiocarpidia sandahanica</i>	78	0.223	2.7	3.3	7.0	10.4	0.120	101	0.202	0.123	0.290
	(10)	(0.023)	(0.2)	(0.5)	(0.3)	(1.3)	(0.020)	(63)	(0.009)	(0.033)	(0.046)
<i>Podocarpus neriifolius</i>	46	<0.200	0.3	2.0	6.7	19.3	<0.090	169	0.201	<0.100	<0.200
	(14)		(0.1)	(1.0)	(1.1)	(2.7)		(91)	(0.006)		
<i>Poikilospermum cordifolium</i>	119	0.370	1.8	1.4	4.8	13.0	0.123	230	0.265	0.176	0.207
	(7)	(0.155)	(0.2)	(0.3)	(0.1)	(1.5)	(0.023)	(21)	(0.009)	(0.023)	(0.007)
<i>Polyalthia sumatrana</i>	47	<0.200	0.4	3.5	10.2	11.2	<0.090	61	<0.200	0.122	2.200
	(5)		(0.1)	(2.0)	(1.3)	(1.0)		(11)		(0.010)	(1.003)
<i>Popowia pisocarpa</i>	131	0.240	0.6	5.8	6.3	12.3	0.112	109	<0.200	<0.100	0.413
	(22)	(0.021)	(0.2)	(1.9)	(0.3)	(1.3)	(0.012)	(5)			(0.107)
<i>Pterospermum stapfianum</i>	35	0.233	0.4	1.9	5.9	12.0	<0.090	55	0.503	0.134	0.267
	(8)	(0.033)	(0.1)	(0.5)	(0.3)	(0.6)		(14.4)	(0.251)	(0.017)	(0.034)
<i>Reinwardtiodendron humile</i>	35	0.228	0.4	1.9	5.9	12.0	0.122	55	0.503	0.111	0.267
	(9)	(0.021)	(0.7)	(1.9)	(0.2)	(1.7)	(0.057)	(4)	(0.053)	(0.003)	(0.080)
<i>Ryparosa hulletii</i>	854	0.297	3.7	2.5	2.8	11.4	0.154	49	0.300	<0.100	0.390
	(567)	(0.052)	(1.2)	(0.7)	(0.8)	(4.3)	(0.011)	(26)	(0.100)		(0.171)
<i>Saurauia ferox</i>	1047	0.320	3.9	4.4	6.0	14.0	<0.090	21	0.289	0.140	0.250
	(257)	(0.069)	(1.5)	(1.1)	(0.17)	(1.3)		(6)	(0.027)	(0.027)	(0.033)
<i>Semecarpus bunburyanus</i>	201	0.202	0.6	3.3	5.6	20.3	<0.090	46	<0.200	0.100	0.216
	(104)	(0.022)	(0.1)	(0.6)	(0.6)	(0.9)		(5.5)		(0.009)	(0.020)
<i>Shorea agami</i>	72	0.270	1.8	2.6	5.3	22.7	<0.090	49	<0.200	0.110	0.260
	(40)	(0.070)	(0.8)	(1.5)	(0.9)	(2.9)		(16)		(0.010)	(0.060)
<i>Shorea fallax</i>	1155	0.217	0.7	5.9	7.6	12.7	0.105	47	0.223	0.102	0.327
	(749)	(0.017)	(0.2)	(1.2)	(1.0)	(1.7)	(0.010)	(8)	(0.022)	(0.007)	(0.090)
<i>Shorea johorensis</i>	180	0.267	0.9	3.8	4.9	10.1	<0.090	33	<0.200	0.154	<0.200
	(135)	(0.034)	(0.2)	(0.9)	(0.9)	(1.6)		(11.6)		(0.018)	
<i>Shorea leprosula</i>	472	0.235	0.5	6.5	10.6	18.0	0.132	30	0.206	0.107	<0.200
	(171)	(0.023)	(0.05)	(2.3)	(1.6)	(0.1)	(0.3)	(7)	(0.006)	(0.003)	
<i>Shorea macrophylla</i>	48	<0.200	0.2	1.9	6.0	14.0	<0.090	149	0.208	0.145	0.256
	(1)		(0.01)	(0.1)	(1.6)	(3.0)		(9)	(0.008)	(0.011)	(0.016)
<i>Sindora irpicina</i>	971	0.347	1.1	5.9	7.3	39.3	0.137	33	0.217	0.117	0.243
	(475)	(0.147)	(0.7)	(1.5)	(1.5)	(12.5)	(0.037)	(6)	(0.017)	(0.017)	(0.043)
<i>Spathiostemon javensis</i>	985	<0.200	1.5	3.3	6.7	18.3	0.101	52	<0.200	<0.100	0.317
	(625)		(1.0)	(0.8)	(1.7)	(2.9)	(0.006)	(16)			(0.072)
<i>Stychnos ignatii</i>	4335	0.299	2.2	62.3	9.9	8.4	0.417	131	<0.200	0.127	2.350

	(648)	(0.028)	(1.0)	(31.5)	(1.1)	(1.5)	(0.166)	(63)	()	(0.027)	(0.958)
<i>Syzygium</i>	47	0.222	0.7	3.0	7.0	20.8	0.122	18	<-0.200	<-0.100	0.800
<i>campanulatum</i>	(27)	(0.012)	(0.2)	(0.6)	(2.9)	(1.2)	(0.011)	(1)			(0.601)
<i>Tarbernaemontana</i>	1510	0.287	0.5	3.9	15.3	31.7	0.109	21	<-0.200	0.110	0.933
<i>macrocarpa</i>	(241)	(0.011)	(0.1)	(1.4)	(2.9)	(1.2)	(0.007)	(1)		(0.016)	(0.734)
	1243	<-0.200	3.6	2.2	7.2	35.3	<-0.090	24		0.267	0.200
<i>Uncaria cordata</i>	(1141)		(2.8)	(0.3)	(0.7)	(18.0)		(4)	(0.040)	(0.023)	(0.005)
	1243	0.202	3.6	2.2	7.2	35.3	0.122	24	0.223	0.123	0.213
<i>Urophyllum glabrum</i>	(43)	(0.013)	(6.2)	(1.5)	(0.7)	(2.3)	(0.097)	(31)	(0.012)	(0.033)	(0.067)
<i>Uvaria</i>	867	<-0.200	0.8	8.6	7.8	12.0	0.130	54	<-0.200	0.107	0.260
<i>sorzogonensis</i>	(234)		(0.1)	(1.2)	(0.6)	(0.6)	(0.010)	(12)		(0.006)	(0.060)
<i>Xanthophyllum</i>	121	0.260	0.4	11.9	8.3	14.3	<-0.090	42	0.222	0.124	0.900
<i>affine</i>	(48)	(0.009)	(0.1)	(5.7)	(2.2)	(0.9)		(10)	(0.013)	(0.008)	(0.701)
<i>Zizyphus</i>	1042	<-0.200	9.5	8.3	5.4	17.0	<-0.090	58	<-0.200	0.137	0.220
<i>angustifolius</i>	(542)		(9.3)	(3.6)	(1.6)	(2.6)		(43)		(0.037)	(0.020)

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Table S4. Foliar concentrations of phenolics and tannins, and morphological foliar traits (Mean, S.E between brackets) of 88 common rainforest plant species in Danum Valley (Borneo). LMA = Leaf mass area. L = Length. R = Roundness. COM = Compactness. P/a = leaf perimeter/leaf area. F = Accumulated standing folivory (% of leaf lost) (n = 3 for chemical analyses and n = 6-37 for morphological and folivory variables).

Species	Phenolics mg g ⁻¹	Tannins mg g ⁻¹	Leaf area (cm ²)	Leaf dry weight (g)	Leaf dry/fresh weight ratio	LMA (Dry weight)	LMA (Fresh weight)	L	R	COM	P/a	F
<i>Agelaea borneensis</i>	2.41 (0.75)	1.49 (0.42)	84.7 (4.8)	0.415 (0.027)	0.332 (0.008)	48.7 (1.4)	146 (2)	2.335 (0.048)	0.623 (0.010)	0.621 (0.008)	52.4 (1.8)	0.053 (0.009)
<i>Alangium javanicum</i>	17.1 (0.00)	16.1 (0.00)	128 (7)	0.633 (0.034)	0.304 (0.004)	49.9 (1.0)	163 (2)	2.768 (0.060)	0.563 (0.011)	0.572 (0.008)	82.6 (3.1)	0.055 (0.011)
<i>Ardisia elliptica</i>	21.5 (5.5)	13.1 (3.74)	80.1 (4.8)	0.717 (0.043)	0.277 (0.005)	90.1 (1.9)	325 (3)	2.950 (0.533)	0.533 (0.008)	0.552 (0.007)	19.5 (0.7)	0.025 (0.006)
<i>Artocarpus anisophyllus</i>	20.3 (5.4)	14.8 (0.448)	3222 (263)	45.7 (2.4)	0.437 (0.028)	155.5 (15.8)	349 (17)	1.556 (0.058)	0.058 (0.006)	0.641 (0.021)	25.1 (3.0)	0.060 (0.030)
<i>Baccaurea lanceolata</i>	11.5 (3.6)	4.19 (1.24)	250 (16)	1.60 (0.12)	0.277 (0.004)	63.2 (1.3)	229 (4)	2.285 (0.625)	0.625 (0.007)	0.641 (0.008)	42.9 (1.2)	0.076 (0.009)
<i>Baccaurea macrocarpa</i>	10.9 (2.3)	5.98 (1.88)	245 (12)	3.30 (0.18)	0.389 (0.008)	137.7 (5.6)	348 (8)	2.001 (0.678)	0.678 (0.005)	0.681 (0.004)	53.4 (2.1)	0.040 (0.010)
<i>Barringtonia sarcostachys</i>	23.5 (7.6)	1.956 (0.635)	554 (44)	7.77 (0.83)	0.316 (0.010)	136.0 (6.4)	427 (13)	3.812 (0.374)	0.374 (0.008)	0.455 (0.007)	186 (10)	0.051 (0.014)
<i>Blumeodendron tokbrai</i>	23.3 (7.6)	1.14 (0.325)	300 (19)	2.80 (0.18)	0.450 (0.006)	92.8 (2.0)	206 (3)	1.838 (0.715)	0.715 (0.007)	0.701 (0.009)	38.4 (0.9)	0.035 (0.007)
<i>Brownlowia peltata</i>	87.0 (17.0)	24.1 (4.8)	478 (34)	3.07 (0.25)	0.383 (0.007)	63.2 (1.6)	166 (4)	1.394 (0.744)	0.744 (0.010)	0.822 (0.010)	7.67 (0.7)	0.091 (0.013)
<i>Caesalpinia major</i>	33.4 (10.7)	4.87 (1.69)	80.7 (4.2)	0.640 (0.039)	0.332 (0.006)	78.8 (2.1)	237 (3)	1.704 (0.106)	0.106 (0.007)	0.657 (0.007)	48.6 (4.2)	0.079 (0.022)
<i>Callicarpa longifolia</i>	16.6 (15.5)	4.27 (3.78)	45.0 (2.4)	0.196 (0.010)	0.364 (0.007)	44.0 (0.6)	122 (2)	2.434 (0.546)	0.546 (0.012)	0.577 (0.009)	25.0 (1.7)	0.086 (0.016)
<i>Canarium denticulatum</i>	20.5 (3.2)	5.17 (0.87)	109 (7)	0.528 (0.029)	0.382 (0.008)	50.4 (1.2)	132 (1)	2.577 (0.536)	0.536 (0.009)	0.596 (0.009)	22.8 (1.3)	0.066 (0.012)
<i>Chionanthus pluriflorus</i>	11.4 (2.9)	7.07 (1.21)	142 (5)	0.917 (0.038)	0.388 (0.005)	64.8 (1.3)	166 (2)	2.763 (0.584)	0.584 (0.008)	0.580 (0.005)	22.9 (0.6)	0.043 (0.007)
<i>Cinnamomum subavenium</i>	2.7 (0.09)	1.34 (0.04)	72.0 (3.9)	0.461 (0.019)	0.385 (0.005)	67.4 (1.3)	174 (2)	3.629 (0.479)	0.479 (0.013)	0.504 (0.009)	65.6 (1.5)	0.049 (0.009)
<i>Clausena excavata</i>	6.8 (4.3)	4.10 (0.30)	20.0 (0.7)	0.112 (0.006)	0.361 (0.004)	55.5 (1.2)	154 (3)	2.845 (0.502)	0.502 (0.005)	0.545 (0.004)	31.1 (0.5)	0.012 (0.002)
<i>Clidemia hirta</i>	35.6	4.94	64.7	0.275	0.340	43.2	128	1.974	0.599	0.663	24.3	0.027

	(12.7)	(1.96)	(2.0)	(0.012)	(0.006)	(1.6)	(5)	(0.599)	(0.006)	(0.005)	(0.4)	(0.005)
<i>Combretum</i>	38.9	1.87	34.6	0.169	0.423	50.3	118	2.525	0.596	0.600	38.2	0.049
<i>nigrescens</i>	(12.7)	(0.49)	(1.8)	(0.008)	(0.004)	(1.5)	(3)	(0.596)	(0.010)	(0.008)	(1.3)	(0.011)
<i>Coscinium</i>	3.0	2.82	303	1.63	0.425	54.2	126	1.280	0.721	0.833	32.0	0.020
<i>blumeianum</i>	(3.0)	(2.17)	(18)	(0.15)	(0.012)	(3.1)	(6)	(0.721)	(0.010)	(0.010)	(0.5)	(0.007)
<i>Dillenia excelsa</i>	32.3	4.16	215	2.95	0.339	138.8	407	1.806	0.705	0.728	81.3	0.018
	(8.2)	(1.09)	(9)	(0.15)	(0.006)	(3.7)	(6)	(0.705)	(0.006)	(0.006)	(2.0)	(0.005)
<i>Dimocarpus</i>	15.0	5.25	134	0.458	0.362	34.3	94.4	2.654	0.436	0.577	16.1	0.031
<i>dentatus</i>	(4.8)	(2.40)	(4)	(0.015)	(0.005)	(0.6)	(0.9)	(0.436)	(0.007)	(0.005)	(0.4)	(0.004)
<i>Dimorphocalyx</i>	1.2	0.977	184	1.11	0.276	61.6	221	2.439	0.584	0.610	94.5	0.063
<i>murinus</i>	(0.5)	(0.340)	(13)	(0.09)	(0.006)	(1.9)	(3)	(0.584)	(0.009)	(0.008)	(0.7)	(0.013)
<i>Diospyros</i>	23.8	6.99	110	1.68	0.474	155.6	323	3.338	0.521	0.549	44.5	0.083
<i>durionoides</i>	(7.3)	(2.05)	(8)	(0.14)	(0.009)	(5.1)	(6)	(0.521)	(0.007)	(0.005)	()	(0.020)
<i>Diospyrus elliptifolia</i>	1.4	1.24	109	0.782	0.338	72.2	213	1.905	0.694	0.699	35.8	0.060
	(0.4)	(0.35)	(5)	(0.037)	(0.004)	(1.3)	(3)	(0.694)	(0.009)	(0.007)	(1.0)	(0.014)
<i>Dipterocarpus</i>	17.4	2.63	842	11.7	0.427	142.3	332	2.141	0.640	0.667	93.4	0.041
<i>applanatus</i>	(8.0)	(1.21)	(43)	(0.6)	(0.006)	(4.1)	(7)	(0.640)	(0.008)	(0.006)	(6.5)	(0.009)
<i>Dipterocarpus</i>	19.4	4.20	295	3.35	0.436	113.1	260	2.486	0.602	0.613	57.3	0.042
<i>gracilis</i>	(4.7)	(0.98)	(24)	(0.29)	(0.006)	(1.9)	(5)	(0.602)	(0.012)	(0.009)	()	(0.011)
<i>Dryobalanops</i>	24.7	4.83	50.4	0.568	0.478	116.5	244	3.162	0.520	0.544	56.9	0.044
<i>lanceolata</i>	(12.8)	(1.53)	(2.3)	(0.020)	(0.004)	(2.0)	(4)	(0.520)	(0.007)	(0.005)	(1.7)	(0.010)
<i>Duabanga</i>	47.1	3.27	209	2.17	0.410	104.7	256	2.519	0.575	0.614	61.6	0.031
<i>moluccana</i>	(1.0)		(18)	(0.18)	(0.004)	(1.9)	(4)	(0.575)	(0.012)	(0.010)	(2.6)	(0.014)
<i>Durio kutejensis</i>	6.61	5.34	108	0.614	0.336	56.0	167	2.865	0.554	0.567	26.4	0.024
	(0.59)	(0.35)	(5)	(0.031)	(0.004)	(0.7)	(1)	(0.554)	(0.006)	(0.003)	()	(0.005)
<i>Etilingera</i>	11.8	7.23	978	10.2	0.334	102.1	303	4.071	0.453	0.499	58.1	0.007
<i>brevilabrum</i>	(3.9)	(2.33)	(40)	(0.7)	(0.007)	(3.3)	(3)	(0.453)	(0.009)	(0.006)	(1.4)	(0.003)
<i>Euphoria</i>			74.0	0.672	0.447		194				16.3	
<i>malaiensis</i> =	36.4	13.5	(5.4)	(0.056)	(0.007)	105.1	(2)	3.042	0.499	0.546	(0.6)	0.047
<i>Dimocarpus longan</i>	(4.8)	(2.4)				(2.1)		(0.499)	(0.010)	(0.006)		(0.013)
<i>Eurycoma longifolia</i>	4.0	2.07	18.2	0.085	0.376	47.0	125	3.335	0.494	0.523	38.6	0.020
	(2.0)	(1.72)	(0.5)	(0.003)	(0.005)	(0.7)	(1)	(0.494)	(0.006)	(0.005)	(0.7)	(0.006)
<i>Eusideroxylon</i>	22.1	16.1	263	3.35	0.418	129.3	310	2.555	0.608	0.614	20.7	0.034
<i>zwageri</i>	(7.0)	(5.9)	(12)	(0.15)	(0.006)	(2.0)	(3)	(0.608)	(0.011)	(0.009)	(0.8)	(0.008)
<i>Fagraea cuspidata</i>	5.21	0.232	392	5.20	0.385	147.6	376	1.884	0.678	0.720	175	0.010
	(4.09)	(0.230)	(30)	(0.30)	(0.007)	(7.8)	(14)	(0.678)	(0.010)	(0.010)	(3.7)	(0.006)
<i>Fordia</i>	23.3	17.4	72.0	0.342	0.379	46.9	124	2.542	0.578	0.592	15.8	0.065
<i>splendidissima</i>	(5.8)	(6.9)	(23.1)	(0.018)	(0.006)	(1.2)	(2)	(0.578)	(0.011)	(0.008)	(1.0)	(0.013)
<i>Goniothalamus</i>	22.8	7.75	470	2.99	0.338	62.7	185	2.764	0.579	0.586	23.4	0.029
<i>uvaroides</i>	(5.0)	(1.32)	(23)	(1.70)	(0.006)	(1.5)	(2)	(0.579)	(0.009)	(0.007)	(0.7)	(0.007)
<i>Helicia</i>	2.7	1.90	1386	16.6	0.402	123.0	306	1.388	0.039	0.597	104	0.120

<i>artocarpoides</i>	(0.8)	(0.55)	(143)	(1.7)	(0.004)	(3.1)	(7)	(0.039)	(0.003)	(0.011)	(8.2)	(0.018)
<i>Hopea nervosa</i>	7.4	6.84	38.1	0.334	0.470	86.6	184	2.586	0.566	0.584	23.6	0.035
	(7.4)	(2.54)	(1.6)	(0.019)	(0.004)	(2.3)	(4)	(0.566)	(0.009)	(0.006)	(0.6)	(0.006)
<i>Hopea nutans</i>	83.1	13.0	50.2	0.537	0.493	107.9	218	2.033	0.631	0.643	12.3	0.036
	(30.4)	(5.2)	(1.5)	(0.017)	(0.004)	(2.4)	(4)	(0.631)	(0.007)	(0.007)	(0.5)	(0.010)
<i>Hopea sangal</i>	34.6	4.38	43.9	0.428	0.473	100.3	212	2.293	0.586	0.615	48.4	0.028
	(15.8)	(2.01)	(2.9)	(0.027)	(0.005)	(1.4)	(2)	(0.586)	(0.009)	(0.006)	(0.9)	(0.007)
<i>Ixora grandifolia</i>	22.6	11.3	105	1.01	0.336	96.0	286	2.434	0.598	0.605	31.9	0.046
	(8.6)	(2.41)	(5)	(0.05)	(0.003)	(1.2)	(2)	(0.598)	(0.007)	(0.005)	(1.2)	(0.006)
<i>Knema latericia</i>	4.5	1.06	47.3	0.256	0.339	55.8	165	4.242	0.425	0.483	21.7	0.055
	(2.0)	(0.49)	(2.6)	(0.014)	(0.008)	(1.4)	(2)	(0.425)	(0.011)	(0.008)	(0.6)	(0.009)
<i>Lansium domesticum</i>	5.0	1.23	96.5	0.692	0.369	71.1	191	2.305	0.646	0.634	67.8	0.090
	(1.6)	(0.41)	(4.7)	(0.038)	(0.005)	(1.9)	(3)	(0.646)	(0.007)	(0.007)	(2.2)	(0.014)
<i>Leea indica</i>	37.5	6.21	109	0.659	0.288	60.7	211	2.576	0.540	0.573	49.7	0.038
	(18.6)	(3.01)	(4)	(0.031)	(0.005)	(1.4)	(3)	(0.540)	(0.007)	(0.005)	(2.1)	(0.006)
<i>Lophoetalum beccarianum</i>	23.0	7.69	188	1.08	0.340	60.7	178	2.807	0.581	0.585	58.6	0.089
	(11.1)	(2.29)	(12)	(0.06)	(0.006)	(1.9)	(4)	(0.581)	(0.010)	(0.008)	(2.1)	(0.010)
<i>Ludekia borneensis</i>	4.86	4.67	49.3	0.567	0.428	115.8	271	1.864	0.709	0.692	29.8	0.047
	(3.52)	(3.08)	(1.7)	(0.020)	(0.006)	(2.1)	(3)	(0.709)	(0.007)	(0.005)	(0.8)	(0.008)
<i>Luvunga heterophylla</i>	17.1	15.0	63.7	0.369	0.304	57.8	191	2.835	0.533	0.550	34.2	0.063
	(8.3)	(9.2)	(4.3)	(0.025)	(0.003)	(0.5)	(2)	(0.533)	(0.007)	(0.006)	(0.9)	(0.010)
<i>Macaranga gigantea</i>	30.7	11.5	2603	19.7	0.361	73.9	205	1.114	0.448	0.846	14.6	0.096
	(5.3)	(2.02)	(214)	(1.9)	(0.007)	(2.0)	(4)	(0.448)	(0.011)	(0.004)	(1.7)	(0.022)
<i>Macaranga hypoleuca</i>	25.1	3.13	232	2.17	0.442	97.2	221	1.264	0.429	0.744	19.9	0.046
	(2.9)	(0.339)	(14)	(0.11)	(0.011)	(2.5)	(4)	(0.429)	(0.008)	(0.007)	(1.6)	(0.011)
<i>Macaranga triloba</i>	21.1	6.01	339	3.16	0.430	96.7	220	1.379	0.482	0.779	53.3	0.143
	(7.6)	(1.54)	(32)	(0.26)	(0.007)	(3.1)	(3)	(0.482)	(0.012)	(0.010)	(7.4)	(0.031)
<i>Macaranga pearsonii</i>	20.6	3.36	377	2.83	0.434	73.5	174	1.219	0.416	0.773	33.7	0.062
	(4.2)	(0.717)	(23)	(0.23)	(0.010)	(2.6)	(9)	(0.416)	(0.007)	(0.008)	(3.3)	(0.020)
<i>Madhuca korthalsii</i>	10.6	0.885	650	5.43	0.325	84.6	260	2.311	0.612	0.628	70.7	0.047
	(2.7)	(0.223)	(34)	(0.30)	(0.007)	(2.2)	(4)	(0.612)	(0.013)	(0.007)	(3.3)	(0.013)
<i>Mallotus mollissimus</i>	27.4	3.01	83.3	0.463	0.458	65.8	124	1.273	0.710	0.803	38.0	0.029
	(14.6)	(1.41)	(5.0)	(0.026)	(0.008)	(2.0)	(3)	(0.710)	(0.006)	(0.006)	(1.6)	(0.007)
<i>Mallotus wrayi</i>	46.2	1.23	122	0.730	0.494	59.2	120	2.839	0.545	0.562	49.0	0.044
	(5.1)	(0.32)	(7)	(0.043)	(0.006)	(0.8)	(1)	(0.545)	(0.013)	(0.009)	(1.9)	(0.008)
<i>Melastoma malabathricum</i>	20.0	5.05	17.8	0.149	0.351	86.2	247	2.779	0.552	0.573	37.0	0.023
	(5.1)	(1.31)	(0.7)	(0.006)	(0.006)	(2.1)	(5)	(0.552)	(0.008)	(0.004)	(0.7)	(0.003)
<i>Memecylon laevigatum</i>	11.9	9.23	98.7	0.821	0.427	84.1	196	2.935	0.545	0.562	35.6	0.048
	(1.8)	(1.52)	(4.9)	(0.043)	(0.004)	(1.8)	(3)	(0.545)	(0.008)	(0.006)	(0.6)	(0.014)
<i>Neonauclea artocarpoides</i>	40.4	34.8	580	6.56	0.350	108.6	307	1.453	0.783	0.808	33.2	0.111
	(12.4)	(7.2)	(44)	(0.75)	(0.014)	(5.5)	(6)	(0.783)	(0.005)	(0.009)	(1.9)	(0.017)
<i>Nephelium ramboutan-ake</i>	48.4	1.26	33.5	0.180	0.414	52.7	127	2.670	0.575	0.585	4.27	0.072
	(16.1)	(0.43)	(1.6)	(0.010)	(0.006)	(0.9)	(2)	(0.575)	(0.009)	(0.007)	(2.1)	(0.009)

<i>Ochanostachys</i>	41.4	1.22	53.5	0.255	0.393	48.7	124	2.235	0.623	0.619	47.7	0.042
<i>amentacea</i>	(7.5)	(0.21)	(2.3)	(0.010)	(0.005)	(0.9)	(1)	(0.623)	(0.007)	(0.005)	(1.4)	(0.009)
<i>Octomeles</i>	11.7	5.55	1122	8.08	0.334	71.5	214	1.237	0.607	0.839	83.8	0.034
<i>sumatrana</i>	(4.8)	(2.23)	(53)	(0.45)	(0.008)	(2.2)	(5)	(0.607)	(0.008)	(0.005)	(2.2)	(0.007)
<i>Parashorea</i>	12.0	11.3	111	0.840	0.456	80.2	174	2.497	0.606	0.614	28.1	0.040
<i>malonaanan</i>	(2.9)	(3.1)	(7)	(0.043)	(0.007)	(2.7)	(4)	(0.606)	(0.008)	(0.006)	(1.4)	(0.006)
<i>Parashorea</i>	24.0	11.7	356	3.06	0.451	84.4	187	2.003	0.687	0.691	17.3	0.066
<i>tomentella</i>	(8.0)	(3.7)	(21)	(0.21)	(0.005)	(1.6)	(3)	(0.687)	(0.008)	(0.007)	(0.9)	(0.014)
<i>Parinari oblongifolia</i>	12.1	7.80	134	0.940	0.507	70.4	139	2.561	0.589	0.591	15.2	0.075
	(5.6)	(3.32)	(5)	(0.037)	(0.006)	(1.4)	(2)	(0.589)	(0.007)	(0.004)	(0.9)	(0.011)
<i>Payena acuminata</i>	19.3	12.4	168	0.979	0.362	59.3	163	3.207	0.494	0.527	23.2	0.032
	(2.1)	(1.8)	(6)	(0.034)	(0.005)	(1.2)	(2)	(0.494)	(0.006)	(0.004)	(0.6)	(0.008)
<i>sandhanica</i>	3.0	1.75	147	1.13	0.321	75.8	236	3.100	0.537	0.554	73.4	0.039
	(1.7)	(1.21)	(11)	(0.09)	(0.003)	(0.8)	(2)	(0.537)	(0.004)	(0.003)	(2.2)	(0.010)
<i>Podocarpus</i>	8.3	4.91	28.0	0.563	0.470	209.5	446	12.910	0.159	0.280	168	0.013
<i>nerifolius</i>	(4.2)	(2.34)	(1.4)	(0.020)	(0.003)	(3.9)	(8)	(0.159)	(0.004)	(0.004)	(4.4)	(0.006)
<i>Poikilospermum</i>	16.9	9.02	348	2.90	0.319	83.4	260	1.415	0.767	0.819	40.2	0.026
<i>cordifolium</i>	(14.0)	(7.56)	(13)	(0.13)	(0.006)	(2.2)	(4)	(0.767)	(0.004)	(0.009)	(2.7)	(0.007)
<i>Polyalthia</i>	5.9	2.03	51.7	0.334	0.367	64.5	176	3.366	0.520	0.532	19.5	0.060
<i>sumatrana</i>	(0.7)	(0.23)	(2.6)	(0.017)	(0.003)	(0.7)	(1)	(0.520)	(0.007)	(0.005)	(0.8)	(0.009)
<i>Popowia pisocarpa</i>	1.0	0.53	27.7	0.129	0.351	47.3	135	2.641	0.585	0.585	41.9	0.049
	(0.5)	(0.70)	(1.4)	(0.006)	(0.005)	(0.7)	(1)	(0.585)	(0.007)	(0.006)	(1.0)	(0.007)
<i>Pterospermum</i>	9.1	2.84	103	0.640	0.397	62.5	159	1.812	0.689	0.730	23.3	0.095
<i>stapfianum</i>	(2.8)	(0.92)	(5)	(0.034)	(0.008)	(1.4)	(3)	(0.689)	(0.009)	(0.007)	(1.4)	(0.012)
<i>Reinwardtiodendron</i>	38.2	36.2	13.0	0.070	0.397	53.7	135	3.252	0.457	0.502	40.0	0.051
<i>humile</i>	(17.8)	(18.3)	(0.6)	(0.004)	(0.005)	(0.8)	(1)	(0.457)	(0.010)	(0.008)	(1.3)	(0.009)
<i>Ryparosa hulletii</i>	40.8	2.40	76.7	0.404	0.274	53.2	194	2.994	0.530	0.546	6.18	0.033
	(11.2)	(0.63)	(3.9)	(0.020)	(0.003)	(0.8)	(2)	(0.530)	(0.007)	(0.005)	(0.2)	(0.006)
<i>Saurauia ferox</i>	42.8	5.57	192	0.893	0.220	47.9	219	3.079	0.483	0.520	62.9	0.048
	(26.8)	(3.47)	(12)	(0.052)	(0.003)	(0.8)	(4)	(0.483)	(0.006)	(0.005)	(3.6)	(0.013)
<i>Semecarpus</i>	14.2	3.14	315	3.51	0.400	112.9	282	2.543	0.519	0.567	50.5	0.047
<i>bunburyanus</i>	(2.6)	(0.63)	(17)	(0.19)	(0.005)	(2.2)	(4)	(0.519)	(0.005)	(0.004)	(1.9)	(0.006)
<i>Shorea agami</i>	86.2	3.51	190	0.972	0.289	50.8	178	2.397	0.640	0.633	50.7	0.080
	(31.1)	(1.30)	(13)	(0.068)	(0.008)	(1.7)	(3)	(0.640)	(0.013)	(0.009)	(7.2)	(0.018)
<i>Shorea fallax</i>	42.8	10.3	118	0.736	0.358	65.6	178	3.014	0.533	0.545	40.4	0.043
	(4.1)	(1.32)	(4)	(0.039)	(0.007)	(3.6)	(7)	(0.533)	(0.006)	(0.004)	(2.0)	(0.008)
<i>Shorea johorensis</i>	16.0	3.50	71.9	0.627	0.435	90.0	205	2.130	0.670	0.671	20.3	0.119
	(2.3)	(0.50)	(3.6)	(0.032)	(0.006)	(2.7)	(5)	(0.670)	(0.009)	(0.007)	(2.1)	(0.019)
<i>Shorea leprosula</i>	48.3	3.42	47.5	0.239	0.399	51.9	131	2.707	0.576	0.583	32.7	0.133
	(2.2)	(0.10)	(2.1)	(0.010)	(0.004)	(0.8)	(2)	(0.576)	(0.008)	(0.005)	(3.2)	(0.018)
<i>Shorea macrophylla</i>	22.2	0.464	256	2.59	0.461	102.7	223	2.357	0.677	0.644	50.7	0.039
	(5.7)	(0.128)	(13.3)	(0.10)	(0.004)	(2.3)	(4)	(0.678)	(0.006)	(0.005)	(2.1)	(0.013)
<i>Sindora irpicina</i>	19.0	6.80	69.9	0.391	0.434	56.2	130	2.100	0.670	0.653	23.0	0.040

	(4.4)	(1.51)	(3.3)	(0.018)	(0.005)	(0.7)	(2)	(0.670)	(0.009)	(0.007)	(0.7)	(0.011)
<i>Spathiostemon</i>	25.9	4.14	64.2	0.338	0.353	51.0	145	2.682	0.540	0.561	19.8	0.082
<i>javensis</i>	(16.0)	(2.63)	(4.1)	(0.027)	(0.004)	(1.5)	(4)	(0.540)	(0.009)	(0.006)	(2.0)	(0.014)
	12.7	11.2	39.0	0.165	0.308	43.4	143	2.647	0.562	0.584	52.1	0.053
<i>Stychnos ignatii</i>	(0.8)	(1.0)	(1.6)	(0.007)	(0.013)	(1.5)	(1)	(0.562)	(0.013)	(0.011)	(1)	(0.013)
<i>Syzygium</i>	99.3	1.14	10.8	0.126	0.491	118.6	244	3.430	0.456	0.494	20.7	0.023
<i>campanulatum</i>	(28.4)	(0.32)	(0.5)	(0.006)	(0.011)	(1.6)	(6)	(0.456)	(0.014)	(0.010)	(0.4)	(0.015)
<i>Tarbetaemontana</i>	14.3	3.80	108	0.570	0.258	53.2	204	2.531	0.563	0.581	43.8	0.023
<i>macrocarpa</i>	(5.1)	(1.22)	(4)	(0.027)	(0.005)	(1.6)	(2)	(0.563)	(0.007)	(0.005)	(1.1)	(0.007)
	28.8	4.69	213	1.91	0.439	94.9	214	1.975	0.692	0.678	39.2	0.068
<i>Uncaria cordata</i>	(4.1)	(0.80)	(15)	(0.12)	(0.005)	(2.7)	(4)	(0.692)	(0.008)	(0.008)	(2.1)	(0.010)
	2.11	1.55	99.0	0.391	0.239	39.9	167	2.668	0.566	0.575	67.5	0.030
<i>Urophyllum glabrum</i>	(0.30)	(0.04)	(4.1)	(0.016)	(0.002)	(0.6)	(2)	(0.566)	(0.006)	(0.005)	(1.8)	(0.009)10.0
<i>Uvaria</i>	9.7	6.54	190	0.896	0.345	46.6	135	2.638	0.578	0.584	14.2	0.035
<i>sorzogonensis</i>	(0.7)	(0.39)	(9)	(0.053)	(0.005)	(1.0)	(2)	(0.578)	(0.008)	(0.006)	(0.4)	(0.005)
	2.3	1.46	116	0.692	0.334	58.5	174	2.309	0.638	0.632	63.1	0.054
<i>Xanthophyllum</i>	(1.1)	(1.51)	(5)	(0.041)	(0.006)	(1.5)	(3)	(0.638)	(0.009)	(0.008)	(1.9)	(0.011)
<i>affine</i>												
<i>Zizyphus</i>	10.6	4.10	82.2	0.412	0.354	50.2	142	3.134	0.539	0.548	48.2	0.070
<i>angustifolius</i>	(8.5)	(3.38)	(5.1)	(0.026)	(0.004)	(0.9)	(2)	(0.539)	(0.008)	(0.006)	(1.0)	(0.013)

Table S5. Pearson's coefficients and levels of significance (p) of the correlations between element contents and ratios with leaf phenolics and tannin contents, A_{mass} (leaf photosynthetic rate per unit of leaf mass), morphological traits and accumulated folivory (F), maximum accumulated folivory (MaxF) and the accumulated folivory coefficient of variation (CVF) in 88 rainforest plants of Borneo. Significant correlations at $p < 0.05$ ($p < 0.001$ after Bonferroni correction) are in bold.

	TP	TT	Area	LMA	LMAF	DF	L	R	COM	Per. larea	A_{mass}	F	MaxF	CVF
C	R=0.120 $p=0.264$	R=0.129 $p=0.230$	R=-0.226 $p=0.034$	R=-0.101 $p=0.333$	R=-0.145 $p=0.178$	R=0.052 $p=0.633$	R=0.084 $p=0.435$	R=-0.080 $p=0.467$	R=-0.156 $p=0.146$	R=-0.163 $p=0.130$	R=-0.129 $p=0.459$	R=0.189 $p=0.079$	R=0.150 $p=0.162$	R=-0.047 $p=0.661$
N	R=-0.235 $p=0.027$	R=-0.344 $p=0.001$	R=-0.038 $p=0.726$	R=-0.334 $p=0.001$	R=-0.291 $p=0.006$	R=-0.168 $p=0.117$	R=-0.023 $p=0.832$	R=-0.083 $p=0.453$	R=0.061 $p=0.573$	R=0.001 $p=0.998$	R=0.413 $p=0.001$	R=0.057 $p=0.597$	R=0.138 $p=0.201$	R=-0.043 $p=0.689$
Ca	R=0.164 $p=0.128$	R=0.153 $p=0.154$	R=0.1393 $p=0.195$	R=0.355 $p<0.001$	R=0.389 $p<0.001$	R=0.044 $p=0.686$	R=0.020 $p=0.857$	R=0.072 $p=0.513$	R=0.136 $p=0.206$	R=-0.014 $p=0.898$	R=0.003 $p=0.986$	R=-0.001 $p=0.993$	R=0.068 $p=0.532$	R=0.094 $p=0.386$
K	R=-0.283 $p=0.007$	R=-0.111 $p=0.302$	R=-0.003 $p=0.979$	R=-0.066 $p=0.544$	R=0.103 $p=0.339$	R=-0.355 $p=0.001$	R=0.068 $p=0.528$	R=-0.138 $p=0.206$	R=-0.072 $p=0.500$	R=-0.101 $p=0.352$	R=0.086 $p=0.623$	R=-0.273 $p<0.001$	R=-0.220 $p=0.040$	R=-0.195 $p=0.069$
Mg	R=-0.188 $p=0.080$	R=-0.073 $p=0.497$	R=0.027 $p=0.802$	R=0.158 $p=0.143$	R=0.264 $p=0.013$	R=-0.170 $p=0.114$	R=0.098 $p=0.362$	R=-0.068 $p=0.535$	R=-0.024 $p=0.823$	R=-0.034 $p=0.754$	R=-0.040 $p=0.820$	R=-0.057 $p=0.588$	R=-0.034 $p=0.752$	R=0.141 $p=0.191$
S	R=-0.160 $p=0.136$	R=-0.290 $p=0.006$	R=0.065 $p=0.548$	R=-0.065 $p=0.546$	R=-0.006 $p=0.953$	R=-0.117 $p=0.278$	R=0.030 $p=0.783$	R=-0.002 $p=0.983$	R=0.046 $p=0.674$	R=-0.095 $p=0.379$	R=0.117 $p=0.502$	R=-0.013 $p=0.908$	R=0.081 $p=0.452$	R=-0.136 $p=0.207$
P	R=0.230 $p=0.832$	R=-0.104 $p=0.337$	R=-0.043 $p=0.690$	R=-0.053 $p=0.623$	R=-0.106 $p=0.326$	R=0.084 $p=0.438$	R=-0.056 $p=0.607$	R=-0.033 $p=0.765$	R=0.183 $p=0.088$	R=-0.106 $p=0.324$	R=0.184 $p=0.289$	R=-0.144 $p=0.182$	R=0.013 $p=0.903$	R=-0.009 $p=0.933$
Na	R=0.200 $p=0.031$	R=0.209 $p=0.050$	R=-0.172 $p=0.110$	R=0.095 $p=0.380$	R=0.044 $p=0.683$	R=0.102 $p=0.329$	R=0.067 $p=0.535$	R=-0.120 $p=0.274$	R=-0.156 $p=0.147$	R=-0.053 $p=0.0623$	R=0.238 $p=0.168$	R=-0.131 $p=0.225$	R=-0.185 $p=0.084$	R=-0.037 $p=0.729$
Fe	R=0.215 $p=0.044$	R=-0.026 $p=0.809$	R=0.083 $p=0.443$	R=-0.142 $p=0.186$	R=-0.167 $p=0.119$	R=0.038 $p=0.726$	R=-0.186 $p=0.083$	R=0.198 $p=0.070$	R=0.217 $p=0.043$	R=-0.240 $p=0.825$	R=0.369 $p=0.029$	R=0.088 $p=0.413$	R=0.175 $p=0.104$	R=0.013 $p=0.902$
Mn	R=-0.020 $p=0.857$	R=-0.200 $p=0.061$	R=0.055 $p=0.614$	R=-0.087 $p=0.421$	R=-0.054 $p=0.616$	R=-0.058 $p=0.595$	R=-0.095 $p=0.380$	R=-0.102 $p=0.353$	R=0.046 $p=0.669$	R=-0.043 $p=0.692$	R=0.111 $p=0.526$	R=0.127 $p=0.240$	R=0.210 $p=0.050$	R=-0.075 $p=0.485$
V	R=0.174 $p=0.105$	R=-0.013 $p=0.904$	R=-0.079 $p=0.464$	R=-0.154 $p=0.153$	R=-0.192 $p=0.073$	R=0.057 $p=0.598$	R=-0.056 $p=0.602$	R=0.137 $p=0.210$	R=0.057 $p=0.598$	R=-0.065 $p=0.547$	R=0.274 $p=0.111$	R=0.031 $p=0.777$	R=0.151 $p=0.160$	R=-0.026 $p=0.809$
Cr	R=0.061 $p=0.575$	R=0.056 $p=0.606$	R=0.2033 $p=0.057$	R=-0.122 $p=0.258$	R=0.072 $p=0.506$	R=-0.117 $p=0.279$	R=-0.201 $p=0.061$	R=0.142 $p=0.195$	R=0.174 $p=0.105$	R=0.044 $p=0.688$	R=0.050 $p=0.776$	R=0.169 $p=0.116$	R=0.158 $p=0.143$	R=0.116 $p=0.281$

Ni	R=-0.267 p=0.012	R=-0.131 p=0.223	R=-0.053 p=0.624	R=-0.159 p=0.138	R=-0.157 p=0.144	R=-0.052 p=0.632	R=-0.040 p=0.709	R=0.029 p=0.793	R=-0.067 p=0.537	R=0.028 p=0.796	R=0.283 p=0.099	R=0.127 p=0.238	R=0.227 p=0.034	R=0.085 p=0.429
Cu	R=-0.176 p=0.102	R=-0.194 p=0.071	R=0.002 p=0.099	R=-0.097 p=0.369	R=-0.124 p=0.252	R=0.014 p=0.898	R=-0.067 p=0.999	R=-0.065 p=0.557	R=0.116 p=0.283	R=0.035 p=0.749	R=0.351 p=0.039	R=-0.013 p=0.902	R=0.063 p=0.559	R=-0.076 p=0.481
Zn	R=0.006 p=0.959	R=-0.102 p=0.347	R=-0.014 p=0.897	R=0.046 p=0.670	R=0.079 p=0.465	R=-0.052 p=0.999	R=0.052 p=0.633	R=-0.022 p=0.840	R=0.019 p=0.861	R=-0.187 p=0.081	R=0.077 p=0.660	R=-0.043 p=0.694	R=0.084 p=0.434	R=-0.160 p=0.137
As	R=-0.086 p=0.428	R=-0.071 p=0.510	R=-0.036 p=0.742	R=-0.111 p=0.305	R=-0.111 p=0.305	R=-0.027 p=0.803	R=-0.056 p=0.999	R=0.043 p=0.698	R=0.061 p=0.575	R=0.065 p=0.545	R=-0.032 p=0.854	R=0.074 p=0.491	R=0.263 p=0.013	R=-0.041 p=0.708
Sr	R=-0.212 p=0.048	R=-0.023 p=0.832	R=0.024 p=0.824	R=0.220 p=0.039	R=0.199 p=0.063	R=0.092 p=0.392	R=0.094 p=0.382	R=-0.014 p=0.900	R=0.083 p=0.440	R=-0.006 p=0.958	R=0.281 p=0.102	R=-0.137 p=0.202	R=-0.083 p=0.444	R=0.022 p=0.838
Mo	R=-0.037 p=0.731	R=0.084 p=0.436	R=0.073 p=0.500	R=0.014 p=0.899	R=0.001 p=0.995	R=0.020 p=0.855	R=-0.105 p=0.330	R=0.097 p=0.379	R=0.090 p=0.404	R=0.193 p=0.072	R=0.016 p=0.927	R=-0.108 p=0.315	R=0.014 p=0.900	R=0.040 p=0.712
Cd	R=0.006 p=0.953	R=-0.058 p=0.589	R=0.016 p=0.884	R=0.032 p=0.770	R=0.045 p=0.674	R=-0.018 p=0.869	R=-0.053 p=0.624	R=-0.116 p=0.291	R=0.065 p=0.547	R=-0.086 p=0.424	R=0.297 p=0.083	R=-0.155 p=0.149	R=0.111 p=0.303	R=-0.087 p=0.419
Pb	R=-0.325 p=0.002	R=-0.134 p=0.212	R=-0.113 p=0.296	R=-0.206 p=0.055	R=-0.159 p=0.138	R=-0.153 p=0.155	R=0.029 p=0.790	R=-0.070 p=0.525	R=0.094 p=0.883	R=-0.009 p=0.934	R=-0.003 p=0.987	R=0.009 p=0.932	R=0.170 p=0.114	R=-0.129 p=0.233
C:N	R=0.258 p=0.015	R=0.346 p=0.001	R=-0.025 p=0.818	R=0.350 p=0.001	R=0.304 p=0.004	R=0.172 p=0.110	R=0.018 p=0.870	R=-0.063 p=0.567	R=-0.059 p=0.586	R=-0.034 p=0.753	R=-0.420 p=0.0012	R=-0.069 p=0.525	R=-0.140 p=0.194	R=-0.024 p=0.824
C:P	R=-0.019 p=0.859	R=0.116 p=0.282	R=0.025 p=0.817	R=0.054 p=0.621	R=0.094 p=0.385	R=-0.059 p=0.588	R=0.037 p=0.729	R=0.051 p=0.645	R=-0.176 p=0.100	R=0.123 p=0.254	R=-0.217 p=0.210	R=0.148 p=0.170	R=0.008 p=0.941	R=0.024 p=0.821
N:P	R=-0.249 p=0.019	R=-0.167 p=0.119	R=0.025 p=0.821	R=-0.185 p=0.084	R=-0.108 p=0.318	R=-0.193 p=0.077	R=0.001 p=0.972	R=0.010 p=0.930	R=-0.123 p=0.255	R=0.167 p=0.119	R=0.203 p=0.242	R=0.152 p=0.156	R=0.077 p=0.477	R=0.012 p=0.910
C:K	R=0.291 p=0.006	R=0.122 p=0.258	R=-0.008 p=0.941	R=0.053 p=0.625	R=-0.100 p=0.355	R=0.322 p<0.001	R=-0.082 p=0.449	R=0.169 p=0.123	R=0.070 p=0.518	R=0.074 p=0.491	R=-0.107 p=0.540	R=0.284 p=0.007	R=0.248 p=0.020	R=0.215 p=0.044
N:K	R=0.187 p=0.081	R=-0.073 p=0.502	R=-0.008 p=0.944	R=-0.124 p=0.250	R=-0.234 p=0.029	R=0.1947 p=0.069	R=-0.103 p=0.340	R=0.145 p=0.185	R=0.109 p=0.313	R=0.067 p=0.537	R=0.157 p=0.368	R=0.292 p=0.006	R=0.302 p=0.004	R=0.202 p=0.060
P:K	R=0.301 p=0.004	R=0.038 p=0.728	R=-0.026 p=0.812	R=0.014 p=0.899	R=-0.165 p=0.123	R=0.359 p=0.001	R=-0.107 p=0.319	R=0.131 p=0.233	R=0.195 p=0.069	R=-0.015 p=0.890	R=0.039 p=0.825	R=0.174 p=0.105	R=0.239 p=0.025	R=0.194 p=0.070

TP = Total leaf phenolics
 TT = Total leaf tannins
 Area = Leaf area
 LMA = Leaf mass area (dry weight)

LMAF = Leaf mass area (fresh weight)
DF = Leaf (dry/fresh) weight
L = Leaf Length
R = Leaf Roundness
COM = Leaf Compactness
Per/Area = Leaf (Perimeter/Area)
 A_{mass} = Photosynthetic rate per unity of leaf mass
MaxF = Maximum accumulated folivory
CvF = Coefficient of variation of accumulated folivory
F = Accumulated folivory

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Table S6. Pearson's coefficients and levels of significance (p) of the correlations between leaf phenolics and tannin contents, A_{mass} (leaf photosynthetic rate per unit of leaf mass), morphological traits with the accumulated folivory (F), maximum accumulated folivory (MaxF) and coefficient of variation of accumulated folivory (CVF) in 88 plants in a Bornean rainforest. Significant correlations at $p < 0.05$ ($p < 0.0025$ after Bonferroni correction) are in bold.

	TP	TT	Area	LMA	LMAF	DF	L	R	COM	Per/area	A_{mass}
MaxF	R=-0.094 $p=0.384$	R=-0.163 $p=0.129$	R=-0.089 $p=0.410$	R=-0.096 $p=0.372$	R=-0.129 $p=0.230$	R=0.044 $p=0.686$	R=-0.086 $p=0.424$	R=0.105 $p=0.338$	R=0.069 $p=0.520$	R=0.020 $p=0.851$	R=-0.044 $p=0.803$
CVF	R=0.053 $p=0.627$	R=0.119 $p=0.270$	R=0.218 $p=0.042$	R=-0.086 $p=0.427$	R=-0.053 $p=0.623$	R=-0.074 $p=0.491$	R=-0.318 $p=0.003$	R=0.240 $p=0.027$	R=0.263 $p=0.013$	R=0.234 $p=0.028$	R=0.147 $p=0.399$
F	R=0.135 $p=0.212$	R=0.092 $p=0.396$	R=0.151 $p=0.162$	R=-0.135 $p=0.210$	R=-0.104 $p=0.333$	R=-0.065 $p=0.549$	R=-0.18 $p=0.090$	R=0.126 $p=0.250$	R=0.201 $p=0.060$	R=0.146 $p=0.175$	R=0.044 $p=0.800$

TP = Total leaf phenolics

TT = Total leaf tannins

Area = Leaf area

LMA = Leaf mass area (dry weight)

LMAF = Leaf mass area (fresh weight)

DF = Leaf (dry/fresh) weight

L = Leaf Length

R = Leaf Roundness

COM = Leaf Compactness

Per/Area = Leaf (Perimeter/Area)

A_{mass} = Photosynthetic rate per unity of leaf mass

MaxF = Maximum accumulated folivory

CvF = Coefficient of variation of accumulated folivory

F = Accumulated folivory

Table S7. Pearson's coefficients and significant levels (p) of the correlations among total leaf phenolics and tannin contents, A_{mass} (leaf photosynthesis rate per unit of leaf mass), morphological traits and accumulated standing folivory in the 88 rainforest plants of the Borneo studied forest. Significant regressions at $p < 0.05$ ($p < 0.001$ after Bonferroni correction) are in bold.

	TT	Area	Dry weight	LMA	LMAF	DF	L	R	COM	Per./area	A_{mass}
TP	R=0.401 p<0.001	R=0.081 p=0.456	R = 0.132 p=0.222	R=0.220 p=0.039	R=0.105 p=0.329	R=0.299 p=0.005	R=-0.068 p=0.532	R=-0.035 p=0.751	R=0.077 p=0.478	R=-0.038 p=0.724	R=-0.079 p=0.652
TT		R=0.028 p=0.799	R=0.064 p=0.556	R=0.132 p=0.220	R=0.048 p=0.660	R=0.191 p=0.075	R=-0.157 p=0.145	R=0.091 p=0.408	R=0.153 p=0.154	R=-0.010 p=0.930	R=0.096 p=0.583
Area			R=0.961 p<0.001	R=0.362 p<0.001	R=0.450 p<0.001	R=-0.090 p=0.402	R=-0.363 p=0.001	R=0.072 p=0.690	R=0.495 p<0.001	R=0.345 p<0.001	R=-0.262 p=0.129
Dry weight				R=0.597 p<0.001	R=0.641 p<0.001	R=0.051 p=0.635	R=-0.271 p=0.011	R=-0.124 p=0.248	R=0.450 p<0.001	R=0.389 p<0.001	R=0. p=0.
LMA					R=0.880 p<0.001	R=0.464 p=0.401	R=0.159 p=0.139	R=-0.019 p=0.864	R=0.072 p=0.508	R=0.282 p=0.008	R=-0.722 p<0.001
LMAF						R=0.006 p=0.959	R=0.157 p<0.001	R=-0.039 p=0.720	R=0.027 p=0.800	R=0.28 p=0.007	R=-0.568 p<0.001
DF							R=0.047 p=0.664	R=0.026 p=0.813	R=0.091 p=0.402	R=0.093 p=0.388	R=-0.320 p=0.061
L								R=-0.693 p<0.001	R=-0.765 p<0.001	R=-0.002 p=0.982	R=-0.241 p=0.162
R									R=0.702 p<0.001	R=-0.768 p<0.001	R=-0.111 p=0.526
COM										R=-0.063 p=0.559	R=0.119 p=0.450
Per./area											R=0.062 p=0.723

TP = Total leaf phenolics
TT = Total leaf tannins

Area = Leaf area
LMA = Leaf mass area (dry weight)
LMAF = Leaf mass area (fresh weight)
DF = Leaf (dry/fresh) weight
L = Leaf Length
R = Leaf Roundness
COM = Leaf Compactness
Per/Area = Leaf (Perimeter/Area)
 A_{mass} = Photosynthetic rate per unity of leaf mass

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Table S8. Association between species leaf traits and phylogeny (phylogenetic effects were estimated with the PHYSIG randomization procedure. Significant associations are highlighted in bold.

Leaf Variable	k	P
Element content		
Log C (%)	0.145	0.26
N (%)	0.182	0.061
Log Ca (%)	0.202	0.020
K (%)	0.168	0.12
Log Mg (%)	0.120	0.48
Log S (%)	0.119	0.40
P (%)	0.110	0.55
Na (%)	0.304	0.10
Log Fe (mg kg ⁻¹)	0.178	0.44
Mn (mg kg ⁻¹)	0.215	0.12
Log V (mg kg ⁻¹)	0.245	0.36
Log Cr (mg kg ⁻¹)	0.220	0.072
Log Ni (mg kg ⁻¹)	0.195	0.25
Log Cu (mg kg ⁻¹)	0.128	0.42
Log Zn (mg kg ⁻¹)	0.179	0.55
Log As (mg kg ⁻¹)	0.209	0.44
Log Sr (mg kg ⁻¹)	0.090	0.95
Log Mo,mg kg ⁻¹)	0.180	0.44
Log Cd (mg kg ⁻¹)	0.113	0.66
Pb (mg kg ⁻¹)	0.247	0.14
Stoichiometry		
C:N	0.189	0.087
Log C:P	0.106	0.54
N:P	0.150	0.16
Log C:K	0.137	0.26
N:K	0.106	0.67
Log P:K	0.192	0.050
Carbon based Compounds		
Log Total phenolics (mg g ⁻¹)	0.172	0.28
Log Total tannins (mg g ⁻¹)	0.106	0.57
Leaf morphological traits		
Log leaf area (m ⁻²)	0.205	0.045
Log leaf fresh weight (g)	0.199	0.024
Log leaf dry weight (g)	0.203	0.020
Log LMA (g m ⁻²) (dry weight)	0.425	0.009
Log LMA (g m ⁻²) (fresh weight)	0.513	<0.0001
Leaf dry/fresh weight ratio	0.170	0.16

Elongation	7.388	<0.00001
Roundness	0.667	0.015
Compactness	0.804	0.002
Leaf perimeter/leaf area	0.238	0.067
Accumulated folivory (%)	0.104	0.894

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Table S9. Range of leaf elemental content of the 20 different elements analyzed in this study and in examples of previous studies in other tropical rainforests.

Element	Danum valley, Borneo (88 sp) This study	Oahu (88 sp) <i>Peñuelas et al. 2010a</i>	New South Wales (12 sp) <i>Specht & Turner 2006</i>	Taiwan (20 sp) <i>Wu et al. 2007</i>	French Guiana (45 sp) <i>Hättenschwiler et al. 2008</i>	French Guiana (14 sp) <i>Coste et al. 2005</i>	Queensland (Australia) (162 sp) <i>Asner et al. 2009</i>	Review of different parts of the world (150 sp) <i>Townsend et al. 2007</i>
C (%)	39.9-57.2	41.9-57.4			44.5-52.4			
N (%)	1.00-3.59	0.74-3.44	0.72-4.21	0.12-3.8	1.0-2.6	2.5-1.1	1.1-2.7	1.83-1.92
Ca (%)	0.23-5.33	0.03-4.31	0.24-2.74	0.01-5.2				
K (%)	0.42-2.30	0.30-2.62	0.07-2.37	0.20-5.4				
Mg (%)	0.10-0.91	0.10-1.61	0.02-0.68	0.02-2.9				
S (%)	0.11-0.43	0.10-1.41						
P (%)	0.04-0.16	0.05-0.42	0.04-0.51	0.03-0.28	0.04-0.12		0.06-0.22	0.08-0.12
Na (%)	<0.01-0.16	0.03-1.65						
Fe (mg kg ⁻¹)	37-1266	30-299		3.8-1010				
Mn (mg kg ⁻¹)	20-4335	30-1676		22.6-4130				
V (mg kg ⁻¹)	0.2-4.6	0.05-0.70						
Cr (mg kg ⁻¹)	0.2-21.0	0.01-2.3						
Ni (mg kg ⁻¹)	1.1-70	0.4-39						
Cu (mg kg ⁻¹)	2.4-23.2	2.5-22.3		3.9-17.0				
Zn (mg kg ⁻¹)	5.4-54.7	5.2-214		0.32-324				
As (mg kg ⁻¹)	<0.10-0.42	0.01-0.44						
Sr (mg kg ⁻¹)	11-343	12-606						
Mo (mg kg ⁻¹)	<0.2-0.5	0.01-2.4						
Cd (mg kg ⁻¹)	<0.1-0.4	0.01-0.40						
Pb (mg kg ⁻¹)	0.20-2.35	0.04-7.6						

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