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

Josep Peñuelas[1,2]*, Jordi Sardans[1,2], Joan Llusià[1,2], Jorge Silva [1,2], Susan M. Owen[1,3], Bernadus Bala-Ola[4], Alona C. Linatoc[5], Mohamed N. Dalimin[5], Ülo Niinemets[6]

[1] *CSIC, Global Ecology Unit, CREAF-CEAB-UAB, Cerdanyola del Vallés 08913, Catalonia, Spain;* [2]*CREAF, Cerdanyola del Valles 08193, Catalonia, Spain;* [3] *Centre for Ecology and Hydrology, Edinburgh, Penicuik, EH26 0QB, Scotland, Great Britain;* [4] *Royal Society SEARRP, Danum Valley Conservation Area, Sabah, Malaysia;* [5] *Faculty of Science, Arts and Heritage, Universiti Tun Hussein Onn, Malaysia , 86400, Parit Raja, Batu Pahat, Johor, Malaysia;* [6] *Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 1, Tartu, 51014, Estonia*

* Corresponding author. E-mail: josep.penuelas@ uab.cat

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 'biogeocheminal 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 Shangguan (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; Mundin 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 succesional stages.

In Borneo, many soils are N- and P-limited (Nomura and Kikuzawa 2003; Paoli et al. 2005; Paoli 2006); e.g., typically, soil ($NH_4OAc/HOAc$)-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-km^2 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-km^2 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 ºC. Temperatures >34 ºC are rare and occur during prolonged dry periods, only. Minimum temperatures below 19 ºC 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 ± 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 (μmol g^{-1} 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 μmol m^{-2} s^{-1}, a leaf temperature of 25 °C, and an ambient CO_2 concentration of 385 μmol 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 ºC 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 (*Caesalpina major, Cassia alata, Clausena excavata, Duabanga moluccana, Fordia splendidissima, Leea indica, Reinwardtiodendron 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 V_2O_5 (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 HNO_3 and H_2O_2 (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, Gaitherburg, 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 $NaBH_4$ (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 polyvinylpolypyrrolidone (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, $S_{\mathrm{A,T}}$. The proportion of each leaf that had been removed by herbivores, F_{R}, was calculated as follows:

$$F_{\mathrm{R}} = 1 - \frac{S_{\mathrm{A}}}{S_{\mathrm{A,T}}}.$$

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} ($N_{area} = 7.46P_{area}^{0.62}$, $P < 0.001$).

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; Eichhom 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..

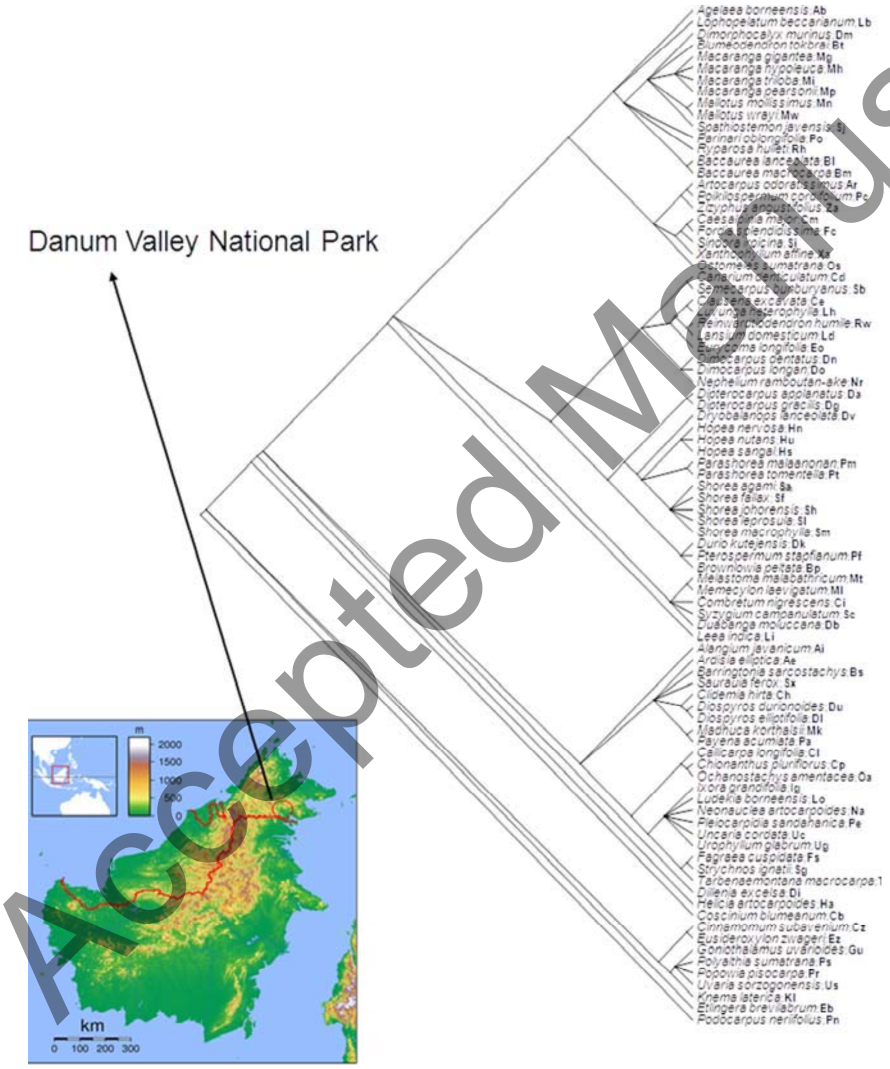


Figure 2. 'Biogeochemical niche', successional stages and folivory. (a) Principal component analysis of the leaf concentrations of the 20 elements analysed, and leaf N:P, N:K, and P:K ratios of different 88 woody species. (b) Relationship between accumulated standing folivory and PC1 scores for each 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).

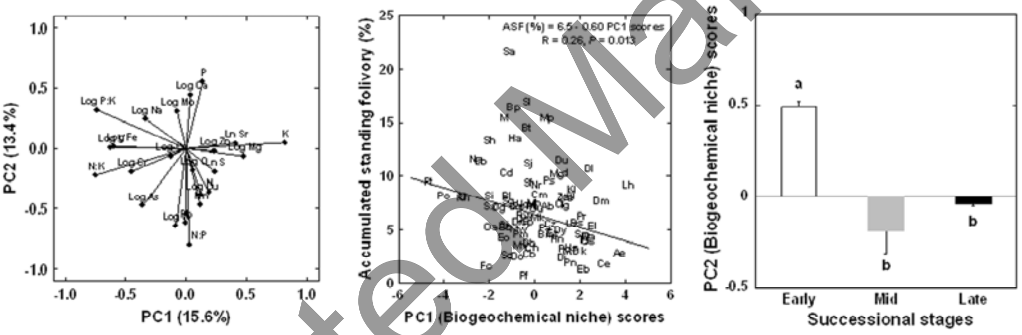


Figure 3. Relationship between accumulated standing folivory and leaf $[K]_{area}$ among 88 woody species in the Bornean rainforest studied. (Species acronyms defined in Figure 1).

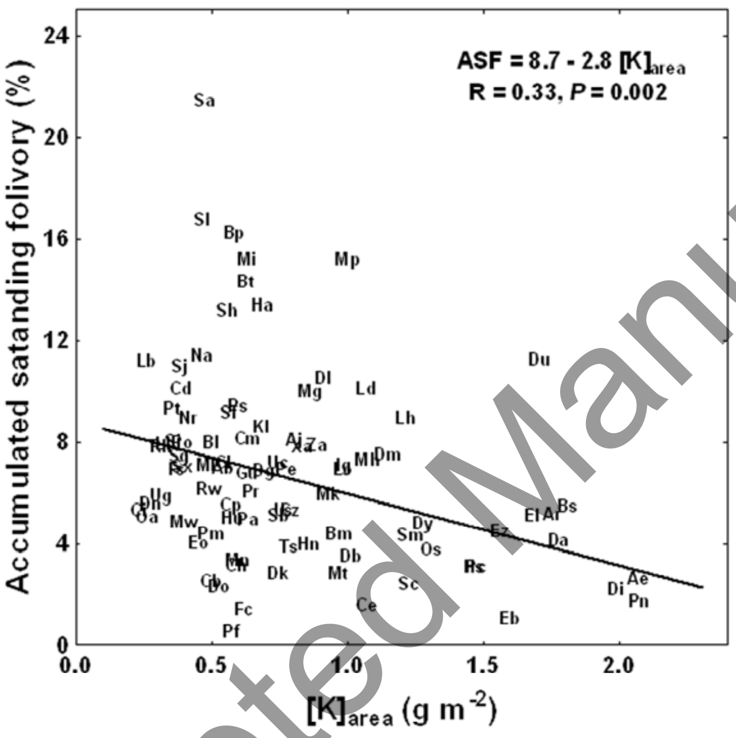


Figure 4. Leaf P concentrations and N:P ratio (means + S.E.) in the species of different successional stages. Different letters indicate significant differences (ANOVA, $P < 0.05$).

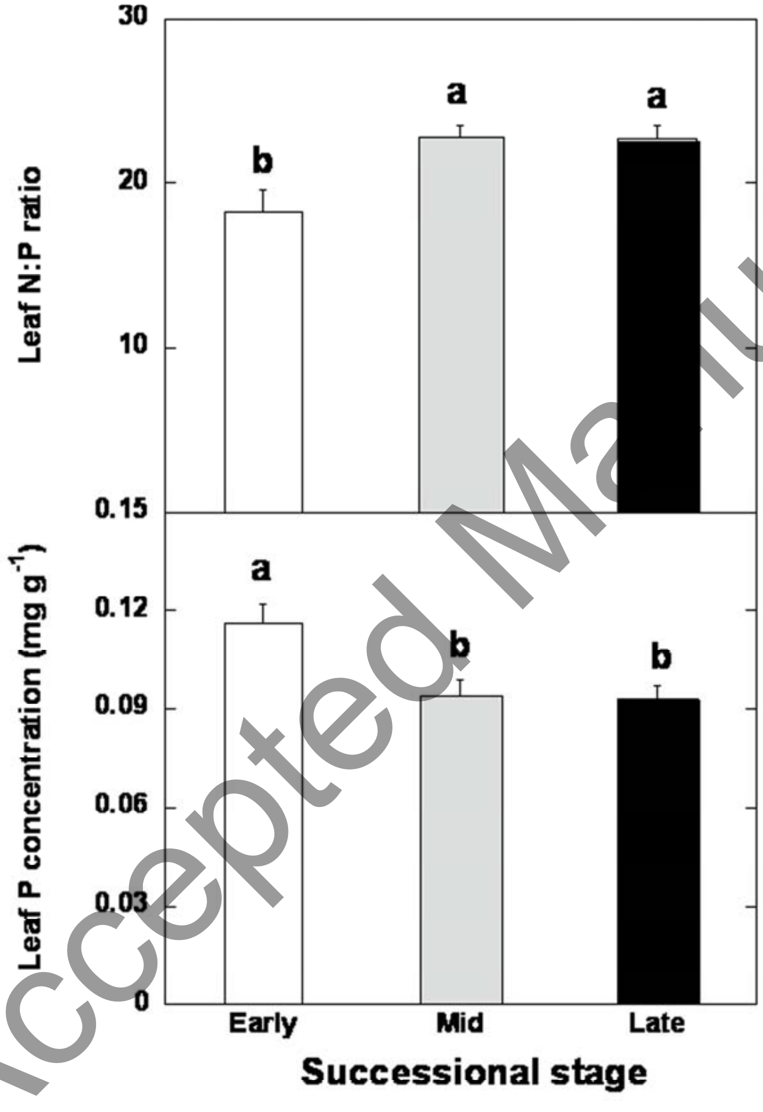


Figure 5. Relationships of LMA and A_{mass} (leaf photosynthetic capacity per unit of leaf weight) with foliar N concentrations (% dry weight) among 88 woody rain forest species in the Danum Valley, Borneo . (Species acronyms defined in Figure 1).

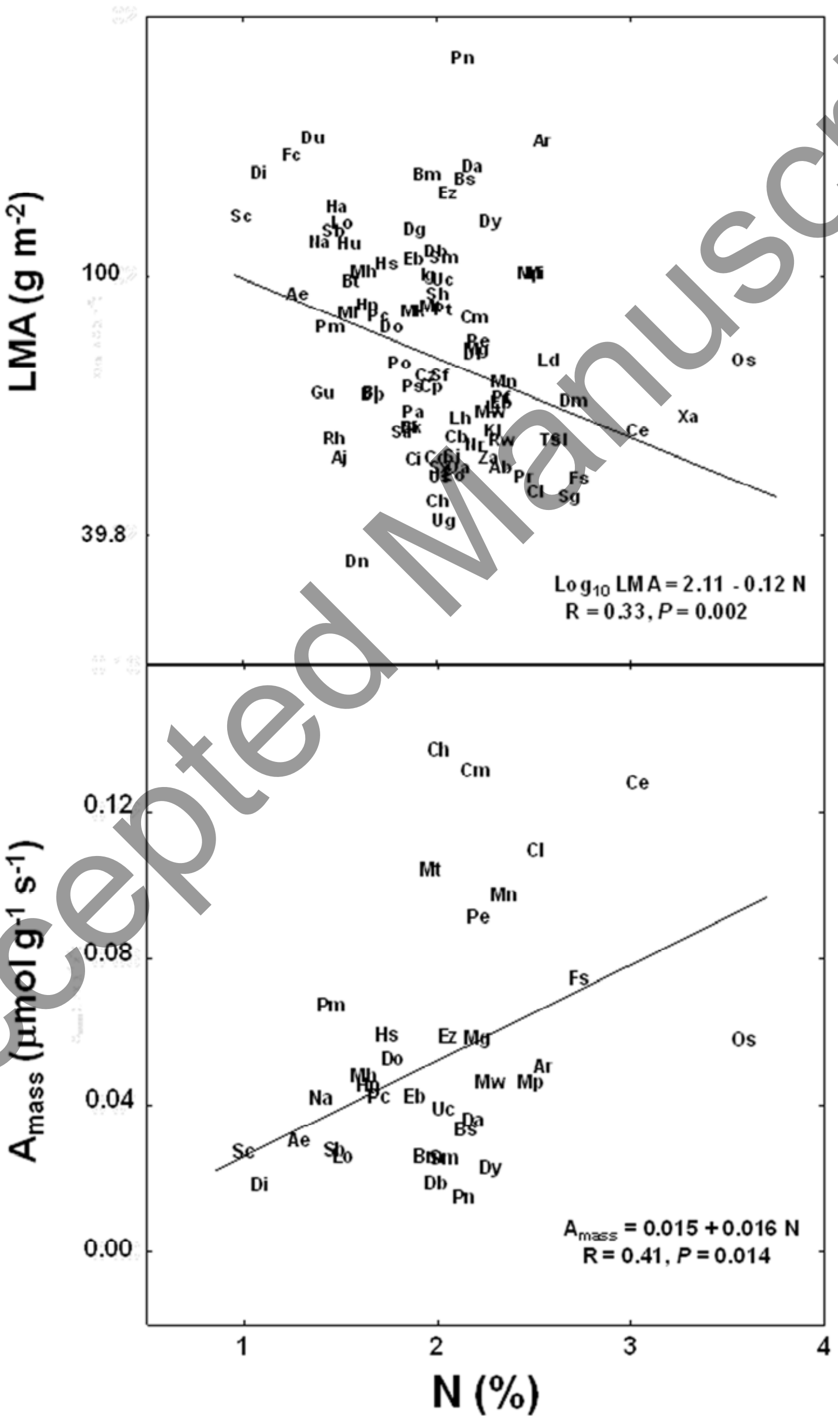
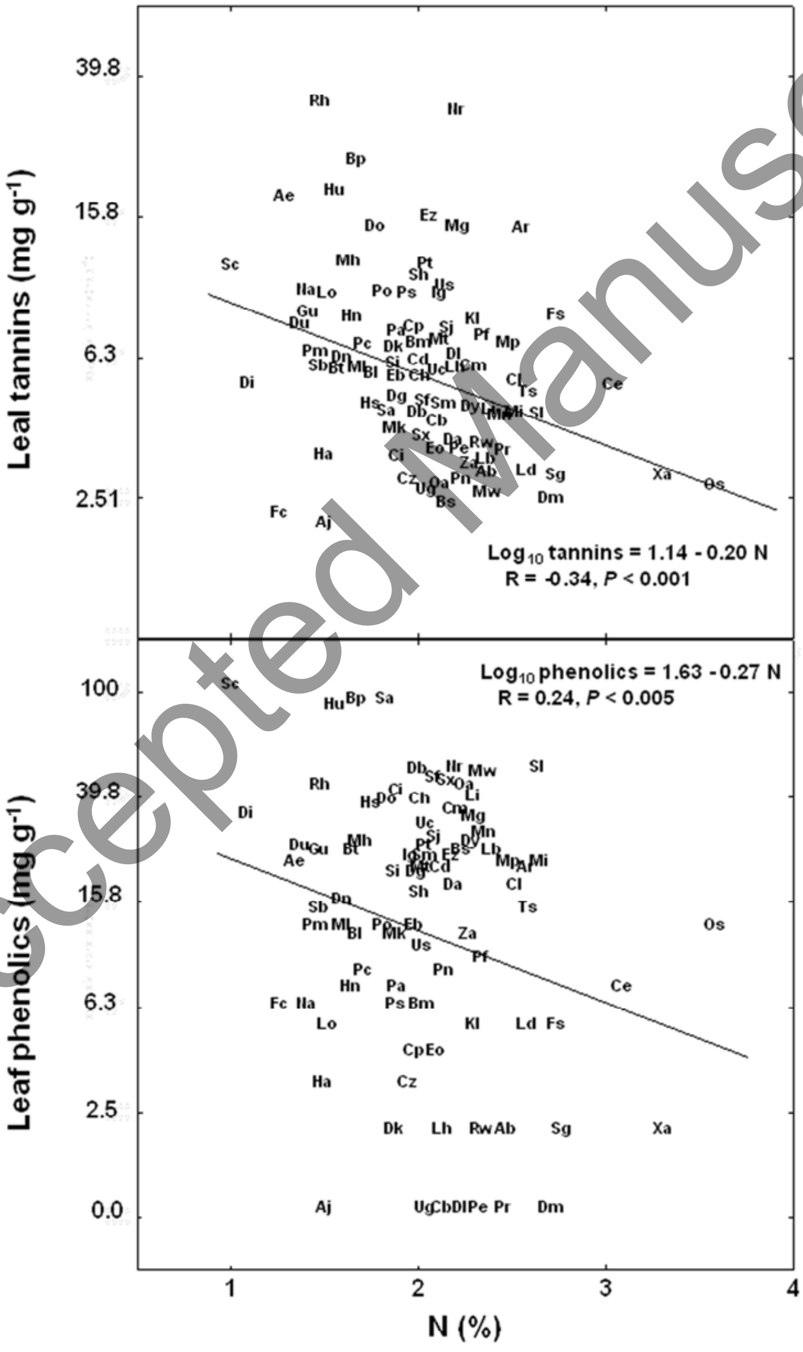


Figure 6. Relationships of concentrations of total leaf phenolics and leaf tannins with foliar N concentrations (% dry weight) of 88 woody species woody rain forest species in the Danum Valley, Borneo. (Species acronyms defined in Figure 1).



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

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

Parinari oblongifolia Hk. f. **Po**	Chrysobalanaceae	tree	40	mid
Payena acuminata (Bl.) Pierre **Pa**	Sapotaceae	tree	30	mid
Pleiocarpidia sandahanica Brem. **Pe**	Rubiaceae	tree	15	early
Podocarpus neriifolius D. Don **Pn**	Podocarpaceae	tree	36	late
Poikilospermum cordifolium (Barg.-Petr.) Merrill **Pc**	Urticaceae	liana		mid
Polyalthia sumatrana (Miq.) Kurz **Ps**	Annonaceae	tree	15	mid
Popowia pisocarpa (Bl.) Endl. **Pr**	Annonaceae	shrub/tree	10	late
Pterospermum stapfianum Ridl. **Pf**	Malvaceae	tree	25	mid
Reinwardtiodendron humile (Hassk.) Mabb. **Rw**	Meliaceae	tree	27	mid
Ryparosa hulletii King. **Rh**	Flacourtiaceae	tree	15	mid
Saurauia ferox Korth. **Sx**	Actinidiaceae	tree	5	mid
Semecarpus bunburyanus Gibbs **Sb**	Anacardiaceae	tree	15	early
Shorea agami P. S. Ashton **Sa**	Dipterocarpaceae	tree	50	late
Shorea fallax Meijer **Sf**	Dipterocarpaceae	tree	50	late
Shorea johorensis Foxw. **Sh**	Dipterocarpaceae	tree	50	late
Shorea leprosula Miq. **Sl**	Dipterocarpaceae	tree	60	late
Shorea macrophylla (de Vriese) P. S. Ashton **Sm**	Dipterocarpaceae	tree	45	mid
Sindora irpicina de Wit **Si**	Leguminosae	tree	40	mid
Spathiostemon javensis Bl. **Sj**	Euphorbiaceae	tree	17	mid
Strychnos ignatii Bergius **Sg**	Loganiaceae	liana	35	mid
Syzygium campanulatum Korth. **Sc**	Myrtaceae	tree	30	early
Tabernaemontana macrocarpa Jack **Ts**	Apocynaceae	shrub/tree	30	mid
Uncaria cordata (Lour.) Merr. **Uc**	Rubiaceae	liana		early
Urophyllum glabrum Wall. sensu Ridl. **Ug**	Rubiaceae	shrub/tree	5	mid
Uvaria sorzogonensis C. Presl. **Us**	Annonaceae	liana		mid
Xanthophyllum affine Korth. **Xa**	Polygalaceae	tree	30	late
Zizyphus angustifolius (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})
Agelaea borneensis	46.2	2.33	0.45	1.11	0.53	0.26	0.09	72.7
	(0.5)	(0.08)	(0.18)	(0.09)	(0.07)	(0.01)	(0.006)	(13.4)
Alangium javanicum	48.7	1.50	0.44	1.60	0.18	0.19	0.12	44.0
	(0.1)	(0.01)	(0.01)	(0.01)	(0.01)	(0.003)	(0.001)	(0.2)
Ardisia elliptica	47.0	1.29	1.27	2.30	0.63	0.11	0.08	39.7
	(0.8)	(0.27)	(0.12)	(0.25)	(0.08)	(0.01)	(0.01)	(5.4)
Artocarpus anisophyllus	45.2	2.55	1.35	1.13	0.13	0.16	0.12	139
	(0.4)	(0.05)	(0.17)	(0.11)	(0.07)	(0.00)	(0.003)	(13.3)
Baccaurea lanceolata	45.7	1.66	2.13	0.79	0.34	0.23	0.08	123
	(4.5)	(0.20)	(0.79)	(0.14)	(0.04)	(0.06)	(0.005)	(44.0)
Baccaurea macrocarpa	46.8	1.96	1.80	0.71	0.59	0.13	0.08	53.0
	(0.5)	(0.48)	(0.20)	(0.20)	(0.03)	(0.02)	(0.01)	(14.7)
Barringtonia sarcostachys	47.2	2.15	2.13	1.33	0.55	0.34	0.11	104
	(0.8)	(0.13)	(0.49)	(0.09)	(0.23)	(0.03)	(0.004)	(26.7)
Blumeodendron tokbrai	47.2	1.56	2.08	0.66	0.27	0.28	0.08	80.0
	(0.6)	(0.13)	(0.68)	(0.14)	(0.10)	(0.13)	(0.008)	(33.3)
Brownlowia peltata	51.1	1.67	0.76	0.93	0.18	0.19	0.10	87.7
	(1.5)	(0.18)	(0.27)	(0.13)	(0.02)	(0.06)	(0.007)	(0.3)
Caesalpinia major	48.4	2.20	2.27	0.76	0.23	0.20	0.11	58.3
	(0.8)	(0.20)	(0.62)	(0.12)	(0.03)	(0.02)	(0.003)	(5.2)
Callicarpa longifolia	48.8	2.51	1.14	1.22	0.23	0.17	0.12	74.0
	(0.9)	(0.56)	(0.23)	(0.24)	(0.02)	(0.01)	(0.02)	(7.1)
Canarium denticulatum	47.6	2.00	0.91	0.77	0.22	0.15	0.10	80.0
	(0.7)	(0.10)	(0.22)	(0.12)	(0.02)	(0.01)	(0.003)	(1.5)
Chionanthus pluriflorus	49.2	1.98	1.18	0.88	0.17	0.13	0.12	41.3
	(0.6)	(0.34)	(0.17)	(0.22)	(0.03)	(0.03)	(0.01)	(3.8)
Cinnamomum subavenium	49.5	1.95	0.76	1.17	0.19	0.16	0.08	71.0
	(0.5)	(0.19)	(0.20)	(0.03)	(0.003)	(0.12)	(0.01)	(22.0)
Clausena excavata	45.5	3.04	1.50	1.93	0.36	0.23	0.14	62.3
	(1.1)	(0.06)	(0.00)	(0.13)	(0.01)	(0.02)	(0.00)	(7.4)
Clidemia hirta	47.9	2.01	0.61	1.37	0.34	0.15	0.10	159
	(1.5)	(0.04)	(0.06)	(0.09)	(0.04)	(0.01)	(0.003)	(90)
Combretum nigrescens	44.7	1.88	1.16	0.46	0.29	0.12	0.10	1266
	(0.3)	(0.14)	(0.10)	(0.08)	(0.06)	(0.01)	(0.02)	(808)
Coscinium blumeanum	49.6	2.11	0.49	0.92	0.14	0.17	0.08	64.5
	(0.02)	(0.17)	(0.05)	(0.03)	(0.01)	(0.02)	(0.01)	(5.7)
Dillenia excelsa	46.5	1.09	0.85	1.43	0.22	0.23	0.08	57.7
	(0.2)	(0.07)	(0.04)	(0.03)	(0.03)	(0.04)	(0.002)	(4.3)
Dimocarpus dentatus	45.0	1.59	1.06	0.80	0.28	0.16	0.11	59.3
	(3.7)	(0.18)	(0.19)	(0.21)	(0.04)	(0.04)	(0.02)	(14.5)
Dimorphocalyx murinus	47.3	2.71	1.23	1.87	0.91	0.14	0.11	75.3
	(0.5)	(0.07)	(0.19)	(0.20)	(0.23)	(0.003)	(0.02)	(24.4)
Diospyros durionoides	47.0	1.37	2.13	1.09	0.46	0.12	0.10	55.7
	(1.5)	(0.54)	(0.26)	(0.12)	(0.25)	(0.02)	(0.003)	(11.9)
Diospyrus elliptifolia	49.2	2.19	1.50	1.25	0.46	0.24	0.08	47.0
	(0.1)	(0.07)	(0.13)	(0.03)	(0.01)	(0.03)	(0.00)	(3.3)
Dipterocarpus applanatus	49.2	2.19	1.50	1.25	0.46	0.24	0.08	47.0
	(2.2)	(0.21)	(0.40)	(0.29)	(0.08)	(0.04)	(0.02)	(25.7)
Dipterocarpus gracilis	53.4	1.89	0.88	0.61	0.24	0.15	0.09	104
	(2.4)	(0.05)	(0.03)	(0.05)	(0.06)	(0.02)	(0.01)	(39.4)
Dryobalanops lanceolata	53.6	2.28	0.90	1.10	0.58	0.20	0.09	81.3
	(6.2)	(0.32)	(0.12)	(0.21)	(0.10)	(0.04)	(0.02)	(9.3)
Duabanga moluccana	47.4	2.00	1.20	0.97	0.30	0.12	0.13	66.0
	(0.0)	(0.01)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.2)
Durio kutejensis	46.4	1.87	0.76	1.33	0.50	0.17	0.07	54.3
	(0.6)	(0.16)	(0.14)	(0.15)	(0.08)	(0.01)	(0.01)	(3.8)

Etlingera brevilabrum	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)
Euphoria malaiensis = Dimocarpus longan	51.4	1.41	0.77	1.13	0.25	0.15	0.10	47.3
	(0.5)	(0.04)	(0.08)	(0.08)	(0.02)	(0.01)	(0.00)	(0.03)
Eurycoma longifolia	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)
Eusideroxylon zwageri	46.6	2.06	0.97	1.21	0.40	0.13	0.12	76.7
	(0.9)	(0.16)	(0.19)	(0.26)	(0.09)	(0.01)	(0.00)	(4.7)
Fagraea cuspidata	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)
Fordia splendidissima	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)
Goniothalamus uvarioides	47.8	1.41	1.09	1.00	0.16	0.15	0.06	64.3
	(1.7)	(0.20)	(0.56)	(0.31)	(0.04)	(0.05)	(0.004)	(14.2)
Helicia artocarpoides	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)
Hopea nervosa	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)
Hopea nutans	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)
Hopea sangal	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)
Ixora grandifolia	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)
Knema latericia	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)
Lansium domesticum	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)
Leea indica	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)
Lophoetalum beccarianum	49.6	2.34	1.37	0.43	0.44	0.24	0.10	38.0
	(0.3)	(0.51)	(0.12)	(0.03)	(0.07)	(0.03)	(0.01)	(3.6)
Ludekia borneensis	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)
Luvunga heterophylla	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)
Macaranga gigantea	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)
Macaranga hypoleuca	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)
Macaranga triloba	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)
Macaranga pearsonii	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)
Madhuca korthalsii	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)
Mallotus mollissimus	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)
Mallotus wrayi	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)
Melastoma malabathricum	45.3	1.97	1.72	1.12	0.60	0.19	0.11	77.5
	(1.9)	(0.35)	(0.36)	(0.31)	(0.09)	(0.06)	(0.01)	(21.8)
Memecylon laevigatum	45.9	1.55	0.87	0.57	0.25	0.43	0.05	44.7
	(0.6)	(0.11)	(0.20)	(0.09)	(0.01)	(0.15)	(0.004)	(1.3)
Neonauclea artocarpioides	47.6	1.40	1.60	0.43	0.43	0.16	0.08	127
	(0.5)	(0.19)	(0.25)	(0.01)	(0.03)	(0.01)	(0.02)	(15.6)
Nephelium ramboutan-ake	50.2	2.20	1.26	0.79	0.53	0.15	0.10	58.3
	(0.6)	(0.32)	(0.32)	(0.19)	(0.11)	(0.02)	(0.01)	(7.0)
Ochanostachys amentacea	50.9	2.12	0.14	0.54	0.12	0.15	0.08	55.0
	(0.5)	(0.09)	(0.02)	(0.04)	(0.02)	(0.01)	(0.001)	(4.0)

Octomeles sumatrana	49.4 (0.6)	3.59 (0.02)	0.93 (0.04)	1.83 (0.12)	0.38 (0.09)	0.17 (0.01)	0.16 (0.01)	102 (26.8)
Parashorea malonaanan	47.0 (0.6)	1.46 (0.44)	1.39 (0.42)	0.63 (0.14)	0.37 (0.11)	0.19 (0.01)	0.07 (0.03)	73.0 (4.6)
Parashorea tomentella	45.5 (0.6)	2.04 (0.10)	1.67 (0.41)	0.42 (0.02)	0.18 (0.06)	0.16 (0.01)	0.10 (0.01)	183 (91.7)
Parinari oblongifolia	46.8 (1.1)	1.81 (0.21)	0.88 (0.11)	0.56 (0.08)	0.19 (0.07)	0.16 (0.03)	0.07 (0.00)	261 (178)
Payena acuminata	52.0 (0.7)	1.89 (0.06)	0.48 (0.09)	1.07 (0.09)	0.22 (0.02)	0.17 (0.01)	0.06 (0.003)	64.7 (11.8)
Pleiocarpidia sandahanica	45.4 (0.5)	2.22 (0.17)	1.20 (0.10)	1.0 (0.08)	0.35 (0.04)	0.27 (0.07)	0.11 (0.01)	97.7 (31.7)
Podocarpus neriifolius	47.2 (1.5)	2.14 (0.08)	1.53 (0.33)	0.99 (0.21)	0.44 (0.15)	0.22 (0.08)	0.10 (0.00)	46.7 (6.4)
Poikilospermum cordifolium	39.9 (1.9)	1.71 (0.13)	5.33 (0.61)	1.77 (0.39)	0.54 (0.16)	0.22 (0.02)	0.15 (0.01)	182 (55.0)
Polyalthia sumatrana	52.8 (0.5)	1.88 (0.01)	0.68 (0.10)	0.93 (0.09)	0.20 (0.00)	0.15 (0.01)	0.07 (0.004)	51.0 (2.6)
Popowia pisocarpa	47.4 (0.03)	2.46 (0.10)	0.52 (0.09)	1.37 (0.12)	0.43 (0.04)	0.26 (0.01)	0.08 (0.004)	61.0 (3.6)
Pterospermum stapfianum	47.3 (0.4)	2.34 (0.18)	2.03 (0.19)	0.92 (0.14)	0.23 (0.05)	0.20 (0.02)	0.18 (0.04)	73.3 (14.2)
Reinwardtiodendron humile	47.3 (0.7)	2.34 (0.02)	2.03 (0.15)	0.92 (0.17)	0.23 (0.07)	0.20 (0.01)	0.18 (0.01)	73.3 (1)
Ryparosa hulletii	49.4 (1.6)	1.48 (0.16)	1.21 (0.62)	0.58 (0.12)	0.28 (0.04)	0.15 (0.02)	0.08 (0.01)	132 (41.4)
Saurauia ferox	48.1 (2.9)	2.02 (0.08)	1.51 (0.66)	0.80 (0.00)	0.16 (0.02)	0.31 (0.08)	0.10 (0.01)	124 (51.1)
Semecarpus bunburyanus	46.6 (0.5)	1.47 (0.06)	1.04 (0.14)	0.66 (0.09)	0.29 (0.03)	0.16 (0.01)	0.15 (0.03)	45.7 (6.2)
Shorea agami	48.6 (1.18)	1.83 (0.19)	1.17 (0.18)	0.86 (0.20)	0.21 (0.07)	0.11 (0.01)	0.08 (0.02)	139 (46.5)
Shorea fallax	50.9 (0.8)	2.02 (0.23)	0.90 (0.36)	0.84 (0.25)	0.29 (0.02)	0.13 (0.01)	0.09 (0.01)	78.3 (41.1)
Shorea johorensis	50.5 (0.2)	2.01 (0.15)	1.08 (0.25)	0.62 (0.07)	0.31 (0.06)	0.18 (0.02)	0.10 (0.004)	138 (41.1)
Shorea leprosula	51.4 (0.1)	2.64 (0.06)	0.86 (0.07)	0.87 (0.05)	0.22 (0.05)	0.15 (0.01)	0.12 (0.003)	60.0 (4.0)
Shorea macrophylla	47.0 (0.0)	2.04 (0.01)	1.80 (0.01)	1.20 (0.02)	0.63 (0.00)	0.29 (0.00)	0.16 (0.003)	50.0 (0.7)
Sindora irpicina	50.7 (0.4)	1.87 (0.21)	0.77 (0.09)	0.64 (0.04)	0.22 (0.05)	0.16 (0.02)	0.08 (0.01)	126 (80.6)
Spathiostemon javensis	48.2 (1.1)	2.08 (0.40)	1.39 (0.33)	0.75 (0.07)	0.30 (0.09)	0.23 (0.07)	0.09 (0.01)	71.3 (11.9)
Stychnos ignatii	46.1 (0.6)	2.69 (0.22)	1.18 (0.40)	0.87 (0.13)	0.43 (0.11)	0.27 (0.07)	0.08 (0.001)	68.0 (9.1)
Syzygium campanulatum	50.6 (0.5)	1.00 (0.05)	0.77 (0.12)	1.03 (0.17)	0.10 (0.05)	0.12 (0.02)	0.09 (0.03)	45.3 (10.6)
Tarbernaemontana macrocarpa	50.8 (0.6)	2.59 (0.08)	0.65 (0.11)	1.47 (0.12)	0.31 (0.04)	0.29 (0.01)	0.09 (0.01)	53.7 (5.6)
Uncaria cordata	51.7 (1.0)	2.04 (0.21)	0.64 (0.14)	0.79 (0.04)	0.21 (0.02)	0.20 (0.03)	0.08 (0.01)	58.3 (9.7)
Urophyllum glabrum	51.7 (0.84)	2.04 (0.22)	0.64 (0.16)	0.79 (0.05)	0.21 (0.16)	0.20 (0.02)	0.08 (0.01)	58.3 (6.6)
Uvaria sorzogonensis	47.2 (3.1)	2.02 (0.12)	0.39 (0.07)	1.63 (0.13)	0.28 (0.03)	0.14 (0.003)	0.10 (0.01)	70.3 (3.2)
Xanthophyllum affine	47.9 (0.62)	3.30 (0.34)	0.37 (0.13)	1.43 (0.29)	0.17 (0.01)	0.23 (0.01)	0.11 (0.03)	45.7 (3.5)
Zizyphus angustifolius	51.1 (2.3)	2.27 (0.60)	0.92 (0.33)	1.77 (0.17)	0.33 (0.06)	0.17 (0.01)	0.13 (0.02)	82.3 (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})
Agelaea borneensis	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)
Alangium javanicum	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)
Ardisia elliptica	20 (0)	<0.200	0.4 (0.1)	1.1 (0.4)	3.1 (0.9)	9.2 (0.9)	0.111 (0.002)	53 (16)	0.209 (0.003)	0.154 (0.010)	0.210 (0.008)
Artocarpus anisophyllus	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)
Baccaurea lanceolata	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)
Baccaurea macrocarpa	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)
Barringtonia sarcostachys	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)
Blumeodendron tokbrai	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)
Brownlowia peltata	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)
Caesalpinia major	1151 (345)	0.268 (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)
Callicarpa longifolia	1534 (918)	0.213 (0.022)	0.6 (0.4)	2.6 (1.0)	12.0 (2.1)	36.0 (13.1)	<0.090	51 (11)	0.207 (0.007)	0.103 (0.011)	<0.200
Canarium denticulatum	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)
Chionanthus pluriflorus	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)
Cinnamomum subavenium	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)
Clausena excavata	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 ()	0.213 (0.013)
Clidemia hirta	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)
Combretum nigrescens	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 ()	0.150 (0.028)	0.750 (0.339)
Coscinium	101	0.298	1.9	2.2	23.2	17.4	0.110	53	<0.200	<0.100	1.080

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

Hopea sangal	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)
Ixora grandifolia	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	0.320 (0.120)
Knema latericia	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)
Lansium domesticum	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	0.457 (0.132)
Leea indica	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
Lophoetalum beccarianum	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)
Ludekia borneensis	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)
Luvunga heterophylla	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)
Macaranga gigantea	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)
Macaranga hypoleuca	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)
Macaranga triloba	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)
Macaranga pearsonii	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)
Madhuca korthalsii	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)
Mallotus mollissimus	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)
Mallotus wrayi	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)
Melastoma malabathricum	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)
Memecylon laevigatum	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
Neonauclea artocarpioides	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)
Nephelium ramboutan-ake	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 ()	0.233 (0.033)
Ochanostachys amentacea	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)
Octomeles sumatrana	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

Parashorea malonaanan	333 (189)	0.288 (0.065)	3.4 (1.9)	24.8 (14.5)	6.2 (2.1)	7.3 (2.0)	<0.090	201 (97)	0.290 (0.060)	0.102 (0.037)	0.205 (0.012)
Parashorea tomentella	294 (209)	0.393 (0.194)	1.8 (1.0)	4.5 (0.7)	6.8 (0.9)	14.0 (3.5)	0.143 (0.043)	41 (5)	0.255 (0.032)	0.177 (0.052)	0.417 (0.096)
Parinari oblongifolia	317 (267)	0.633 (0.434)	7.4 (5.3)	76.8 (35.5)	7.2 (0.3)	12.3 (3.9)	0.100 (0.012)	38 (9)	0.220 (0.020)	0.154 (0.017)	0.437 (0.185)
Payena acuminata	45 (12)	<0.200	0.9 (0.4)	3.4 (0.8)	2.4 (1.0)	10.2 (0.4)	<0.090	44 (15)	0.200 (0.006)	<0.100	1.333 (0.988)
Pleiocarpidia sandahanica	78 (10)	0.223 (0.023)	2.7 (0.2)	3.3 (0.5)	7.0 (0.3)	10.4 (1.3)	0.120 (0.020)	101 (63)	0.202 (0.009)	0.123 (0.033)	0.290 (0.046)
Podocarpus neriifolius	46 (14)	<0.200	0.3 (0.1)	2.0 (1.0)	6.7 (1.1)	19.3 (2.7)	<0.090	169 (91)	0.201 (0.006)	<0.100	<0.200
Poikilospermum cordifolium	119 (7)	0.370 (0.155)	1.8 (0.2)	1.4 (0.3)	4.8 (0.1)	13.0 (1.5)	0.123 (0.023)	230 (21)	0.265 (0.009)	0.176 (0.023)	0.207 (0.007)
Polyalthia sumatrana	47 (5)	<0.200	0.4 (0.1)	3.5 (2.0)	10.2 (1.3)	11.2 (1.0)	<0.090	61 (11)	<0.200	0.122 (0.010)	2.200 (1.003)
Popowia pisocarpa	131 (22)	0.240 (0.021)	0.6 (0.2)	5.8 (1.9)	6.3 (0.3)	12.3 (1.3)	0.112 (0.012)	109 (5)	<0.200	<0.100	0.413 (0.107)
Pterospermum stapfianum	35 (8)	0.233 (0.033)	0.4 (0.1)	1.9 (0.5)	5.9 (0.3)	12.0 (0.6)	<0.090	55 (14.4)	0.503 (0.251)	0.134 (0.017)	0.267 (0.034)
Reinwardtiodendron humile	35 (9)	0.228 (0.021)	0.4 (0.7)	1.9 (1.9)	5.9 (0.2)	12.0 (1.7)	0.122 (0.057)	55 (4)	0.503 (0.053)	0.111 (0.003)	0.267 (0.080)
Ryparosa hulletii	854 (567)	0.297 (0.052)	3.7 (1.2)	2.5 (0.7)	2.8 (0.8)	11.4 (4.3)	0.154 (0.011)	49 (26)	0.300 (0.100)	<0.100	0.390 (0.171)
Saurauia ferox	1047 (257)	0.320 (0.069)	3.9 (1.5)	4.4 (1.1)	6.0 (0.17)	14.0 (1.3)	<0.090	21 (6)	0.289 (0.027)	0.140 (0.027)	0.250 (0.033)
Semecarpus bunburyanus	201 (104)	0.202 (0.022)	0.6 (0.1)	3.3 (0.6)	5.6 (0.6)	20.3 (0.9)	<0.090	46 (5.5)	<0.200	0.100 (0.009)	0.216 (0.020)
Shorea agami	72 (40)	0.270 (0.070)	1.8 (0.8)	2.6 (1.5)	5.3 (0.9)	22.7 (2.9)	<0.090	49 (16)	<0.200	0.110 (0.010)	0.260 (0.060)
Shorea fallax	1155 (749)	0.217 (0.017)	0.7 (0.2)	5.9 (1.2)	7.6 (1.0)	12.7 (1.7)	0.105 (0.010)	47 (8)	0.223 (0.022)	0.102 (0.007)	0.327 (0.090)
Shorea johorensis	180 (135)	0.267 (0.034)	0.9 (0.2)	3.8 (0.9)	4.9 (0.9)	10.1 (1.6)	<0.090	33 (11.6)	<0.200	0.154 (0.018)	<0.200
Shorea leprosula	472 (171)	0.235 (0.023)	0.5 (0.05)	6.5 (2.3)	10.6 (1.6)	18.0 (0.1)	0.132 (0.3)	30 (7)	0.206 (0.006)	0.107 (0.003)	<0.200
Shorea macrophylla	48 (1)	<0.200	0.2 (0.01)	1.9 (0.1)	6.0 (1.6)	14.0 (3.0)	<0.090	149 (9)	0.208 (0.008)	0.145 (0.011)	0.256 (0.016)
Sindora irpicina	971 (475)	0.347 (0.147)	1.1 (0.7)	5.9 (1.5)	7.3 (1.5)	39.3 (12.5)	0.137 (0.037)	33 (6)	0.217 (0.017)	0.117 (0.017)	0.243 (0.043)
Spathiostemon javensis	985 (625)	<0.200	1.5 (1.0)	3.3 (0.8)	6.7 (1.7)	18.3 (2.9)	0.101 (0.006)	52 (16)	<0.200	<0.100	0.317 (0.072)
Stychnos ignatii	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)
Syzygium campanulatum	47 (27)	0.222 (0.012)	0.7 (0.2)	3.0 (0.6)	7.0 (2.9)	20.8 (1.2)	0.122 (0.011)	18 (1)	<0.200	<0.100	0.800 (0.601)
Tarbernaemontana macrocarpa	1510 (241)	0.287 (0.011)	0.5 (0.1)	3.9 (1.4)	15.3 (2.9)	31.7 (1.2)	0.109 (0.007)	21 (1)	<0.200	0.110 (0.016)	0.933 (0.734)
Uncaria cordata	1243 (1141)	<0.200	3.6 (2.8)	2.2 (0.3)	7.2 (0.7)	35.3 (18.0)	<0.090	24 (4)	0.267 (0.040)	0.123 (0.023)	0.200 (0.005)
Urophyllum glabrum	1243 (43)	0.202 (0.013)	3.6 (6.2)	2.2 (1.5)	7.2 (0.7)	35.3 (2.3)	0.122 (0.097)	24 (31)	0.223 (0.012)	0.123 (0.033)	0.213 (0.067)
Uvaria sorzogonensis	867 (234)	<0.200	0.8 (0.1)	8.6 (1.2)	7.8 (0.6)	12.0 (0.6)	0.130 (0.010)	54 (12)	<0.200	0.107 (0.006)	0.260 (0.060)
Xanthophyllum affine	121 (48)	0.260 (0.009)	0.4 (0.1)	11.9 (5.7)	8.3 (2.2)	14.3 (0.9)	<0.090	42 (10)	0.222 (0.013)	0.124 (0.008)	0.900 (0.701)
Zizyphus angustifolius	1042 (542)	<0.200	9.5 (9.3)	8.3 (3.6)	5.4 (1.6)	17.0 (2.6)	<0.090	58 (43)	<0.200	0.137 (0.037)	0.220 (0.020)

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**
Agelaea borneensis	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)
Alangium javanicum	17.1 (0.00)	16.1	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)
Ardisia elliptica	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)
Artocarpus anisophyllus	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)
Baccaurea lanceolata	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)
Baccaurea macrocarpa	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)
Barringtonia sarcostachys	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)
Blumeodendron tokbrai	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)
Brownlowia peltata	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)
Caesalpinia major	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)
Callicarpa longifolia	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)
Canarium denticulatum	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)
Chionanthus pluriflorus	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)
Cinnamomum subavenium	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)
Clausena excavata	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)
Clidemia hirta	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)
Combretum nigrescens	38.9 (12.7)	1.87 (0.49)	34.6 (1.8)	0.169 (0.008)	0.423 (0.004)	50.3 (1.5)	118 (3)	2.525 (0.596)	0.596 (0.010)	0.600 (0.008)	38.2 (1.3)	0.049 (0.011)
Coscinium blumeanum	3.0 (3.0)	2.82 (2.17)	303 (18)	1.63 (0.15)	0.425 (0.012)	54.2 (3.1)	126 (6)	1.280 (0.721)	0.721 (0.010)	0.833 (0.010)	32.0 (0.5)	0.020 (0.007)
Dillenia excelsa	32.3 (8.2)	4.16 (1.09)	215 (9)	2.95 (0.15)	0.339 (0.006)	138.8 (3.7)	407 (6)	1.806 (0.705)	0.705 (0.006)	0.728 (0.006)	81.3 (2.0)	0.018 (0.005)
Dimocarpus dentatus	15.0 (4.8)	5.25 (2.40)	134 (4)	0.458 (0.015)	0.362 (0.005)	34.3 (0.6)	94.4 (0.9)	2.654 (0.436)	0.436 (0.007)	0.577 (0.005)	16.1 (0.4)	0.031 (0.004)
Dimorphocalyx murinus	1.2 (0.5)	0.977 (0.340)	184 (13)	1.11 (0.09)	0.276 (0.006)	61.6 (1.9)	221 (3)	2.439 (0.584)	0.584 (0.009)	0.610 (0.008)	94.5 (0.7)	0.063 (0.013)
Diospyros durionoides	23.8 (7.3)	6.99 (2.05)	110 (8)	1.68 (0.14)	0.474 (0.009)	155.6 (5.1)	323 (6)	3.338 (0.521)	0.521 (0.007)	0.549 (0.005)	44.5 ()	0.083 (0.020)
Diospyrus elliptifolia	1.4 (0.4)	1.24 (0.35)	109 (5)	0.782 (0.037)	0.338 (0.004)	72.2 (1.3)	213 (3)	1.905 (0.694)	0.694 (0.009)	0.699 (0.007)	35.8 (1.0)	0.060 (0.014)
Dipterocarpus applanatus	17.4 (8.0)	2.63 (1.21)	842 (43)	11.7 (0.6)	0.427 (0.006)	142.3 (4.1)	332 (7)	2.141 (0.640)	0.640 (0.008)	0.667 (0.006)	93.4 (6.5)	0.041 (0.009)
Dipterocarpus gracilis	19.4 (4.7)	4.20 (0.98)	295 (24)	3.35 (0.29)	0.436 (0.006)	113.1 (1.9)	260 (5)	2.486 (0.602)	0.602 (0.012)	0.613 (0.009)	57.3 ()	0.042 (0.011)
Dryobalanops lanceolata	24.7 (12.8)	4.83 (1.53)	50.4 (2.3)	0.568 (0.020)	0.478 (0.004)	116.5 (2.0)	244 (4)	3.162 (0.520)	0.520 (0.007)	0.544 (0.005)	56.9 (1.7)	0.044 (0.010)
Duabanga moluccana	47.1 (1.0)	3.27	209 (18)	2.17 (0.18)	0.410 (0.004)	104.7 (1.9)	256 (4)	2.519 (0.575)	0.575 (0.012)	0.614 (0.010)	61.6 (2.6)	0.031 (0.014)
Durio kutejensis	6.61 (0.59)	5.34 (0.35)	108 (5)	0.614 (0.031)	0.336 (0.004)	56.0 (0.7)	167 (1)	2.865 (0.554)	0.554 (0.006)	0.567 (0.003)	26.4 ()	0.024 (0.005)
Etlingera brevilabrum	11.8 (3.9)	7.23 (2.33)	978 (40)	10.2 (0.7)	0.334 (0.007)	102.1 (3.3)	303 (3)	4.071 (0.453)	0.453 (0.009)	0.499 (0.006)	58.1 (1.4)	0.007 (0.003)
Euphoria malaiensis = Dimocarpus longan	36.4 (4.8)	13.5 (2.4)	74.0 (5.4)	0.672 (0.056)	0.447 (0.007)	105.1 (2.1)	194 (2)	3.042 (0.499)	0.499 (0.010)	0.546 (0.006)	16.3 (0.6)	0.047 (0.013)
Eurycoma longifolia	4.0 (2.0)	2.07 (1.72)	18.2 (0.5)	0.085 (0.003)	0.376 (0.005)	47.0 (0.7)	125 (1)	3.335 (0.494)	0.494 (0.006)	0.523 (0.005)	38.6 (0.7)	0.020 (0.006)
Eusideroxylon zwageri	22.1 (7.0)	16.1 (5.9)	263 (12)	3.35 (0.15)	0.418 (0.006)	129.3 (2.0)	310 (3)	2.555 (0.608)	0.608 (0.011)	0.614 (0.009)	20.7 (0.8)	0.034 (0.008)
Fagraea cuspidata	5.21 (4.09)	0.232 (0.230)	392 (30)	5.20 (0.30)	0.385 (0.007)	147.6 (7.8)	376 (14)	1.884 (0.678)	0.678 (0.010)	0.720 (0.010)	175 (3.7)	0.010 (0.006)
Fordia splendidissima	23.3 (5.8)	17.4 (6.9)	72.0 (23.1)	0.342 (0.018)	0.379 (0.006)	46.9 (1.2)	124 (2)	2.542 (0.578)	0.578 (0.011)	0.592 (0.008)	15.8 (1.0)	0.065 (0.013)
Goniothalamus uvarioides	22.8 (5.0)	7.75 (1.32)	470 (23)	2.99 (1.70)	0.338 (0.006)	62.7 (1.5)	185 (2)	2.764 (0.579)	0.579 (0.009)	0.586 (0.007)	23.4 (0.7)	0.029 (0.007)
Helicia	2.7	1.90	1386	16.6	0.402	123.0	306	1.388	0.039	0.597	104	0.120

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

Ochanostachys amentacea	41.4 (7.5)	1.22 (0.21)	53.5 (2.3)	0.255 (0.010)	0.393 (0.005)	48.7 (0.9)	124 (1)	2.235 (0.623)	0.623 (0.007)	0.619 (0.005)	47.7 (1.4)	0.042 (0.009)
Octomeles sumatrana	11.7 (4.8)	5.55 (2.23)	1122 (53)	8.08 (0.45)	0.334 (0.008)	71.5 (2.2)	214 (5)	1.237 (0.607)	0.607 (0.008)	0.839 (0.005)	83.8 (2.2)	0.034 (0.007)
Parashorea malonaanan	12.0 (2.9)	11.3 (3.1)	111 (7)	0.840 (0.043)	0.456 (0.007)	80.2 (2.7)	174 (4)	2.497 (0.606)	0.606 (0.008)	0.614 (0.006)	28.1 (1.4)	0.040 (0.006)
Parashorea tomentella	24.0 (8.0)	11.7 (3.7)	356 (21)	3.06 (0.21)	0.451 (0.005)	84.4 (1.6)	187 (3)	2.003 (0.687)	0.687 (0.008)	0.691 (0.007)	17.3 (0.9)	0.066 (0.014)
Parinari oblongifolia	12.1 (5.6)	7.80 (3.32)	134 (5)	0.940 (0.037)	0.507 (0.006)	70.4 (1.4)	139 (2)	2.561 (0.589)	0.589 (0.007)	0.591 (0.004)	15.2 (0.9)	0.075 (0.011)
Payena acuminata	19.3 (2.1)	12.4 (1.8)	168 (6)	0.979 (0.034)	0.362 (0.005)	59.3 (1.2)	163 (2)	3.207 (0.494)	0.494 (0.006)	0.527 (0.004)	23.2 (0.6)	0.032 (0.008)
Pleiocarpidia sandahanica	3.0 (1.7)	1.75 (1.21)	147 (11)	1.13 (0.09)	0.321 (0.003)	75.8 (0.8)	236 (2)	3.100 (0.537)	0.537 (0.004)	0.554 (0.003)	73.4 (2.2)	0.039 (0.010)
Podocarpus neriifolius	8.3 (4.2)	4.91 (2.34)	28.0 (1.4)	0.563 (0.020)	0.470 (0.003)	209.5 (3.9)	446 (8)	12.910 (0.159)	0.159 (0.004)	0.280 (0.004)	168 (4.4)	0.013 (0.006)
Poikilospermum cordifolium	16.9 (14.0)	9.02 (7.56)	348 (13)	2.90 (0.13)	0.319 (0.006)	83.4 (2.2)	260 (4)	1.415 (0.767)	0.767 (0.004)	0.819 (0.009)	40.2 (2.7)	0.026 (0.007)
Polyalthia sumatrana	5.9 (0.7)	2.03 (0.23)	51.7 (2.6)	0.334 (0.017)	0.367 (0.003)	64.5 (0.7)	176 (1)	3.366 (0.520)	0.520 (0.007)	0.532 (0.005)	19.5 (0.8)	0.060 (0.009)
Popowia pisocarpa	1.0 (0.5)	0.53 (0.70)	27.7 (1.4)	0.129 (0.006)	0.351 (0.005)	47.3 (0.7)	135 (1)	2.641 (0.585)	0.585 (0.007)	0.585 (0.006)	41.9 (1.0)	0.049 (0.007)
Pterospermum stapfianum	9.1 (2.8)	2.84 (0.92)	103 (5)	0.640 (0.034)	0.397 (0.008)	62.5 (1.4)	159 (3)	1.812 (0.689)	0.689 (0.009)	0.730 (0.007)	23.3 (1.4)	0.095 (0.012)
Reinwardtiodendron humile	38.2 (17.8)	36.2 (18.3)	13.0 (0.6)	0.070 (0.004)	0.397 (0.005)	53.7 (0.8)	135 (1)	3.252 (0.457)	0.457 (0.010)	0.502 (0.008)	40.0 (1.3)	0.051 (0.009)
Ryparosa hulletii	40.8 (11.2)	2.40 (0.63)	76.7 (3.9)	0.404 (0.020)	0.274 (0.003)	53.2 (0.8)	194 (2)	2.994 (0.530)	0.530 (0.007)	0.546 (0.005)	6.18 (0.2)	0.033 (0.006)
Saurauia ferox	42.8 (26.8)	5.57 (3.47)	192 (12)	0.893 (0.052)	0.220 (0.003)	47.9 (0.8)	219 (4)	3.079 (0.483)	0.483 (0.006)	0.520 (0.005)	62.9 (3.6)	0.048 (0.013)
Semecarpus bunburyanus	14.2 (2.6)	3.14 (0.63)	315 (17)	3.51 (0.19)	0.400 (0.005)	112.9 (2.2)	282 (4)	2.543 (0.519)	0.519 (0.005)	0.567 (0.004)	50.5 (1.9)	0.047 (0.006)
Shorea agami	86.2 (31.1)	3.51 (1.30)	190 (13)	0.972 (0.068)	0.289 (0.008)	50.8 (1.7)	178 (3)	2.397 (0.640)	0.640 (0.013)	0.633 (0.009)	50.7 (7.2)	0.080 (0.018)
Shorea fallax	42.8 (4.1)	10.3 (1.32)	118 (4)	0.736 (0.039)	0.358 (0.007)	65.6 (3.6)	178 (7)	3.014 (0.533)	0.533 (0.006)	0.545 (0.004)	40.4 (2.0)	0.043 (0.008)
Shorea johorensis	16.0 (2.3)	3.50 (0.50)	71.9 (3.6)	0.627 (0.032)	0.435 (0.006)	90.0 (2.7)	205 (5)	2.130 (0.670)	0.670 (0.009)	0.671 (0.007)	20.3 (2.1)	0.119 (0.019)
Shorea leprosula	48.3 (2.2)	3.42 (0.10)	47.5 (2.1)	0.239 (0.010)	0.399 (0.004)	51.9 (0.8)	131 (2)	2.707 (0.576)	0.576 (0.008)	0.583 (0.005)	32.7 (3.2)	0.133 (0.018)
Shorea macrophylla	22.2 (5.7)	0.464 (0.128)	256 (13.3)	2.59 (0.10)	0.461 (0.004)	102.7 (2.3)	223 (4)	2.357 (0.678)	0.677 (0.006)	0.644 (0.005)	50.7 (2.1)	0.039 (0.013)
Sindora irpicina	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)
Spathiostemon javensis	25.9 (16.0)	4.14 (2.63)	64.2 (4.1)	0.338 (0.027)	0.353 (0.004)	51.0 (1.5)	145 (4)	2.682 (0.540)	0.540 (0.009)	0.561 (0.006)	19.8 (2.0)	0.082 (0.014)
Stychnos ignatii	12.7 (0.8)	11.2 (1.0)	39.0 (1.6)	0.165 (0.007)	0.308 (0.013)	43.4 (1.5)	143 (1)	2.647 (0.562)	0.562 (0.013)	0.584 (0.011)	52.1 ()	0.053 (0.013)
Syzygium campanulatum	99.3 (28.4)	1.14 (0.32)	10.8 (0.5)	0.126 (0.006)	0.491 (0.011)	118.6 (1.6)	244 (6)	3.430 (0.456)	0.456 (0.014)	0.494 (0.010)	20.7 (0.4)	0.023 (0.015)
Tarbernaemontana macrocarpa	14.3 (5.1)	3.80 (1.22)	108 (4)	0.570 (0.027)	0.258 (0.005)	53.2 (1.6)	204 (2)	2.531 (0.563)	0.563 (0.007)	0.581 (0.005)	43.8 (1.1)	0.023 (0.007)
Uncaria cordata	28.8 (4.1)	4.69 (0.80)	213 (15)	1.91 (0.12)	0.439 (0.005)	94.9 (2.7)	214 (4)	1.975 (0.692)	0.692 (0.008)	0.678 (0.008)	39.2 (2.1)	0.068 (0.010)
Urophyllum glabrum	2.11 (0.30)	1.55 (0.04)	99.0 (4.1)	0.391 (0.016)	0.239 (0.002)	39.9 (0.6)	167 (2)	2.668 (0.566)	0.566 (0.006)	0.575 (0.005)	67.5 (1.8)	0.030 (0.009)10.0
Uvaria sorzogonensis	9.7 (0.7)	6.54 (0.39)	190 (9)	0.896 (0.053)	0.345 (0.005)	46.6 (1.0)	135 (2)	2.638 (0.578)	0.578 (0.008)	0.584 (0.006)	14.2 (0.4)	0.035 (0.005)
Xanthophyllum affine	2.3 (1.1)	1.46 (1.51)	116 (5)	0.692 (0.041)	0.334 (0.006)	58.5 (1.5)	174 (3)	2.309 (0.638)	0.638 (0.009)	0.632 (0.008)	63.1 (1.9)	0.054 (0.011)
Zizyphus angustifolius	10.6 (8.5)	4.10 (3.38)	82.2 (5.1)	0.412 (0.026)	0.354 (0.004)	50.2 (0.9)	142 (2)	3.134 (0.539)	0.539 (0.008)	0.548 (0.006)	48.2 (1.0)	0.070 (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. /area**	**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=.0230 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=-.0240 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=0116 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=0.383	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=0.071*	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

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 R=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

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

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) Peñuelas *et al*. 2010a	New South Wales (12 sp) Specht & Turner 2006	Taiwan (20 sp) Wu *et al*. 2007	French Gaiana (45 sp) Hättenschwiler *et al*. 2008	French Guaiana (14 sp) Coste *et al*. 2005	Quensland (Australia) (162 sp) Asner *et al*. 2009	Review of different parts of the world (150 sp) Townsend *et al*. 2007
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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