Dear Referees

We would like to thank you for many useful comments on our manuscript and suggestions for improvement. Our responses are made separately for each referee. Pleases find them below.

Dear Referee #1

Your remarks and our responses are presented below in black and blue, respectively. All changes are shown in blue in the revised manuscript.

[RC] Main comments: This paper brings some new informations regarding the Si content of different tropical species, on the Si concentration in litterfall in eight plots sampled at three dates and on Si concentration in soil (0-10 cm depth horizon) obtained through water extraction, in these eight plots for one date. These 8 plots are located at 4 different elevations (700, 1700, 2700 and 3100 m). For each elevation plots are placed on different bedrocks, i.e., acidic sediment and ultrabasic igneous rock; except for 3100 m where sediment bedrock was replaced by granite. These situations lead to strong differences between ecosystems (structure, vegetation composition, production rate, littefall, litter decomposition, soil fertility. . .) previously published in Kitayama and Aiba 2002. For examples, wood biomass ranged from 3.5 to 43.3 Kg.m-2, leaf biomass varied between 0.17 to 0.56 kg.m-2 and leaf litterfall between 121 to 1113 g.m-2.yr-1, litter decomposition constant ranged between 0.44 and 1.69 yr-1 and pH water ranged from 3.4 to 5.4. These data from Kitayama and Aiba (2002) in a tropical ecosystem are exceptional. So you have different ecosystems with very contrasting production and recycling rates (as well as floristic composition).

> [AC] We appreciate the positive comments on our study. We now have clearly summarized differences in ecosystem properties reported by Kitayama and Aiba (2002) in Table 1.

[RC] INTRODUCTION I am not convinced by the hypotheses presented in the introduction which are based on indirect factors. The total Si concentration of a rock type is not a determining factor of the flux of Si in the soil and the soil can act indirectly via its fertility on the biological cycle of the Si. The elevation is an indirect factor which can affect various components of the recycling of an element via the production and the decomposition of litters notably. To use indirect variables strongly limits the interpretations. Beyond elevation and rock type, the differences of production and of litter decomposi- tion rate of these 8 ecosystems seem to be fundamental and direct factors affecting the concentrations of Si in leaves. The hypothesis of this article could be for example that the influence of

1

the recycling rate of Si by the stand on the Si concentration in leaves in the long term. See the paper of Cornelis and Delvaux (2016) which is cited in this manuscript.

> [AC] Thank you for your insightful comments and suggestions. Although we generally agree that we cannot tease apart direct and indirect effects of elevation and bedrocks, they clearly show trends. However, as you mentioned and we do in our discussion, elevation and bedrock affect various biotic (e.g., transpiration, other plant physiology) and abiotic processes (e.g., temperature), thereby influencing leaf Si concentration and Si cycling. Even though using elevation and bedrock may limit the interpretations, they are the ultimate factors in this study that govern the various components related to Si cycling, and our results on the ecosystem-level variations in relation to elevation and bedrocks are novel findings. Nevertheless, we have changed proses to avoid an impression that we are inferring direct causality in introduction (e.g., difference with elevations, rather than difference by elevations). [1 Introduction].

[RC] METHOD Tropical ecosystems are complex. In consequence, you have to well describe the ecosystems (see Tab 1 Kitayama and Aiba 2002), with matter stocks and fluxes.

> [AC] We added a sentence and a table to describe our study sites. [2.1 Study site, Table 1].

[RC] Specify whether they are affected by forest management and understory vegetation.

> [AC] We added sentences about the history of forest management and understory vegetation and a table that provides information about vegetation cover on the ground. [2.1 Study Site].

[RC] Describe soil and their properties.

> [AC] We added sentences and soil properties are better described in Table 1. [2.1 Study Site].

[RC] Justify that you measures only Si concentrations in the samples collected at three dates (April 1997, May and August 1998) and during two weeks while the annual concentration was aimed.

> [AC] We have clarified how and why we arbitrarily used collections from these three times. As our leaf-litter Si concentrations correlate across the plots among different collection times (Fig. S1), we believe that the arbitrary selection of these three sampling months had little effect on the overall results. [2.2 Leaf and litter sampling].

[RC] What are the limits of detection and uncertainties of our measurement devices?

[AC] We added sentences to clarify them. [2.4 Si extraction and measurements].

[RC] Soil description was absence.

[AC] We added soil description in Table 1, as explained earlier.

[RC] RESULTS The original results of the Si concentrations in leaves are not enough valorized (except figure 2 which is a global figure). For example add the values of Si concentration for each species in the table S1.

[AC] According to your suggestion, we added the mean values to the figure. [Figure 2].

[RC] DISCUSSION I suggest to rework a part of the discussion by dealing with the relations between direct factors such as litter production, litter decomposition, Si recycling, and Si concentration in leaves.

[AC] We revised discussion to address your concerns. [4 Discussion].

[RC] In conclusion, in the current state, this manuscript is not publishable in Biogeosciences because the research question is not enough relevant and not supported by an adequate device of observation allowing to conclude (three factors: species, elevation, bedrock and 2 indirect factors on the cycle of Si). However, the set of data stemming from this article could be better exploited by associating the data on the production and the decomposition of litters published in Kitayama and Aiba (2002).

[AC] We respectfully disagree that our research question is not relevant enough for publication. In a more general term, our key hypothesis is that community-wide patterns of biogenic Si flux via litter fall differ with elevation. This is a novel hypothesis that no other researchers had tested. The natural world is full of confounding environmental factors, and many biogeochemical phenomena are aggregate of multiple causal factors as you point out. We hope that rewording in introduction and discussion avoids misunderstanding that we are trying to prove a direct causality of elevation on ecosystem processes. Our study has examined multiple factors that potentially give direct and indirect effects on litter Si flux, enough to suggest some previously unrecognized factors that influence litter Si flux.

Dear Referee #2

Your remarks and our responses are presented below in black and blue, respectively. All changes are shown in blue in the revised manuscript.

[RC] This paper presents a thorough study of the Si concentrations in multiple tree species across an elevation gradient in a tropical forest. It also calculates the annual litterfall associated Si fluxes, based on annual litterfall fluxes and Si concentrations. This is related to Si availability in the soil water.
The authors have done a great job in analysing a large set of tropical trees for Si concentration, and the consequent calculation of associated tree litter Si fluxes is inter- esting. The study has a strong merit for that, as it is one of the first –and probably the first at this scale – to analyse this potentially interesting component of tropical forest Si cycling.

[AC] We appreciate positive comments on our study.

That said, in my opinion, the study cannot deliver any strong new information on the effect of elevation or bedrock on the Si cycling by trees. My main concern is that the Si concentration in the leaves, and the associated Si litter flux, could just be a reflection of the Si availability in the soil water. The latter is highest at lowest elevation, and this results in generally higher Si concentrations in biomass. It is well known that all species, even those not accumulating Si but acquiring it passively, will show a higher Si concentration in biomass when availability is higher. The question thus is: why is Si availability higher at lowest elevation? Is it because of higher Biogenic Si concentrations in the soil? Is it because of alterations in soil water source?
The authors cannot provide a response to that with this analysis or dataset. In order to move this study from an interesting local observation, to a study that truly moves knowledge on Si cycling in tropical forest sites, a lot of extra context is needed, e.g. -How much BSi is present in the soils? -Indication of Si concentrations in porewater and Si leaching / import from / to groundwater. -Decomposition experiments with the litter.
Now, it is impossible to assess what the observed changes in Si concentrations in leaves, and associated litterfall Si fluxes, mean in the context of ecosystem Si cycling.
The dataset has large merit in itself, since it is quite unique in analysing tropical tree litterfall Si fluxes in such detail. However, it is difficult to currently make any strong conclusion on interaction between tropical trees and tropical Si cycling based on this study alone. For that, more information on soil Si pools and Si leaching / Si groundwater input is needed.
Still, as a scientist interested in Si cycling, I enjoyed reading this paper and am puzzled by its results. I am therefore hesitant to just indicate that the paper should not be published. Indeed, this paper could

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be a trigger for future work on the Si cycling in tropical forests. I would therefore recommend that, if possible, authors include some of the suggested information on the local Si biogeochemistry.

If that is not available, I would recommend authors to focus more on linking plant traits to Si concentrations observed. Is that different between elevations? Can you find an explanation for the large observed differences between species? I think the data are much more suited for that purpose, than for trying to put it in a larger biogeochemical context.

[AC] Thank you for your positive and thoughtful comments. In response to your main concern that the elevational trends may simply reflect soluble Si at deeper soil layers, we added the result of water-extractable Si at different soil horizons from a single deep soil pit from each of the eight plots. The figure clearly shows that Si availability across the soil profile is not necessarily higher at the lowest elevation plots. Even more puzzlingly, B horizon Si availability was actually the highest at 2700 m and 3100 on the ultrabasic rock. Thus, the community-wide (ecosystem-wide) trends with elevation (and lack of difference between the bedrock types) cannot be explained by differences in rock and soil weathering among plots. In other words, our result strongly suggests that Si concentration in the leaves and the parallel differences in Si litter flux do not merely reflect the Si availability in the soil water.

Proximate factor alone cannot explain large inter-community differences in relation to elevation. Leaf Si concentrations of low Si accumulating species at the lowest elevation plots are on the same level as those of species at the higher elevation plots (Fig. 2). This should support the idea that leaf Si concentration in leaves is more likely a reflection of plant Si uptake traits than that of Si availability in topsoil.

We added the data on water-extractable Si per unit soil mass along soil profiles to the revised manuscript as new supplementary material. We hope this change may reduce your concern. [2.3 Soil sampling, 3.3 Si bioavailability, 4 Discussion, Figure S4].

Yours sincerely,

Ryosuke Nakamura, lead & corresponding author

on behalf of all coauthors

Silicon cycled by tropical forest trees: effects of species, elevation and bedrock on Mount Kinabalu, Malaysia

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Abstract. Plant species differ in degrees of silicon (Si) uptake and accumulation, and may differentially influence biogeochemical cycles of Si, possibly in interaction with other environmental factors. Here, we report how patterns of Si cycling by vegetation differ with species composition, elevation and bedrock types for species-rich tropical forests on Mt. Kinabalu, Borneo. We used eight forest monitoring plots established in 1995 at four altitudes (700, 1,700, 2,700 and 3,100 m above sea level) on two geological substrates (acidic sedimentary and ultrabasic igneous rock), where tree species composition, abundance, biomass and litterfall had been monitored. For live leaves of 71 dominant tree species (total relative basal area > 60% in each plot) and leaf litter collected in traps, Si concentration was determined after alkaline extraction. Si availability in the upper 10 cm of mineral soil was determined as Si dissolved to water after shaking overnight. Tree species with high leaf Si concentrations occurred mostly in the lowest elevation plots. The community-mean Si concentration in live leaves, as well as Si concentration in leaf litter, decreased with increasing elevation. The estimated annual flux of leaf litter mass and Si also decreased with increasing elevation. Leaf and litter Si concentrations showed no difference between the two bedrock types without interaction with elevation. Due to large turnovers of species composition with elevation and bedrock types, most species occurred only in one plot. For 11 species that occurred at two or three plots, only one species showed a weakly significant difference in leaf Si concentration between bedrock types. Surface soil Si availability was greater at lower elevation plots and differed with bedrock types only at 1,700 m. This pattern was consistent with a hypothesis that Si input via litter in the form of plant opal, rather than bedrock types, should influence the soluble Si in the upper soil horizons. These results suggest that Si cycling by vegetation is more active in lower elevation forests regardless of bedrock types, most likely because Si accumulating species are more abundant in lowland tropical forests.

1 Introduction

Silicon (Si) is a beneficial element for many plant species (Ma and Takahasi, 2002; Cooke and Leishman, 2011), and as such, soil availability of Si is an important aspect of plant communities and ecosystems (Cooke and Leishman, 2012). Whereas the ultimate source of Si is the earth's crust and rocks, it is increasingly recognized that terrestrial Si dynamics is influenced by

plants as they uptake Si from soil water and return to the soil via litterfall (Bartoli, 1983; Lucas et al., 1993; Alexandre et al., 1997). Once absorbed by roots, Si accumulates in plant organs as opal phytoliths, which have higher solubility than Si in aluminosilicate in clay and quartz in sand (Fraysse et al., 2009). The study by Lucas et al. (1993) from a lowland Amazonian forest was the first that demonstrated that Si returned to topsoil via litterfall significantly enriched the upper soil horizon. The

5   importance of such Si cycled by vegetation is increasingly recognized in temperate forests as well (Struyf and Conley, 2012). Yet, far greater levels of Si cycling by vegetation may exist in lowland tropical forests (Lucas et al., 1993; Alexandre et al., 1997). Furthermore, it remains unknown how tree species may differ in their leaf Si accumulation and differentially influence biogeochemical cycling of Si in species-rich tropical forest ecosystems.

Recently developed conceptual models on biogeochemical Si cycles incorporate the role of terrestrial vegetation in

10   addition to lithospherical and limnological processes (e.g., Gérard et al., 2008). The bedrock containing siliceous minerals of variable weatherability is the source of Si-containing soil particles, including aluminosilicate complex of secondary clay minerals. In the traditional pedological view, Si dissolved in soil water is mainly derived from rocks (lithogenic) and soils (pedogenic), which may exist at 0.1-0.6 mM concentrations as orthosilicic acid (H_4SiO_4) (Epstein, 1994). However, it is increasingly recognized that plants influence Si movement in the soil. Plants absorb orthosilicic acid (uncharged molecules)

15   along with water through roots, and transport it to the shoot, where it may form opal phytoliths ($SiO_2 \cdot nH_2O$) (Epstein, 1999). Since Si does not re-dissolve from opal phytoliths within a live plant, it accumulates as plant organs age, especially in leaves (as reported by Motomura et al., 2004 for a bamboo). When plant organs containing Si die, their decomposition releases Si to the soil. It is increasingly recognized that opal phytoliths in dead plant tissues significantly contribute to biogenic silica (BSi) in the soil, although siliceous shells of soil protozoans (Clarke, 2003), diatoms and sponges (Conley and Schelske, 1993)

20   may also contribute to the soil BSi pool in some soils. Through decomposition of leaf litter, BSi is incorporated in the topsoil and becomes a potential source of dissolved Si through dissolution to soil water (Bartoli, 1983).

Biological Si cycling rate via litterfall varies widely among vegetation types (0.5-4.9 g Si m^{-2} yr^{-1}) (reviewed by Lucas, 2001), possibly because plant species differ in Si uptake patterns. Using active transport mechanisms in roots, some species reject Si uptake, while others actively concentrate Si into root xylems (Ma and Takahasi, 2002). Si concentrations in

25   leaves of 735 plant species from 125 studies compiled by Hodson et al. (2005) demonstrate that leaf Si concentration differs widely among phylogenetic groups. But, their analysis is strongly biased to temperate plant taxa, in which only six studies encompassing 27 species are tropical. For mechanistic understanding of Si cycling in a tropical forest, we need data on species composition and abundance, as well as Si uptake of dominant tree species.

Elevation is a factor that may significantly influence Si cycling, because temperature regimes, soil weathering rates,

30   plant productivity, litter decomposition rate and nutrient cycling patterns change with elevation. Forest structure and tree species composition also change with elevation. Such changes have been well documented from 700 m to 3,100 m elevation on Mount Kinabalu (Aiba and Kitayama, 1999; Kitayama and Aiba, 2002). We predict that Si cycling rates should decline with elevation, not only because annual leaf litterfall mass and litter decomposition rate decrease with increasing elevation, but also because tree species composition changes with elevation. On Mt. Kinabalu, lowland taxa such as Dipterocarpaceae

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dominate at 700 m above sea level (asl), whereas Fagaceae and Myrtaceae dominate at 1,700 m asl, and Podocarpaceae (gymnosperm) and Myrtaceae dominate at 2,700 m asl and above (Aiba et al., 2002). As gymnosperms accumulate less amount of Si in leaves than angiosperms (Takahashi et al., 1981; Hodson et al., 2005; Piperno, 2006), the increasing dominance of gymnosperm trees with increasing elevation on Mt. Kinabalu may decrease community-wide concentrations Si

5   in leaves.

        Bedrock type may also influence forest Si cycling because bedrocks differ in amounts of various siliceous minerals and influence plant species composition via mineral nutrient availability. On Mt. Kinabalu, plant communities differ greatly due to different soil fertility on acidic sedimentary rock (> 50% SiO_2) and ultrabasic igneous rock (41% SiO_2). But, total Si contents of bedrocks may not indicate the rates of Si release from them, because weathering rates tend to be slower in quartz-
10   rich sedimentary rocks than in ultrabasic rocks (Brooks, 1987). Litter fall rate does not systematically differ between the bedrock types along elevation on Mt. Kinabalu, even though the soil derived from ultrabasic rock is less fertile than that from sedimentary rock (Jacobson, 1970; Kitayama and Aiba, 2002). It is important to recognize Si concentration in leaves may not be a simple function of Si solubility of bedrocks, because plant species differ in their Si uptake strategies. Active uptake may compensate for low-Si availability in the soil, whereas rejective-uptake species avoid accumulation of Si even in
15   soils of high Si availability. Hence, it is difficult to predict how plant communities of high species diversity, such as tropical forests, on different bedrocks may differ in their influences on Si cycling by vegetation, and no empirical studies compared ecosystem Si cycling on different bedrocks.

        Here, we report how leaf Si accumulation and the community-wide estimate of annual Si flux via litterfall change with elevation and bedrock types, taking advantage of the long-term forest monitoring plots on Mt. Kinabalu (Aiba
20   and Kitayama, 1999). These plots, located from 700 to 3,100 m asl on two contrasting bedrocks, offered an opportunity to explore how Si cycling by vegetation changes with tree species composition, elevation and bedrock types in tropical forest ecosystems. We evaluated three apriori predictions. Firstly, we predicted that annual Si flux via leaf litterfall should be smaller in higher elevation plant communities. Our second prediction was that Si cycling via vegetation may differ between sedimentary and ultrabasic rocks that differ in Si contents and solubility and their soil fertility. Thirdly, we predicted that
25   litter Si flux should reflect the abundance-weighted leaf Si concentrations of dominant tree species. For species that occurred at multiple plots spanning a range of elevations and bedrock types, we examined within-species variation in leaf Si concentrations. We also compared water extractable Si concentration across the elevation range and bedrock types as an indicator of Si availability in the soil, and also as a possible correlate of variation in Si returned to the soil via leaf litter. Doing so, our study quantifies for the first time in a forest ecosystem how Si flux varies in relation to species composition,
30   elevation and bedrock types.

2 Methods

2.1 Study site

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This study was conducted in the humid tropical montane forests on Mt. Kinabalu, Sabah, Malaysia (summit height 4,095 m asl, 6˚05'N, 160˚33'E). Samples were collected from eight plots laid at four elevation levels (700, 1,700, 2,700 and 3,100 m asl) corresponding to four vegetation zones (hill dipterocarp, sub-montane, montane and sub-alpine) and two bedrock types (sedimentary rock with SiO_2 content > 50% and ultrabasic rock with SiO_2 content $\simeq$ 41%). A slight deviation from this

5   scheme was that the "sedimentary" rock site at 3,100 m elevation was actually on a granitic rock (> 60% SiO_2). The plot size varied from 1 ha to 0.06 ha (smaller size at higher elevation with lower forest statue near the tree line, see Table S1). In total, 380 species were recorded across the eight plots ($\geq$ 10 cm dbh) (Aiba and Kitayama, 1999). The climate was humid tropical with minor seasonal temperature fluctuations (Kitayama, 1992). The mean annual temperature ranges from 23.9ºC at 700 m asl to 10.6ºC at 3,100 m asl (calculated from Kitayama, 1992). The annual rainfall is approximately 2,300 mm yr^{-1}, with little

10   change with the elevation (Kitayama and Aiba, 2002). Canopy height, decomposition rate and litterfall decrease largely with increasing elevation, while the level of organic matter accumulation inconsistently varies among the eight plots (Table 1). The region containing these study plots was declared as a national park in 1964. To our best knowledge, no logging and fire events have been documented. The forest is thought to be old-growth, and understory is sparsely covered with herbs and grasses (Table 1) except that a climbing bamboo (*Racemobambos gibbsiae)* is abundant at 2,700 m elevation on sedimentary

15   rock. Soil weathering and mineralogy differ among elevation levels and rock types in our study system. The 700 m elevation areas show no signs of glacier influence (Jacobson, 1970), and soils are more highly weathered, with deep pedon (>1 m), high clay and pedogenic iron contents, and more advanced clay mineralogy. They are thus classified as Ultisol and Oxisol (Wagai et al., 2008, also see Table 1). Soils at the intermediate elevation sites (at 1700 and 2700 m) are less weathered and classified as Inceptisols on both rock types. Soils at the 3100 m sites were shallow (pedon depth < 30 cm), presumably

20   affected by glacier, and classified as Entisol/Inceptisol. The 3100-m ultrabasic site may be influenced by glacial deposit due to relatively high clay and pedogenic iron contents (R. Wagai, unpublished data). At each elevation pair, in comparison to the sedimentary / granite site, ultrabasic site always had higher soil pH in water by 0.8-1.3 units and higher clay and pedogenic iron contents (Table 1, Wagai and Mayer, 2007).

25   **2.2 Leaf and litter sampling**

Dominant species that together accounted for > 60% relative basal area (RBA) of canopy trees ($\geq$ 10 cm dbh) in each plot (Aiba et al., 2002) were sampled, resulting in a total of 71 species belonging to 28 families across the eight plots (Table S1 in the Supplement). The majority of the 71 species occurred at a single plot, with 11 species occurring at more than one plot (8 and 3 species occurred at 2 and 3 plots, respectively (Table S2 in the Supplement). Terminal branches were collected from a

30   sun-lit portion of each crown of at least three individuals per species per plot with combination of slingshot and rope-climbing techniques from July to November, 2001. For three species, just a single individual was available for leaf collection. Samples were immediately transported to a field laboratory, where fully expanded and matured leaves were oven dried at 70˚C. The dried leaves, excluding petioles, were ground and stored in airtight plastic bags in air-conditioned laboratories until further analysis in the laboratory.

Litter was collected at two-week intervals throughout 1997 and 1998 in litter traps, each consisting a 0.5 m^2 frame covered with a fine-meshed net in the shape of inverted cones, from 20 traps at 700 and 1,700 m elevation plots and from 10 traps at 2,700 and 3,100 m elevation plots. We arbitrarily selected three monthly collections (April 1997, May 1998, August 1998), representing one dry and two wet seasons in the study region. Preliminary analyses show that there were no obvious seasonality in nitrogen, phosphorus, or Si concentrations in leaf litter samples (Kitayama and Aiba 2002, Fig. S1 in the Supplement). The litter was dried at 70°C and separated to leaves, branches, reproductive parts, and dusts. Each type of litter samples were combined to make a pooled sample per plot before grinding for analysis of elemental concentrations. Ground samples were sealed in plastic bags and preserved in air conditioned laboratories. We report only Si concentration of leaf litter, which had far greater Si concentration and total mass compared to other types of litter, as well as high correlation between collection times (Fig. S1). .

2.3 Soil sampling

Soil samples were collected in March 2015 from the upper mineral horizon (0-10 cm, largely corresponding to A-horizon) where most fine roots occur (Wagai et al., 2011). In each plot, five transects were set parallel to each other, along which five cores were taken every 5 to 10 m using a stainless steel sampler (4.8 cm diameter) after removing O-horizon. The five cored samples were combined by transect and homogenized, and visible roots were removed by hand before air-drying and sieving to pass 2 mm mesh. Additionally, a deep soil pit was excavated in the adjacent land of each plot to collect soil samples from different horizons along the profile.

2.4 Si extraction and measurements

Dried leaf and leaf litter samples were milled to a fine powder. From ca. 30 mg of ground sample, Si was extracted with alkaline extraction of BSi with 1% sodium carbonate in water (20 ml in a polycarbonate bottle, shaking at 85°C overnight) in 2015, adopting the method of Conley and Schelske (1993). The Si concentration in the extract was immediately measured with the molybdate blue colourimetry (Sauer et al., 2006; Faisal et al., 2012). Each sample was measured at least twice, and the difference between the values was less than 3.0 mg Si g^{-1} dry weight or 20% Si.

For measurements of water extractable Si concentration, about 3 g each of air-dried soil was mixed in 20 ml of distilled water in a 50 ml centrifuge tube in 2015. The tube was shaken for 20 hours at room temperature (ca. 180 oscillations per minute), then centrifuged at 10,000 rpm (ca. 12,000 g) for one hour. The supernatant was suction-filtered through a 0.025 μm membrane filter, and 1 ml of the filtrate was immediately analyzed with the molybdate blue colourimetry. The values of three repeated analyses were averaged for each sample. Our measurement values of the leaf, leaf-litter and soil sample extracts were above the detection limit of the spectrophotometer (absorbance of blank + 2.8σ) (UV-1650PC, Shimadzu Corporation, Kyoto, Japan). Soil analyses were conducted at the Institute for Agro-Environmental Sciences, Tsukuba, Japan.

2.5 Statistical analyses

For each plot, abundance-weighted community mean of the leaf Si concentration was calculated as follows:

$$\text{Abundance-weighted leaf Si concentration} = \sum_{i=1}^{s} L_i \times \frac{RBA_i}{TRBA}$$

L_i is mean leaf Si concentration of species i, RBA_i is RBA of species i, and $TRBA$ is total RBA of all the target species at each plot (Aiba et al., 2002). Leaf litter Si flux was determined by multiplying leaf litter Si concentration by leaf litterfall dry

5   mass (kg ha^{-1} yr^{-1}) reported previously (Kitayama and Aiba, 2002). Difference among elevation levels (700, 1,700, 2,700 and 3,100 m asl) and bedrock types (sedimentary and ultrabasic) in species leaf, leaf litter and water extractable Si concentrations among the plots were tested with analysis of variance (ANOVA). Leaf Si concentration was log-transformed to improve normality before ANOVA. Si concentration linearly increases with leaf age (Motomura et al., 2004). Because we were interested in estimating the maximum leaf Si concentration that would be found in old and senescing leaves, we used the

10 90th percentile of measured leaf Si concentrations as a species trait observed in each plot. For the 11 species that occurred at more than one plot, we used ANOVA to examine to test within-species variation after applying Bonferroni correction for multiple comparisons.

Phylogenetic independent contrasts (PICs; Felsenstein, 1985) were calculated for the mean leaf Si concentration and elevational distribution of the 71 species in the data set, using the software Phylomatic (version 3; Webb and Donoghue,

15 2005), the latest updates from the Angiosperm Phylogeny Group III (Bremer et al., 2009), and the ape package (Paradis et al., 2004). The observed patterns of PICs were compared with a null model assuming a unit branch length (except for polytomies, for which a negligibly small branch length was assumed) and the Brownian motion of evolutionary change, using the ape package. Pearson's r for PIC correlations was calculated between foliar Si concentration and elevation values (Garland et al., 1992). Blomberg's K statistic was also calculated to examine the degree of phylogenetic signals (Blomberg et al., 2003),

20 using the phytools package (version 0.5.64; Revell, 2012). All statistical analyses were performed in R 3.1.3 GUI 1.65 (R Development Core Team, 2016) with a significance level of alpha = 0.05.

3 Results

3.1 Si cycling via leaf litterfall

25 The annual leaf litter Si flux differed substantially in relation to elevation differences among the eight forest monitoring plots on Mt. Kinabalu, with little difference between the bedrock types (Fig. 1). The Si concentration per unit leaf-litter dry mass was the highest at 700 m elevation plots (6.0 and 5.0 mg Si g^{-1} for sedimentary and ultrabasic rocks, respectively), and decreased with increasing elevation (Fig. 1a). Leaf-litter Si concentration strongly differed with elevation but not between bedrock types without a significant interaction between elevation and bedrock (Table 2). Annual leaf litterfall mass

30 decreased with increasing elevation and was higher on the sedimentary rock than the ultrabasic rock except at 2,700 m asl (reproduced from Kitayama and Aiba 2002, Fig. 1b). Consequently, annual Si flux via leaf litterfall (Fig. 1c) decreased with

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increasing elevation, without noticeable differences between the sedimentary and ultrabasic rocks, except at the highest two elevations on the sedimentary rock.

3.2 Variations of leaf Si concentration among species and communities

Mass-based leaf Si concentration differed substantially among the 71 tree species and the elevation levels (Fig. 2). The mean leaf Si concentration varied up to 57 folds among the species (0.24-13.6 mg Si g^{-1}) (Table S2 in the Supplement). The interspecific variation of leaf Si concentration within a plot was greater in the lower elevation plots. Species leaf Si concentration significantly differed with elevation but not between bedrock types, with similar elevational trends on two bedrock types (Table 2). Abundance-weighted leaf Si concentration was the highest at 700 m asl on both bedrocks (Fig. 3).

Because species composition changed almost completely from plot to plot (Table S1 in the Supplement), the observed among-plot differences in leaf Si concentration may reflect species traits, environmental responses of each species or both. Thus, we compared leaf Si concentrations for the 11 species that occurred at more than one plot, most of which occurred in the higher elevation plant communities (Table S2 in the Supplement). Of the 11 species, only *Leptospermum recurvum* showed significant difference among three plots ($P < 0.005$, after applying the Bonferroni correction) (Fig. 4), showing that physiological responses of each species had very limited effects on observed differences among plots if any.

The Blomberg's K statistic showed a significant phylogenetic signal for elevation ($K = 0.37$, $P < 0.05$) (see Fig. S2 in the Supplement), reflecting the affinity of gymnosperms, Theaceae, Symplocaceae and oaks to the high elevation plots, and the affinity of the clade containing Dipterocarpaceae, Thymelaeaceae, Bombacaceae, and Sterculiaceae to the lowest elevation. In contrast, phylogenetic signal was weaker and non-significant for leaf Si concentration ($K = 0.27$) (see Fig. S3 in the Supplement). PIC values of elevation explained 15% of the variation in PIC values of leaf Si concentration ($r = -0.39$, $P < 0.001$), suggesting that evolutionary shifts of clade distribution to a higher elevation are associated with less leaf Si accumulation.

3.3 Si bioavailability in soil

Water extractable Si concentration per unit soil mass differed among elevations and between the bedrock types with a significant interaction between elevation and bedrock (Table 2). The mean water extractable Si concentration at 700 m elevation plots (0.021 mg Si g^{-1} for both bedrock types) was much higher compared to other elevations (0.007-0.015 mg Si g^{-1}) (Fig. 5). The Si value differed by bedrock only at 1,700 m elevation. Using samples from different horizons along a deep soil pit near each plot, we made preliminary examination how our shallow soil samples differ from deeper soil. Water extractable Si concentration showed variable trends with soil depth across elevation and bedrock types (Fig. S4). In most soil pits, change of water extractable Si with soil depth was small, except for two highest elevation sites on ultrabasic rock where water extractable Si concentration increased with soil depth.

4 Discussion

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We predicted that litter Si flux should differ with elevation and bedrock types, in association with differences in leaf Si concentrations of dominant tree species and soil Si availability. The results supported this prediction in terms of elevation, but we found no significant differences in litter or leaf Si concentrations between the two bedrock types. These results likely reflected cooler temperature regimes, lower productivity and slow litter decomposition at higher elevation, as well as species differences that result in difference in leaf Si concentrations in relation to elevation. We did not directly measure Si release rates from standing leaf litter, but lower decomposition rates (Kitayama and Aiba 2002) in combination with lower Si concentration in leaf litter, mean lower annual rates of BSi release from leaf litter to the soil.

The annual leaf litter Si flux was greater at lower elevation plant communities, with large difference between 700 m and 1,700 m asl. We suspect that Si cycling rates by vegetation would be even faster in lowland forests below 700 m asl due to even greater forest productivity, litter decomposition rate and high diversity of angiosperm trees. The published data on Si flux via leaf litter measured in lowland tropical forests (lowland Amazonia, Lucas et al., 1993; Congo, Alexandre et al., 1997) show even higher values (3.3-7.6 g Si m^{-2} yr^{-1}) than our 700 m elevation plots (3.1-4.4 g Si m^{-2} yr^{-1}). We are not aware of published litter flux data from other lowland tropical forests, but unpublished data for lowland dipterocarp forests from our research group show high values (e.g., 8.5 g Si m^{-2} yr^{-1} for Pasoh, Peninsula Malaysia, per undergraduate thesis of Hidehiro Ishizawa, Kyoto University, and similar values for lowland Borneo sites). These litter Si flux values for tropical lowland forests are high compared to European forests (ranging from 0.2 g Si m^{-2} yr^{-1} for a black pine stand to 4.2 g Si m^{-2} yr^{-1} for a Norway spruce stand) (Cornelis et al., 2010). Such high litter Si flux values in tropical lowland forests strongly support a notion that BSi released from leaf litter to soil is a dominant source of Si taken up by plants (Cornelis and Delvaux, 2016).

The higher litter Si flux at lower elevation sites reflected both greater productivity and high litter Si concentrations. The latter, in turn, reflected higher community-level means of live leaf Si concentrations in lower elevation plots. Whilst the turnover of dominant tree species with elevation most likely explains the community-wide trend of foliar Si concentrations on Mt. Kinabalu, we cannot completely rule out other possible explanations. Firstly, all else being equal, warmer climate at lower elevation may mean greater transpiration and faster rate of Si transport to leaves with xylem water. With cucumber, which is a moderate active uptaker of Si, experimental manipulation of transpiration results in different levels of Si accumulation (Faisal et al., 2012). At the same time, this and other studies with herbaceous species (e.g., Liang et al., 2006) show that Si accumulation rate is not merely transpiration-dependent, but also modulated by active uptake by roots, such that high Si accumulating species compensate for low Si availability from the soil. To isolate the physiological effect of transpiration rates on Si accumulation at different elevations, a reciprocal transplanting of high and low elevation species should be conducted in the future.

The second temperature-related abiotic factor that might increase leaf and litter Si concentration is the faster weathering of silicate minerals under warmer climate (Wagai et al., 2008). Faster weathering can potentially enhance the pool size of soluble Si, which may be absorbed by plants and returned to the soil as BSi contained in dead plant tissues (Cornelis and Delvaux, 2016). More advanced weathering in the upper soil horizons (compared to deeper soil) or lower

elevation (compared to higher elevation) means lower Si:Al ratios in clay, and lower water-extractable Si. But, the lack of such trends with soil depth (Fig. S4) and elevation (the opposite of this expectation) in our study suggests the role of Si cycle by plants and Si pools in plants and leaf litter. As BSi is more soluble than Si contained in rock and clay (Fraysse et al., 2009), a positive feedback to accelerate Si cycling by vegetation may develop. Greater annual production and faster

5   decomposition of Si-rich leaf litter at lower elevation should increase Si availability to plants, thereby escalating Si accumulation in leaves. While we cannot totally discount such direct and indirect effects of temperature regime on the observed elevational trends of leaf and litter Si concentrations, within-species variations for species that occurred at multiple elevations (Fig. 4) favor biological factors over abiotic and proximate environmental factors.

       A likely biological explanation for the high leaf Si concentrations in lowland trees is an evolutionary one. Strong

10   phylogenetic signals exist for Si accumulation among a broad range of land plant species (Takahasi et al., 1981; Hodson et al., 2005) even though the signal was weak within our 71 species dataset, and high Si accumulating species up-regulate active uptake mechanisms (Ma and Takahashi, 2002; Liang et al., 2006). In other words, each plant regulates Si uptake rates as a species-specific trait. A key trend found in our study was that tree species with high leaf Si concentrations occurred more in lower elevation forests. This suggests a tantalizing possibility that active Si uptake is adaptive in relation to biotic

15   and abiotic stress factors in lowland tropical forests compared to forests of higher altitudes and latitudes. Grasses and other herbaceous species are known to use silica to enhance defense against herbivory and disease (McNaughton and Terrants, 1983; Ma and Takahashi, 2002; Hartley et al., 2015). While such defensive use of silica has been reported only sporadically for tropical woody plants (e.g., Korndorfer and Del Claro, 2006), it is worth testing with many other tropical trees which are exposed to a diverse array of herbivores and disease agents year around. Another potential stress factor in lowland tropical

20   forests is a high risk of aluminum toxicity, especially where soils are highly weathered and acidic. It is possible that some lowland tropical tree species have evolved Si accumulation as part of their strategies to ameliorate aluminum and heavy metal toxicity as reported in some temperate herbaceous and tree species (Epstein, 1994; Hodson and Sangster, 1999). As these are speculative ideas, we need more data from tropical taxa about their Si uptake patterns, as well as experiments to test these possible benefits of Si accumulation.

25   Our study found no differences in leaf and litter Si concentrations between the two bedrock types contrasting in total Si contents. This result may indicate that total Si content of rocks is poor indicator of rates of weathering and Si solubility. Sedimentary rocks contain more Si than ultrabasic rocks (Brooks, 1987), but abundance of quartz in some sedimentary rocks (such as sandstones) may mean slower Si dissolution from such rocks than from ultrabasic rocks (Goldich, 1938; Schulz and White, 1999). Indeed, at high elevation sites, water soluble Si in the soil B horizon was much higher in

30   ultrabasic rocks (Fig. S4). But, this high Si availability in the B horizon at high elevation on Ultrabasic rocks did not result in high leaf and litter Si concentrations at these sites. Hence, the lack of difference between the bedrocks suggest that plant Si uptake traits override the effect of bedrock. The latter possibility is in line with a recent finding by Shaller et al. (2018) from Panamanian tropical forests, in which intraspecific variation in foliar Si content that does not respond to soil Si availability. In our study, species composition was almost completely different between the two bedrock types. Similarly to our results,

community-wide leaf Si concentration does not depend on Si availability differences between contrasting soil types in Australia (Cooke and Leishman, 2012). These results strongly suggest that species traits influence biogeochemical cycles of Si more than proximate environmental factors, such as temperature or rock and soil weathering. In order to test these possibilities, future studies need to evaluate Si availability from greater soil depths where trees may also obtain water, while

5   simultaneously distinguishing biogenic *vs.* rock-derived Si.

In our dataset, it is intriguing that lowland trees in the family Dipterocarpaceae differed substantially in leaf Si concentrations, from 0.46 mg Si g^{-1} (*Shorea parvistipulata*) to 9.87 mg Si g^{-1} (*Shorea gibbosa*). Dipterocarpaceae represents the major group of dominant tall trees in lowland tropical forests in Asia (Richards, 1952; Ashton, 2015), and as such, further investigation on their Si uptake patterns can reveal significant insights on Si cycling by vegetation in this region. In

10   addition, Dipterocarp-dominated forests have been severely logged during recent decades (Ashton, 2015), and this may have strongly impacted biogeochemical cycles of Si in the tropics. Conley et al. (2008) suggest that conversion of forests to agricultural and open lands cause significant losses of DSi from the soil and may adversely affect temperate terrestrial ecosystems. The potential impacts of deforestation and forest degradation on Si cycling may be even greater in the tropics given the abundance of high Si accumulating species in lowland tropical forests. In order to analyze these potential impacts

15   over longer time spans, quantification of plant parts other than leaves (e.g., coarse woody debris and tree roots) that also contribute to forest Si cycling will be needed (Clymans et al*.,* 2016; Turpault et al., 2018).

Greater understanding of both proximate and ultimate factors that regulate biogeochemical cycles of Si in tropical ecosystems is urgently needed, including how species diversity matters for Si cycle by tropical vegetation. Our study has scratched just the surface of this topic.

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Data availability

All data used in this manuscript will be available in the Dryad Digital Repository.

Authors' contribution

25   K. Kitajima conceived the ideas; K. Kitajima, K. Kitayama and R. Nakamura designed methodology; R. Wagai, S. Suzuki and K. Kitayama collected samples; R. Nakamura and H. Ishizawa performed the chemical analyses; K. Kitayama and R. Wagai provided critical information on the forest monitoring plots on Mt. Kinabalu; R. Nakamura and K. Kitajima led data analyses; R. Nakamura wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Description of the eight plots on Mt. Kinabalu.

		Sites on sedimentary rock				Sites on ultrabasic rock			
		700 m	1700 m	2700 m	3100 m	700 m	1700 m	2700 m	3100 m
Ecosystem properties	Canopy height (m) [a]	46.8	30	20.6	15	65.4	22.6	14.2	6.1
	Decomposition k (yr^{-1}) [a]	1.69	1.18	1	0.87	1.67	0.71	0.8	0.44
	Ground herbs or grasses [b]	++	++	+	+++	++	++	+++	+
	Litterfall (g m^{-2} yr^{-1}) [a]	1110	799	532	631	1113	628	594	164
	Standing litter (kg m^{-2}) [a]	0.66	0.68	0.53	0.73	0.67	0.88	0.74	0.37
Soil properties	Bulk density (g cm^{-3}) [c]	0.89	1.09	0.48	0.42	0.83	0.62	0.51	0.47
	C:N [a]	13.8	13.7	19.2	14.3	11.4	12.1	9.9	13.3
	Clay content (%) [c]	37.8	9.5	14.8	2.8	45.6	16.6	24.3	15.8
	pH (H$_2$O) [c]	3.9	4.1	3.9	4.6	4.8	5.4	4.9	5.4
	pH (CaCl$_2$) [c]	3.5	3.4	3.1	3.8	4.0	4.6	4.2	4.4
	Total active P (g m^{-2}) [d]	39.2	24.2	41.4	24.5	27.6	4.0	11.4	9.0

+++ abundant, ++ frequent, + few

a from Kitayama and Aiba (2002) using top 10 cm soil

Litterfall consists of leaves, reproductive organs, twigs, epiphytes, palms, bamboos and dust.

Standing litter consists of twigs ≤ 2 cm girth, leaves and other fractions ≥ approximately 1 cm^2.

Decomposition rate constant (k) is determined by dividing annual litterfall by standing litter.

b from Aiba et al. (2002)

c from Wagai et al. (2008) using top 10 cm soil except 3100 m plots from R. Wagai (unpublished data)

d from Kitayama et al. (2000) using top 30 cm soil

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Table 2. ANOVA results for the effects of elevation (700, 1,700, 2,700 and 3,100 m asl) and bedrock type (sedimentary and ultrabasic) on species mean leaf Si concentration (log-transformed for normalization), leaf litter Si concentration and water extractable Si concentration on a basis of sample dry mass. Species leaf Si concentration was defined as the maximum capacity to accumulate Si in leaves, and represented by 90th percentile of measured values by species in this study. In the case the species occurred at multiple plots, species leaf concentration was determined by plot.

	Elevation			Bedrock type			Interaction		
	df	F	P	df	F	P	df	F	P
Log_{10} (Species leaf Si concentration (mg g^{-1}))	3	8.74	**< 0.001**	1	0.7	0.41	3	0.97	0.41
Leaf litter Si concentration (mg g^{-1})	3	20.4	**< 0.001**	1	0.36	0.56	3	0.35	0.79
Soil water extractable Si (mg g^{-1})	3	22.1	**< 0.001**	1	5.0	**0.032**	3	3.2	**0.036**

Notes: Significant terms ($P < 0.05$) are shown in bold. Leaf Si concentration had at least three replicates per species but *Shorea parvistipulata*, No.14 on ultrabasic rock, *Tristania* sp.2, No.49 and *Heritiera simplicifolia*, No.64 in Table S2 (n = 1). Leaf litter and water extractable Si concentrations had three and five replicates, respectively.

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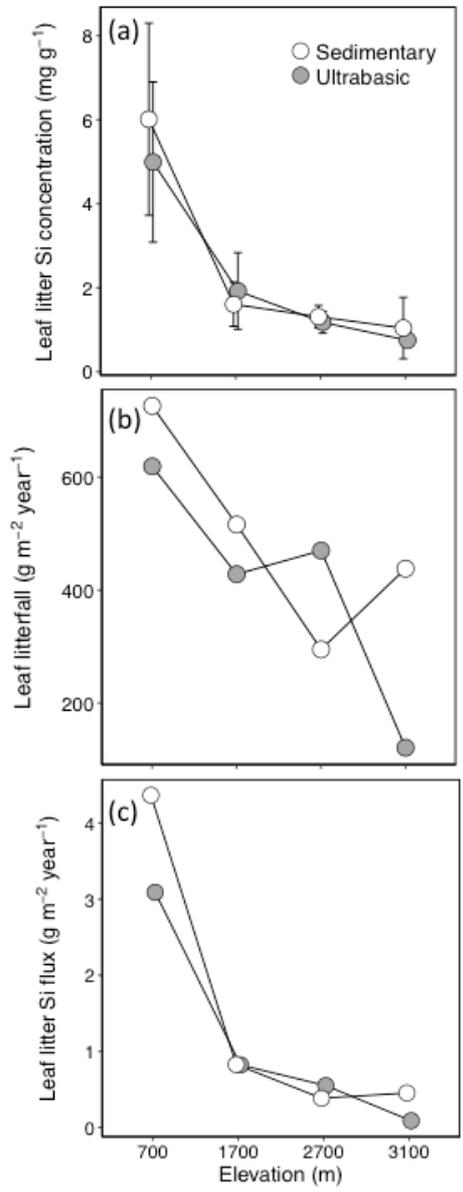
Figure 1. (a) Leaf litter Si concentration (means ± s.d. for three two-week-interval collections), (b) annual leaf litter mass (data from Kitayama and Aiba (2002), showing the mean from two years of data), and (c) leaf litter Si flux (n = 1) at different elevations for sedimentary (white circles) and ultrabasic (grey circles) rocks.

Elevation

Leaf Si concentration (mg g^{-1})

| 700 m | 1700 m | 2700 m | 3100 m | Sedimentary |
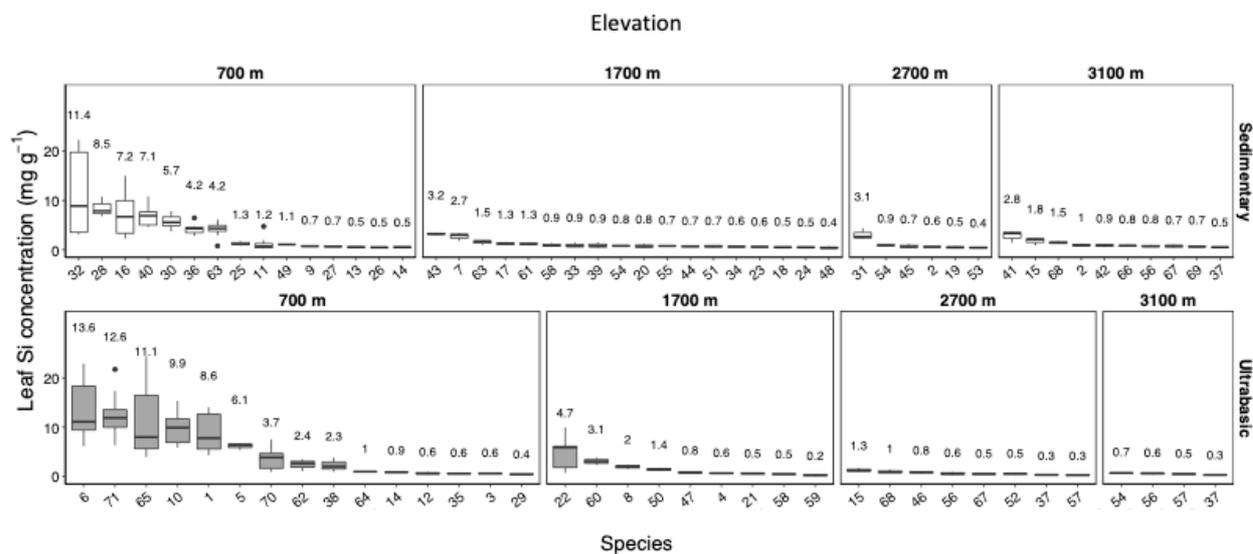
Species

Figure 2. Variations of leaf Si concentrations among species and plots, showing the species median (thick horizontal line) with 25-75th percentiles (box) and 95% confidence interval (whiskers) for each species. Mean values of species are shown above the whiskers. Species identity is indicated by the number on the horizontal axis (see Table S1 in the Supplement). There was a large species turn-over among the eight plots located at different elevations on two types of bedrock. Open and shaded boxes indicate sedimentary and ultrabasic rocks (sedimentary and ultrabasic rocks, upper and lower panels, respectively). Eleven of the 71 species occurred at multiple plots and are shown at more than one panel (8 species at two plots, 3 species at three plots, see Fig. 4 and Table S2 in the Supplement). Plot ID is indicated in each panel.

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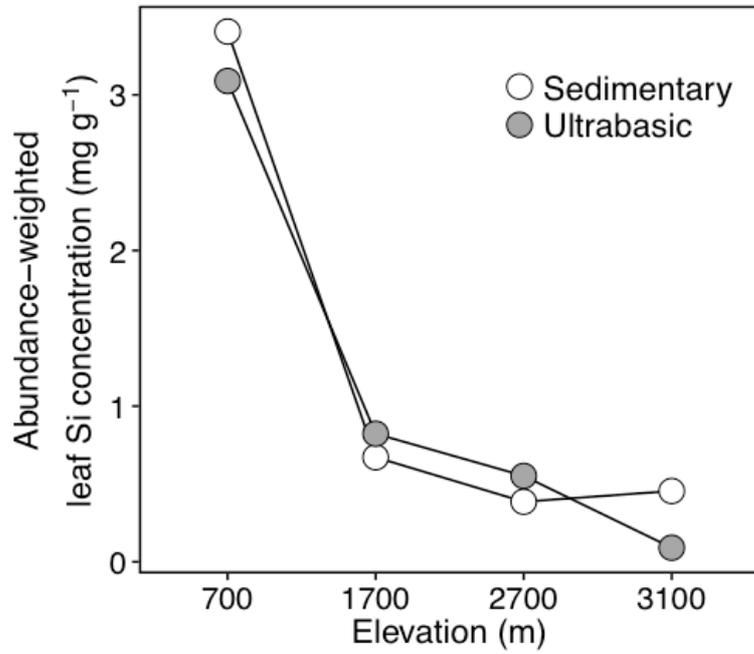
Figure 3. Abundance-weighted leaf Si concentration (n = 1) at different elevations for sedimentary (white circles) and ultrabasic (grey circles) rocks. Each point represents a plot at the elevation.

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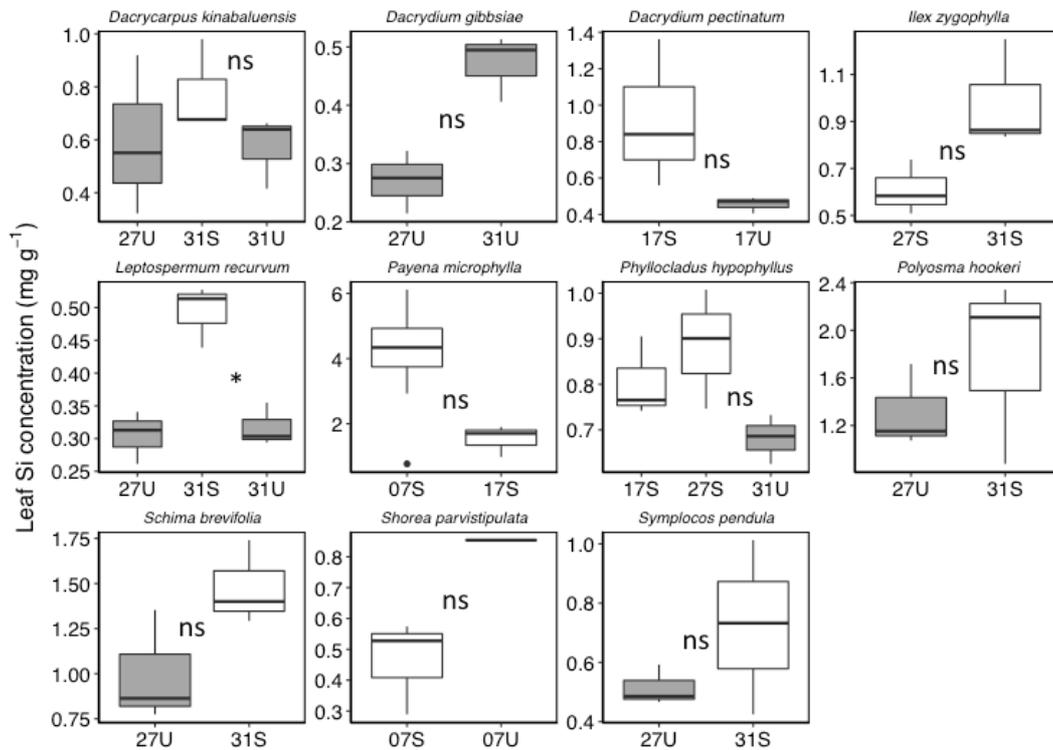
Figure 4. Boxplots for leaf Si concentration for 11 tree species that occurred at multiple plots. Open and shaded boxes indicate sedimentary and ultrabasic rocks. See Fig. 2 for Plot ID. Significant site effect was found for one species * ($P < 0.0045$ with Bonferroni correction) by ANOVA.
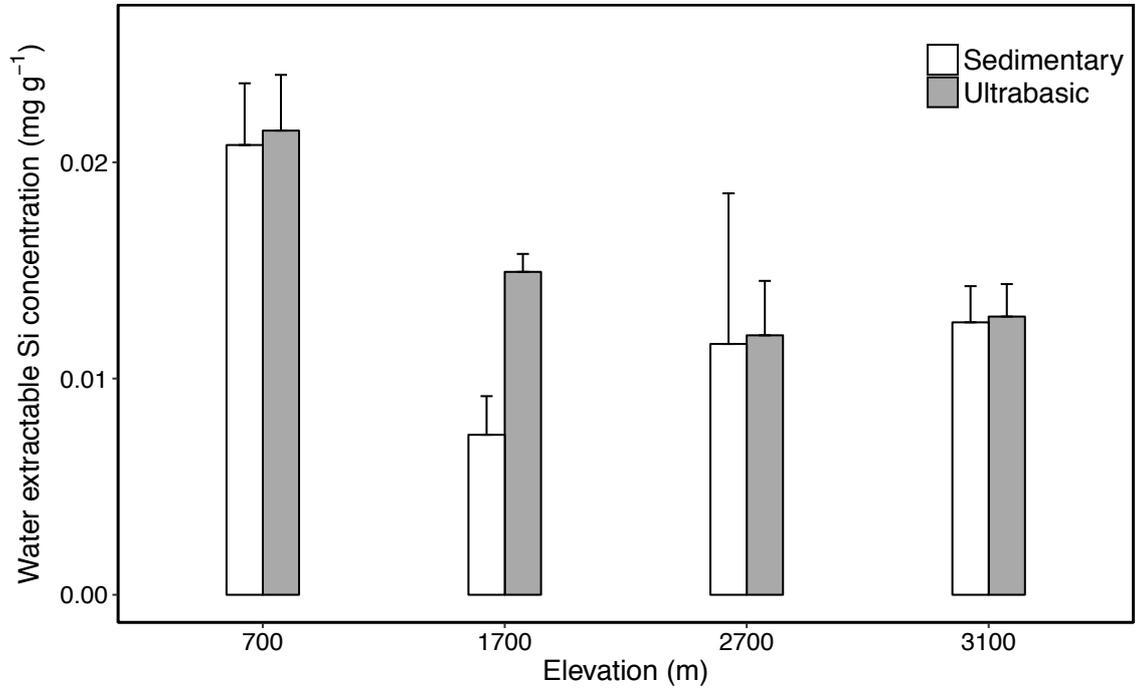
Figure 5. Water extractable Si concentration per unit dry mass of soil for the plots at specified elevations on sedimentary (white bars) and ultrabasic (grey bars) rocks. Data are means + s.d. (n = 5).
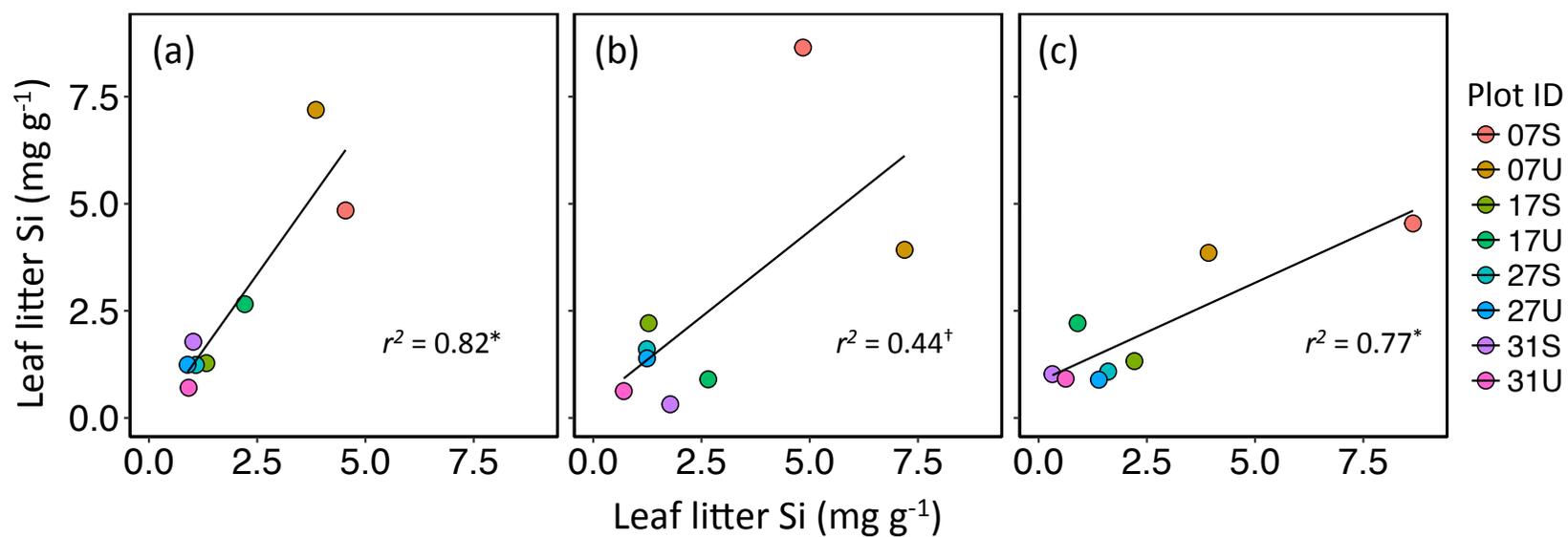
Figure S1. Correlation of leaf litter Si between different collection months. (a) May 1998 (vertical axis) vs. April 1997 (horizontal axis), (b) August 1998 vs. May 1998, (c) April 1997 vs. August 1998. Each point represents a plot (see Figure 2 legend for plot ID), and for which samples from all litter traps were combined before grinding for chemical analysis. $^{†}P <0.1$, $^{*}P <0.05$.

Figure S2. Interpolated elevation values based on the phylogenetic tree for the 71 species focused in this study. Different colors represent different elevation values. The Blomberg's *K* statistic showed significant and weak phylogenetic signal ($K = 0.37$, $P < 0.05$). This map was generated with the phytools package (version 0.5.64; Revell 2012) in R.
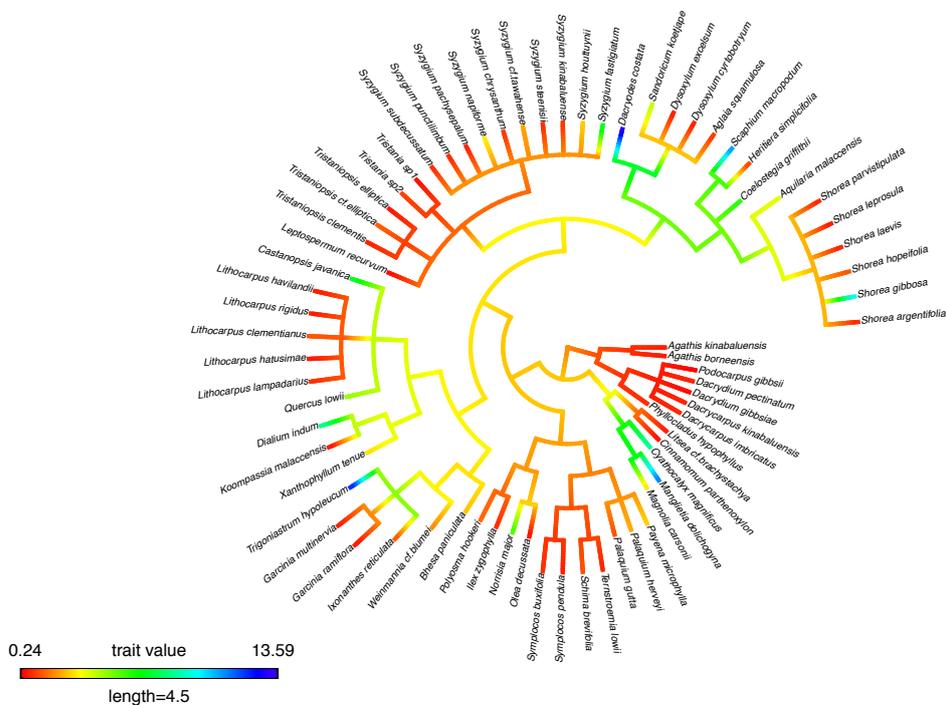
Figure S3. Interpolated leaf Si concentrations per unit leaf mass based on the phylogenetic tree for the 71 species focused in this study. Different colors represent different leaf Si concentrations. The Blomberg's *K* statistic showed non-significant and weak phylogenetic signal (*K* = 0.27). This map was generated with the phytools package (version 0.5.64; Revell 2012) in R.
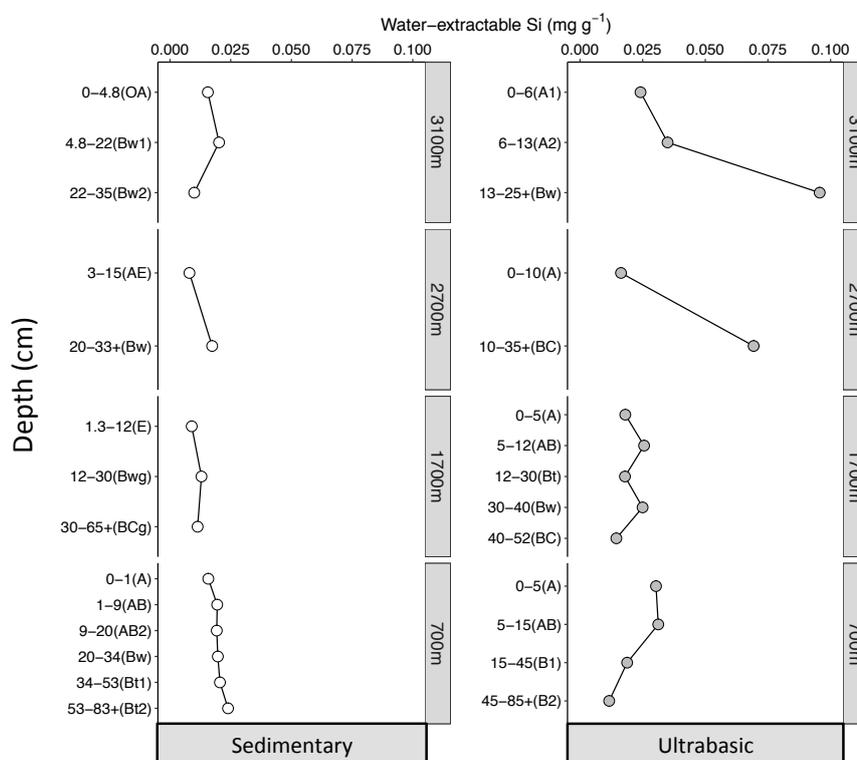
Figure S4. Water extractable Si per unit dry mass along the soil depth profile from one deep soil pit on two rock types (sedimentary and ultrabasic) at four elevations (700, 1700, 2700, 3100 m). Each soil horizon and its depth are indicated.

Table S1. The list of 71 species included in the study, and their relative basal area of stems ≥ 10 cm dbh (RBA, %) in eight plots. The ID number

is given in Fig. 2. The plot ID indicates elevation and bedrock type: 07S, 17S, 27S and 31S indicate 700, 1,700, 2,700 and 3,100 m elevation

on sedimentary rock, respectively, and 07U, 17U, 27U and 31U indicate 700, 1,700, 2,700 and 3,100 m elevation on ultrabasic rock,

respectivcely. Species occuring at multiple plots are highlighted in yellow.

ID	Family	Species	07S 1.0 ha	07U 1.0 ha	17S 1.0 ha	17U 0.2 ha	27S 0.25 ha	27U 0.2 ha	31S 0.2 ha	31U 0.06 ha
1	Annonaceae	*Cyathocalyx magnificus*	-	1.5	-	-	-	-	-	-
2	Aquifoliaceae	*Ilex zygophylla*	-	-	-	-	8.2	-	5.9	-
3	Araucariaceae	*Agathis borneensis*	-	3.5	-	-	-	-	-	-
4	Araucariaceae	*Agathis kinabaluensis*	-	-	-	19.2	-	-	-	-
5	Bombacaceae	*Coelostegia griffithii*	-	2.9	-	-	-	-	-	-
6	Burseraceae	*Dacryodes costata*	-	4.2	-	-	-	-	-	-
7	Celastraceae	*Bhesa paniculata*	-	-	1.3	-	-	-	-	-
8	Cunoniaceae	*Weinmannia* cf. *blumei*	-	-	-	3.9	-	-	-	-
9	Dipterocarpaceae	*Shorea argentifolia*	6.4	-	-	-	-	-	-	-
10	Dipterocarpaceae	*Shorea gibbosa*	-	1.9	-	-	-	-	-	-
11	Dipterocarpaceae	*Shorea hopeifolia*	4.4	-	-	-	-	-	-	-
12	Dipterocarpaceae	*Shorea laevis*	-	30.5	-	-	-	-	-	-

			C1	C2	C3	C4	C5	C6	C7	C8
13	Dipterocarpaceae	*Shorea leprosula*	7.3	-	-	-	-	-	-	-
14	Dipterocarpaceae	*Shorea parvistipulata*	4.5	3.1	-	-	-	-	-	-
15	Escalloniaceae	*Polyosma hookeri*	-	-	-	-	-	2.8	5.1	-
16	Fagaceae	*Castanopsis javanica*	4.3	-	-	-	-	-	-	-
17	Fagaceae	*Lithocarpus clementianus*	-	-	4.6	-	-	-	-	-
18	Fagaceae	*Lithocarpus hatusimae*	-	-	2.5	-	-	-	-	-
19	Fagaceae	*Lithocarpus havilandii*	-	-	-	-	8.2	-	-	-
20	Fagaceae	*Lithocarpus lampadarius*	-	-	1.7	-	-	-	-	-
21	Fagaceae	*Lithocarpus rigidus*	-	-	-	2.3	-	-	-	-
22	Fagaceae	*Quercus lowii*	-	-	-	3.3	-	-	-	-
23	Guttiferae	*Garcinia multinervia*	-	-	1.5	-	-	-	-	-
24	Guttiferae	*Garcinia ramiflora*	-	-	2.7	-	-	-	-	-
25	Ixonanthaceae	*Ixonanthes reticulata*	8.0	-	-	-	-	-	-	-
26	Lauraceae	*Cinnamomum parthenoxylon*	2.4	-	-	-	-	-	-	-
27	Lauraceae	*Litsea* cf. *brachystachya*	2.8	-	-	-	-	-	-	-
28	Leguminosae	*Dialium indum*	1.8	-	-	-	-	-	-	-
29	Leguminosae	*Koompassia malaccensis*	-	2.2	-	-	-	-	-	-
30	Loganiaceae	*Norrisia major*	3.5	-	-	-	-	-	-	-
31	Magnoliaceae	*Magnolia carsonii*	-	-	-	-	18.3	-	-	-
32	Magnoliaceae	*Manglietia dolichogyna*	2.2	-	-	-	-	-	-	-
33	Meliaceae	*Aglaia squamulosa*	-	-	2.9	-	-	-	-	-
34	Meliaceae	*Dysoxylum cyrtobotryum*	-	-	1.4	-	-	-	-	-

			C1	C2	C3	C4	C5	C6	C7	C8
35	Meliaceae	*Dysoxylum excelsum*	-	2.0	-	-	-	-	-	-
36	Meliaceae	*Sandoricum koetjape*	3.1	-	-	-	-	-	-	-
37	Myrtaceae	*Leptospermum recurvum*	-	-	-	-	-	21.6	6.9	89.4
38	Myrtaceae	*Syzygium* cf. *tawahense*	-	1.9	-	-	-	-	-	-
39	Myrtaceae	*Syzygium chrysanthum*	-	-	3.1	-	-	-	-	-
40	Myrtaceae	*Syzygium fastigiatum*	2.0	-	-	-	-	-	-	-
41	Myrtaceae	*Syzygium houttuynii*	-	-	-	-	-	-	10.4	-
42	Myrtaceae	*Syzygium kinabaluense*	-	-	-	-	-	-	6.8	-
43	Myrtaceae	*Syzygium napiforme*	-	-	3.4	-	-	-	-	-
44	Myrtaceae	*Syzygium pachysepalum*	-	-	5.0	-	-	-	-	-
45	Myrtaceae	*Syzygium punctilimbum*	-	-	-	-	40.7	-	-	-
46	Myrtaceae	*Syzygium steenisii*	-	-	-	-	-	4.6	-	-
47	Myrtaceae	*Syzygium subdecussatum*	-	-	-	2.1	-	-	-	-
48	Myrtaceae	*Tristania* sp.1	-	-	4.3	-	-	-	-	-
49	Myrtaceae	*Tristania* sp.2	3.0	-	-	-	-	-	-	-
50	Myrtaceae	*Tristaniopsis* cf. *elliptica*	-	-	-	31.4	-	-	-	-
51	Myrtaceae	*Tristaniopsis clementis*	-	-	6.9	-	-	-	-	-
52	Myrtaceae	*Tristaniopsis elliptica*	-	-	-	-	-	6.8	-	-
53	Oleaceae	*Olea decussata*	-	-	-	-	9.1	-	-	-
54	Phyllocladaceae	*Phyllocladus hypophyllus*	-	-	1.8	-	7.9	-	-	1.3
55	Podocarpaceae	*Dacrycarpus imbricatus*	-	-	5.7	-	-	-	-	-
56	Podocarpaceae	*Dacrycarpus kinabaluensis*	-	-	-	-	-	19.1	36.3	7.5

	Family	Species								
57	Podocarpaceae	*Dacrydium gibbsiae*	-	-	-	-	-	32.5	-	1.7
58	Podocarpaceae	*Dacrydium pectinatum*	-	-	5.9	4.0	-	-	-	-
59	Podocarpaceae	*Podocarpus gibbsii*	-	-	-	6.8	-	-	-	-
60	Polygalaceae	*Xanthophyllum tenue*	-	-	-	6.9	-	-	-	-
61	Sapotaceae	*Palaquium gutta*	-	-	1.6	-	-	-	-	-
62	Sapotaceae	*Palaquium herveyi*	-	2.3	-	-	-	-	-	-
63	Sapotaceae	*Payena microphylla*	6.7	-	6.2	-	-	-	-	-
64	Sterculiaceae	*Heritiera simplicifolia*	-	2.6	-	-	-	-	-	-
65	Sterculiaceae	*Scaphium macropodum*	-	2.5	-	-	-	-	-	-
66	Symplocaceae	*Symplocos buxifolia*	-	-	-	-	-	-	3.9	-
67	Symplocaceae	*Symplocos pendula*	-	-	-	-	-	1.3	2.5	-
68	Theaceae	*Schima brevifolia*	-	-	-	-	-	7.2	10.0	-
69	Theaceae	*Ternstroemia lowii*	-	-	-	-	-	-	4.2	-
70	Thymelaeaceae	*Aquilaria malaccensis*	-	3.4	-	-	-	-	-	-
71	Trigoniaceae	*Trigoniastrum hypoleucum*	-	1.3	-	-	-	-	-	-
		Total RBA	62.4	65.8	62.5	79.9	92.4	95.9	92	99.9

Table S2. Plot-and-species mean leaf Si concentration for the 71 tree species from 28 families. The ID number is used in Fig 2. Mean leaf Si

concentration was found by averaging at least three replicates per species except n = 1 for *Shorea parvistipulata* (No.14) on ultrabasic rock,

Tristania sp.2 (No.44) and *Heritiera simplicifolia* (No.64) (indicated by asterisk). Species occuring at multiple plots are highlighted in

yellow.

ID	Family	Species	07S 1.0 ha	07U 1.0 ha	17S 1.0 ha	17U 0.2 ha	27S 0.25 ha	27U 0.2 ha	31S 0.2 ha	31U 0.06 ha
1	Annonaceae	*Cyathocalyx magnificus*	-	8.61	-	-	-	-	-	-
2	Aquifoliaceae	*Ilex zygophylla*	-	-	-	-	0.61	-	0.98	-
3	Araucariaceae	*Agathis borneensis*	-	0.57	-	-	-	-	-	-
4	Araucariaceae	*Agathis kinabaluensis*	-	-	-	0.62	-	-	-	-
5	Bombacaceae	*Coelostegia griffithii*	-	6.13	-	-	-	-	-	-
6	Burseraceae	*Dacryodes costata*	-	13.59	-	-	-	-	-	-
7	Celastraceae	*Bhesa paniculata*	-	-	2.69	-	-	-	-	-
8	Cunoniaceae	*Weinmannia* cf. *blumei*	-	-	-	1.97	-	-	-	-
9	Dipterocarpaceae	*Shorea argentifolia*	0.70	-	-	-	-	-	-	-
10	Dipterocarpaceae	*Shorea gibbosa*	-	9.87	-	-	-	-	-	-
11	Dipterocarpaceae	*Shorea hopeifolia*	1.25	-	-	-	-	-	-	-
12	Dipterocarpaceae	*Shorea laevis*	-	0.64	-	-	-	-	-	-

13	Dipterocarpaceae	*Shorea leprosula*	0.51	-	-	-	-	-	-	-
14	Dipterocarpaceae	*Shorea parvistipulata*	0.46	0.85*	-	-	-	-	-	-
15	Escalloniaceae	*Polyosma hookeri*	-	-	-	-	-	1.31	1.78	-
16	Fagaceae	*Castanopsis javanica*	7.16	-	-	-	-	-	-	-
17	Fagaceae	*Lithocarpus clementianus*	-	-	1.29	-	-	-	-	-
18	Fagaceae	*Lithocarpus hatusimae*	-	-	0.51	-	-	-	-	-
19	Fagaceae	*Lithocarpus havilandii*	-	-	-	-	0.54	-	-	-
20	Fagaceae	*Lithocarpus lampadarius*	-	-	0.79	-	-	-	-	-
21	Fagaceae	*Lithocarpus rigidus*	-	-	-	0.55	-	-	-	-
22	Fagaceae	*Quercus lowii*	-	-	-	4.73	-	-	-	-
23	Guttiferae	*Garcinia multinervia*	-	-	0.57	-	-	-	-	-
24	Guttiferae	*Garcinia ramiflora*	-	-	0.50	-	-	-	-	-
25	Ixonanthaceae	*Ixonanthes reticulata*	1.25	-	-	-	-	-	-	-
26	Lauraceae	*Cinnamomum parthenoxylon*	0.50	-	-	-	-	-	-	-
27	Lauraceae	*Litsea* cf. *brachystachya*	0.67	-	-	-	-	-	-	-
28	Leguminosae	*Dialium indum*	8.47	-	-	-	-	-	-	-
29	Leguminosae	*Koompassia malaccensis*	-	0.42	-	-	-	-	-	-
30	Loganiaceae	*Norrisia major*	5.73	-	-	-	-	-	-	-
31	Magnoliaceae	*Magnolia carsonii*	-	-	-	-	3.07	-	-	-
32	Magnoliaceae	*Manglietia dolichogyna*	11.38	-	-	-	-	-	-	-
33	Meliaceae	*Aglaia squamulosa*	-	-	0.91	-	-	-	-	-
34	Meliaceae	*Dysoxylum cyrtobotryum*	-	-	0.59	-	-	-	-	-

#	Family	Species								
35	Meliaceae	*Dysoxylum excelsum*	-	0.59	-	-	-	-	-	-
36	Meliaceae	*Sandoricum koetjape*	4.23	-	-	-	-	-	-	-
37	Myrtaceae	*Leptospermum recurvum*	-	-	-	-	-	0.30	0.49	0.32
38	Myrtaceae	*Syzygium* cf. *tawahense*	-	2.27	-	-	-	-	-	-
39	Myrtaceae	*Syzygium chrysanthum*	-	-	0.90	-	-	-	-	-
40	Myrtaceae	*Syzygium fastigiatum*	7.15	-	-	-	-	-	-	-
41	Myrtaceae	*Syzygium houttuynii*	-	-	-	-	-	-	2.80	-
42	Myrtaceae	*Syzygium kinabaluense*	-	-	-	-	-	-	0.87	-
43	Myrtaceae	*Syzygium napiforme*	-	-	3.24	-	-	-	-	-
44	Myrtaceae	*Syzygium pachysepalum*	-	-	0.66	-	-	-	-	-
45	Myrtaceae	*Syzygium punctilimbum*	-	-	-	-	0.75	-	-	-
46	Myrtaceae	*Syzygium steenisii*	-	-	-	-	-	0.79	-	-
47	Myrtaceae	*Syzygium subdecussatum*	-	-	-	0.82	-	-	-	-
48	Myrtaceae	*Tristania* sp.1	-	-	0.43	-	-	-	-	-
49	Myrtaceae	*Tristania* sp.2	1.07*	-	-	-	-	-	-	-
50	Myrtaceae	*Tristaniopsis* cf. *elliptica*	-	-	-	1.44	-	-	-	-
51	Myrtaceae	*Tristaniopsis clementis*	-	-	0.65	-	-	-	-	-
52	Myrtaceae	*Tristaniopsis elliptica*	-	-	-	-	-	0.50	-	-
53	Oleaceae	*Olea decussata*	-	-	-	-	0.42	-	-	-
54	Phyllocladaceae	*Phyllocladus hypophyllus*	-	-	0.80	-	0.89	-	-	0.68
55	Podocarpaceae	*Dacrycarpus imbricatus*	-	-	0.74	-	-	-	-	-
56	Podocarpaceae	*Dacrycarpus kinabaluensis*	-	-	-	-	-	0.60	0.78	0.57

	Family	Species								
57	Podocarpaceae	*Dacrydium gibbsiae*	-	-	-	-	-	0.27	-	0.47
58	Podocarpaceae	*Dacrydium pectinatum*	-	-	0.92	0.46	-	-	-	-
59	Podocarpaceae	*Podocarpus gibbsii*	-	-	-	0.24	-	-	-	-
60	Polygalaceae	*Xanthophyllum tenue*	-	-	-	3.06	-	-	-	-
61	Sapotaceae	*Palaquium gutta*	-	-	1.25	-	-	-	-	-
62	Sapotaceae	*Palaquium herveyi*	-	2.40	-	-	-	-	-	-
63	Sapotaceae	*Payena microphylla*	4.16	-	1.53	-	-	-	-	-
64	Sterculiaceae	*Heritiera simplicifolia*	-	0.98*	-	-	-	-	-	-
65	Sterculiaceae	*Scaphium macropodum*	-	11.08	-	-	-	-	-	-
66	Symplocaceae	*Symplocos buxifolia*	-	-	-	-	-	-	0.80	-
67	Symplocaceae	*Symplocos pendula*	-	-	-	-	-	0.51	0.72	-
68	Theaceae	*Schima brevifolia*	-	-	-	-	-	1.00	1.48	-
69	Theaceae	*Ternstroemia lowii*	-	-	-	-	-	-	0.67	-
70	Thymelaeaceae	*Aquilaria malaccensis*	-	3.74	-	-	-	-	-	-
71	Trigoniaceae	*Trigoniastrum hypoleucum*	-	12.65	-	-	-	-	-	-