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Sellan, G, Thompson, J, Majalap, N and Brearley, FQ (2019) Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest. Plant and Soil, 438 (1-2). pp. 173-185. ISSN 0032-079X

DOI: https://doi.org/10.1007/s11104-019-04000-5

Publisher: Springer Verlag

Version: Accepted Version

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

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Cite as: Sellan, G., Thompson, J., Majalap, N. Brearley, F.Q. Plant Soil (2019). https://doi.org/10.1007/s11104-019-04000-5

Abstract:

Background and aims: Whilst several studies have shown that edaphic variability influences species composition in nutrient-poor tropical forests, the determinants of local species distributions and, in particular, how these change from younger to mature individuals in such forests are still under debate, and have been poorly explored in tropical heath forests that are among the least fertile tropical forest ecosystems.

Methods: We investigated the influence of soil fertility and topography on a Bornean heath forest species composition, α-, β-diversity and tree size structure among size classes by recording all trees ≥ 1 cm DBH in 16 forest plots totalling 0.36 ha.

Results: Tree species distributions generally followed gradients in available Al and soil depth; α- and β-diversity were linked to soil depth, and to some extent also to pH and the H:Al ratio. In contrast, forest structural attributes (basal area and stem density) were negatively correlated with both available and total P and a wider suite of soil nutrients, although trees ≥ 10 cm DBH were positively correlated with total P.

Conclusion: Our study shows that heath forest species distribution, richness and structure is related to both edaphic and topographic characteristics and that soil acidity might have a strong influence in shaping these forests' features. Among size classes, small trees are less influenced by soil and topography, whereas the sensitivity to these variables increases with tree size. We thus highlight that multiple edaphic factors influence different aspects of tropical forest structure, including different tree life stages, and species composition.

Keywords: Al toxicity; Kabili-Sepilok Forest Reserve; kerangas; nutrient limitation; species diversity; spodosol; white sand forest.

INTRODUCTION:

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

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

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

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

METHODS:

Our experimental site is the Kabili-Sepilok Forest Reserve (KSFR), located in the Malaysian state of Sabah on the island of Borneo (5° 51' N, 117° 58' E) (Figures 1a & 1b in Supplementary information). Local bedrock consists of sandstone interbedded with occasional mudstone inclusions. The climate is equatorial with an annual precipitation of c. 3000 mm; only one month (April) receives less than 100 mm on average (Fox 1973, Nilus 2003).

We installed sixteen 15 m x 15 m plots within the *kerangas* forest of the KSFR, all at least 30 m apart from one another (Figure 1c in Supplementary information) over podzol (USDA soil classification) soils. The plots were located on a gently sloping (c. 15 °), north-facing hillside. Plot slope was determined as the mean value of four measurements of the angle from the top to the bottom of each plot using a hypsometer (Vertex IV, Haglöf, Långsele, Sweden). Plot elevation was determined with a GPS (Garmin Etrex 10, Garmin Ltd, Kansas City, KS, USA). Within all plots, trees and lianas ≥1 cm diameter at breast height (DBH; diameter measured at 1.3 m from the ground) were permanently tagged and their DBH recorded. Furthermore, we recorded the height of 25 randomly selected trees per plot spanning the tallest to the shortest tree with a hypsometer (Vertex IV, Haglöf, Långsele, Sweden) to relate the DBH to position in the canopy. Lianas were measured at 1.3 metres from their last rooting point. We then binned trees with DBH: ≥1-<2 cm, ≥2-<5 cm, ≥5-<10 cm and ≥10 cm (from now on referred as <2, 2-5, 5-10, and >10 cm DBH). Species identification was carried out by staff from Kabili-Sepilok Forest Research Centre Herbarium.

SOIL SAMPLING AND SOIL CHEMICAL ANALYSIS- Within every plot, a single soil pit of approximately 30 cm x 30 cm was dug to compare soil depths across the plots. Each plot was divided into four subplots (7.5 m x 7. 5 m) and a soil sample from the top 5 cm was collected in each subplot following removal of roots and coarse undecomposed leaves by digging a hole of approximately 10 cm x 10 cm using a knife; we collected 64 samples from the 16 plots in total. Each soil sample was split in two subsamples. The first subsample (approximately 2 g) was added to 30 ml of 1 M KCl and shaken for one hour in the field, allowed to equilibrate in a refrigerator for 18 hours, then filtered and analysed for NH_4^+ and NO_3^- on a segmented flow analyser (Astoria-Pacific A2, Clackamas, OR, USA). On the second subsample, we measured moisture content, pH, available and total nutrients, C and N as well as exchangeable acidity and Al. Soil moisture content was determined gravimetrically after drying 3 g of soil to a constant weight at 105ºC. To measure pH, 5 g of fresh soil was shaken in 12.5 ml of distilled water overnight and pH recorded with a Corning 240 pH meter. We then oven dried at 50°C and ground the remaining soil for use in macro and micro-nutrient analysis. Samples (0.25 g) were microwave-digested (Mars Xpress 5, CEM Corporation, Matthews, NC, USA) for total Al and P analysis with a solution of 8 ml HNO_3 and 2 ml deionised H_2O. Extractable soil P, Fe and Mn were extracted with a Mehlich I solution (2 g of soil shaken with 20 ml of Mehlich I solution for 5 minutes on a reciprocating shaker at 120 oscillations per minute ;Wuenscher et al. 2015). For soil exchangeable Ca, Na, Mg and K, we added 2 g of soil to 20 ml of 1 M ammonium acetate and shook for two hours using a reciprocating shaker at 120 oscillations per minute (modified from Van Reeuwijk 2002). We determined exchangeable acidity (H^+ and Al) through titration of a 1 M KCl extraction (5 g soil and 50 ml KCl shaken for one hour) with 0.02 M NaOH and 0.01 % phenolphthalein (modified from Van Reeuwijk 2002). We also measured exchangeable Al on the 1 M KCl extracts. Cation and metal concentrations were quantified using an iCAP Duo 6300 inductively coupled plasma optical emission spectrometer (Thermo Scientific, Waltham, MA, USA). Cation exchange capacity was calculated as sum of bases and exchangeable acidity. Total C and N concentrations were determined by combusting 0.15 g of soil in a Leco TruSpec CN analyser (St Joseph, MI, USA).

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

We calculated α-diversity with the Shannon-Wiener (*H'*) index, whereas for β-diversity we calculated a matrix of total dissimilarity between plots with Jaccard dissimilarity index (function *beta.pair()* of the R package *betapart*; Baselga & Orme 2012). A preliminary exploration of community composition across our plots was carried out using a detrended correspondence analysis (DCA). We then identified associations of selected species to soil variables following Shenbrot et al. (1991) who considered the position of the species centroids with respect to the standard error of the CCA ordination main centroid. If a species' centroid was located within the triplot main centroid's standard deviation, the species was labelled as a "generalist", whereas species that had a positive or negative position along an axis were considered a "specialist" (Table S3). The criterion to select species were a) their abundance among the plots using Shannon-Wiener diversity index and b) their score on the first two CCA axes. We centred and scaled the chemical, topographic variables as well as the absolute species abundances before the CCA, down-weighted the importance of rare species with the "*downweight()*" function in R package *vegan* (Oksanen 2015) and visualised the results using a CCA triplot. The significance of edaphic and topographic variables was obtained with a permutational ANOVA (999 permutations; Oksanen 2015) by terms that also report a *pseudo F* test (i.e. the ratio of constrained and unconstrained total inertia, each divided by their respective degrees of freedom). We performed a non- parametric Spearman correlation to determine correlations among α-diversity, stem density and basal area with the same chemical and topographical variables used in the CCA, whereas we performed a Mantel test (9999 permutations) to assess whether β-diversity correlated with soil or topographic variables selected with PCA. We used a Mantel test because β-diversity is presented as a dissimilarity matrix. The CCA, Spearman correlations and Mantel test were performed with all trees combined and then re-run with the four tree size classes (<2, 2-5, 5-10 and >10 cm DBH).

RESULTS:

The forest plots were characterized by a typical short-statured heath forest with a canopy height of approximately 28 m. In total, we tagged 3336 living individuals ≥ 1cm DBH. The understorey was dense with a mean of 0.73 trees 1-5 cm DBH per m^2 and 0.19 trees ≥ 5 cm DBH per m^2; lianas were scarce (a mean across 16 plots of 217 individuals per ha). Trees < 2 cm DBH had a mean height of 2.9 m (± 0.9 SD), trees 2-5 cm DBH had a mean height of 5.9 m (± 1.7), trees 5-10 cm DBH had a mean height of 11.4 m (± 2.8) and trees > 10 cm DBH had a mean height of 21.0 m (± 5.3). Throughout our plots, there was a mean of 199.7 (± 30.1) stems $plot^{-1}$ whereas basal area had a mean of 36.3 (±10.9) m^2 ha^{-1}. Relative basal area and stem density for the 20 most abundant species is shown in Table 1.

TREE DIVERSITY - In total we identified 2398 trees and shrubs to species level and 784 trees to genus, 12 to family with 142 not identified. We found 124 species within 48 families of which Myrtaceae (19 %) and Rubiaceae (14%) were most abundant. Myrtaceae had the greatest basal area (31 %), followed by Dipterocarpaceae (19 %), Clusiaceae (11 %), Euphorbiaceae (10 %) and Sapotaceae (5 %). Alpha diversity (*H'*) throughout the plots had a mean of 3.48 (±0.23 SD). The DCA (Figure S2, Supplementary information) revealed three main plot groupings that reflected plot position on the hillslope, with strong floristic similarity between plot I, J and L near the ridge crest, A, F, G, H, K and M in the middle of the hill and B, C, D, E, N, O and P at the base (Figure S1c, Supplementary information).

TOPOGRAPHY, SOIL CHEMISTRY AND PCA GRADIENT - The plots lay on a gently sloping hill with an elevation spanning 50 m between the highest and the lowest plot. Plots at the top of the slope had deeper (i.e. > 90 cm in plot I) podzolised soil than lower elevation plots (i.e. 24 cm in plot D). Generally, all plots were acidic (pH < 4) with a high concentration of total Al (mean 247 ± 28 SD $\mu g\ g^{-1}$) and a very low CEC (mean 3.75 ± 0.3 $cmol_c\ kg^{-1}$), due largely to the high exchangeable acidity. Soil C:N ratio was high (mean 22.9 ± 0.7). Low soil N was reflected by low ammonium (mean 8.5 ± 1.1 $\mu g\ g^{-1}$) and nitrate (mean 0.59 ± 0.1 $\mu g\ g^{-1}$) concentrations (Table S1). The RDA first axis was characterised by a plot slope gradient (loading on the first axis: 0.99, $p<0.05$) showing that flatter plots to have less acidic pH, and lower exchangeable acidity and CEC. The second RDA axis was characterised by plot elevation (loading on the second axis: 0.99, $p<0.01$) and, to a lesser extent, by soil depth (loading on the second axis: 0.83, $p<0.05$) showing that higher elevation plots had deeper soil with high available aluminium, low H:Al ratio and total as well as available P (Figure 1). The PCA found seven variables exhibited collinearity (total Al, exchangeable acidity and available Fe, Na, K, Mg and Ca) so these were removed along with variables with non-significant loadings. The PCA first and second axes explained 40.8 % and 28.8 % of the variability in soil properties, respectively. The first axis was related to CEC, total and available P, pH and NH_4^+ whereas the second axis was linked to the H:Al ratio, available Al and Mn and the C:N ratio. The variables that exceeded the expected average contribution to the two first principal components were CEC, total P, available Al and P, H:Al ratio and pH (Table S2, Supplementary information); these were retained for the CCA, Spearman and Mantel analyses along with topographic variables (elevation, slope) and soil depth.

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

SPECIES EDAPHIC ASSOCIATIONS AND SOIL GRADIENTS - From the CCA analyses, 51 species retained both high importance for among-plot diversity and high scores on the first two ordination axes. Of these species, 19 were associated with a low H:Al ratio and deep soil, whereas no species was associated with shallow soil and a high H:Al ratio (CCA first axis, Table S3). Furthermore, we identified another 18 species as generalists, but their association changed among the DBH classes considered. The only species that maintained a generalist species distribution among all DBH classes was *Cotylolebium melanoxylon* (Dipterocarpaceae). *Garcinia gaudichaudii* (Clusiaceae), *Gaertnera junghuhniana* (Rubiaceae), *Dracaena elliptica* (Asparagaceae), *Syzygium cauditilimbum* (Myrtaceae) and *Syzygium* sp. were generalists in at least two size classes (Table S3).

FOREST STRUCTURE, ALPHA- AND BETA- DIVERSITY - Soil heterogeneity clearly influence forest structure although the Spearman and Mantel tests, consistent with the CCA, showed different influences of soil and topographic variables among DBH classes (Tables 3 & 4). In particular, stem density and basal area decreased with high soil P. Density of all trees, and particularly those <2 cm DBH ($p<0.01$) were negatively correlated with available Mn and density and basal area of trees 5-10 cm DBH was negatively correlated with CEC, available Al and pH in addition to slope and soil depth (all $p < 0.05$).

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

The results of the Mantel test for β-diversity (Table 4) showed topography to be consistently significant among size classes, although at different degrees and with different variables. In particular, soil depth was most significant for trees 2-5 cm DBH ($p <0.01$) and 5-10 cm DBH ($p <0.001$) along with plot elevation for trees 5-10 cm DBH ($p <0.01$). Soil chemistry was only correlated with β-diversity for trees 2-5 cm DBH (H:Al ratio at $p <0.05$) and 5-10 cm DBH (pH and H:Al ratio at $p <0.05$ and $p <0.01$).

DISCUSSION:

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

The heath forest in our study site had a basal area of trees > 5 cm DBH (34.4 m^2 ha^{-1}) and stem density of trees > 5 cm DBH (1997 stems ha^{-1}), similar to other Bornean heath forests (e.g. Proctor et al. 1983; Davies & Becker 1991; Miyamoto et al. 2007). When compared to the adjacent lowland evergreen rain forest, stem density was approximately doubled (1002 stems ha^{-1}; Nilus 2003) whilst basal area was very similar (35 m^2 ha^{-1}; Nilus 2003). The most abundant families were rather different to other Bornean tropical heath forests. In comparison to the extensive study undertaken by Newbery (1991) in Brunei and Sarawak heath forests, our site lacked Myrsinaceae, Annonaceae and Chrysobalanaceae. This might be due to the limited area of our study (0.36 ha), requiring caution when comparing with results from other studies because such a small area might not be sufficient to exhaustively capture forest structure and biodiversity indices that are sample size dependent (Condit et al. 1996).

The soil (podzol) underlying our plots had a greater concentration of available P and a lower concentration of Al compared with the heath forest plots (acrisol) of Nilus (2003) in the same KSFR, suggesting that the soils in our plots had likely gone through a longer or more intense podzolisation process. During podzolisation, the soil is weathered and clay is eluviated (Bravard & Righi 1989) so Al and Fe are deposited in deeper layers of the mineral soil (Andriesse 1975), which often forms an indurated hardpan (Andriesse 1968). Usually, in tropical soils, available P is bound to Fe and Al, but the low concentration of these cations in podzols increases P availability in the soil solution (as also seen by Medina & Cuevas 1989, Coomes 1997, Metali et al. 2015).

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

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

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

DIFFERENT INFLUENCES OF EDAPHIC AND TOPOGRAPHIC VARIABLES AMONG SIZE CLASSES - The diverse influence of nutrients and topography on tree species distribution, plot α- and β-diversity as well as community structure clearly changes among size classes. In particular, trees <5 cm DBH showed weak correlations among structure, floristic variation and diversity with edaphic and topographic variables when compared to individuals > 5 cm DBH. This differential effect among size classes was documented elsewhere in Asian forests (e.g. Paoli et al. 2008, Sukri et al. 2012, Xu et al. 2016, Yang et al. 2016) and we propose this dissimilarity to be the effect of light competition. Small understorey trees are primarily limited by light availability as they are growing below the forest canopy (Coomes & Allen 2007, Cai et al. 2008) and only secondarily from other resources. Despite heath forest's low leaf area index (Vernimmen et al. 2007) and high light availability at ground level (Richards 1936), leaves of understorey saplings (Cao 2000, Cao and Booth 2001) had adaptations to low light availability when compared to leaves of the same species growing in brighter environments. Based on our results, indeed, the smallest size classes had a mean height of 2.9 m (< 2 cm DBH) and 5.7 m (2-5 cm DBH), well below the canopy height of 28 m, whereas trees 5-10 cm DBH had a mean height of c. 11 m, which might be sufficient to free them from light limitation. In this case, nutrient availability would have a greater influence on the distribution of trees >5 cm DBH. The poor correlation of tree species distribution with topo-edaphic factors for trees > 10 cm DBH might be explained by the dynamic nature of soil chemistry. In both tropical (Bauters et al. 2017) and temperate (Mueller et al. 2012; Vesterdal et al. 2008) forest plantations, changes in topsoil nutrient content and acidity have been recorded after just a few decades. Tropical trees can be as old as 1000 years (Chambers et al. 1998; Kurokawa et al. 2003) and in heath forests trees, diameter growth is slow compared to lowland evergreen forest (Nilus 2003; Brearley et al. unpublished data). Although we have no information on tree age in our forest, it is likely that trees > 10 cm DBH developed in a soil with different nutrient characteristics from the ones we see today. Alternatively, the lack of correlation between trees > 10 cm DBH species distribution and topo-edaphic variables might be due to the random mortality of big trees in our plots. It is also interesting to note that trees > 10 cm DBH show an opposite correlation of basal area with soil total P and of α-diversity with soil pH if compared to trees 5-10 cm DBH. This might highlight different strategies to overcome soil acidity and absorb nutrients between different tree life stages.

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

The cumulative number of species following the soil depth- H:Al gradient through the split size classes (18 species) instead of the CEC-pH gradient (19 species) was very similar. However, the higher score of the first CCA axis gives us a further reasonable criterion to suggest a greater influence of the depth-H:Al gradient rather than the CEC-pH gradient on species distribution. A secondary result is that, among the heath forest generalist species, we found *Gaertnera junghuhniana*, which is an Al accumulator. This characteristic might allow

G. junghuhniana to succeed throughout our heath forest site because of its capacity of attenuate H^+ toxicity through Al-rich leaf litterfall.

Our study demonstrated that there are complex interactions among topography, nutrient limitation and soil acidity that influence different aspects of forest tree species distributions and forest structure in this Bornean heath forest. These variables showed a greater importance for trees 5- 10 cm DBH, confirming a recently developed hypothesis suggesting that environmental filtering is almost absent in the early stages of plant development and become cumulative with age (Jabot et al. 2008). Generally, we suggest soil acidity to be a factor of primary importance in shaping this heath forest's floristic variation and structure. Given the high conservation value of this fragile forest type (Oktavia et al. 2015; Whitmore 1984) we underscore its susceptibility to changes in soil pH and encourage careful management and protection of heath forests.

Acknowledgements: This research was funded by Manchester Metropolitan University's Environmental Science Research Centre. We would like to thank the Sabah Biodiversity Council, the Soil Chemistry section, Ecology section and Herbarium staff from Sabah Forest Research Centre and in particular the research assistants Juanis Runcin, Jemson Jumian, Postar Miun, Spincer Sitim, Lioba Sawadon and Yun Len Lee. We are indebted to David McKendry and Graham Tinsley for the assistance in the laboratory, Yannis Kougoulous for preparing the map and Liam Trethowan, Matteo Giacomazzo and anonymous reviewers for the valuable suggestions and discussions.

Conflict of Interest: The authors declare that they have no conflict of interest.

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FIGURE 1. Redundancy analysis (RDA) biplot with the main soil chemical variables (grey) constrained by plot topography (blue) in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA ordination.

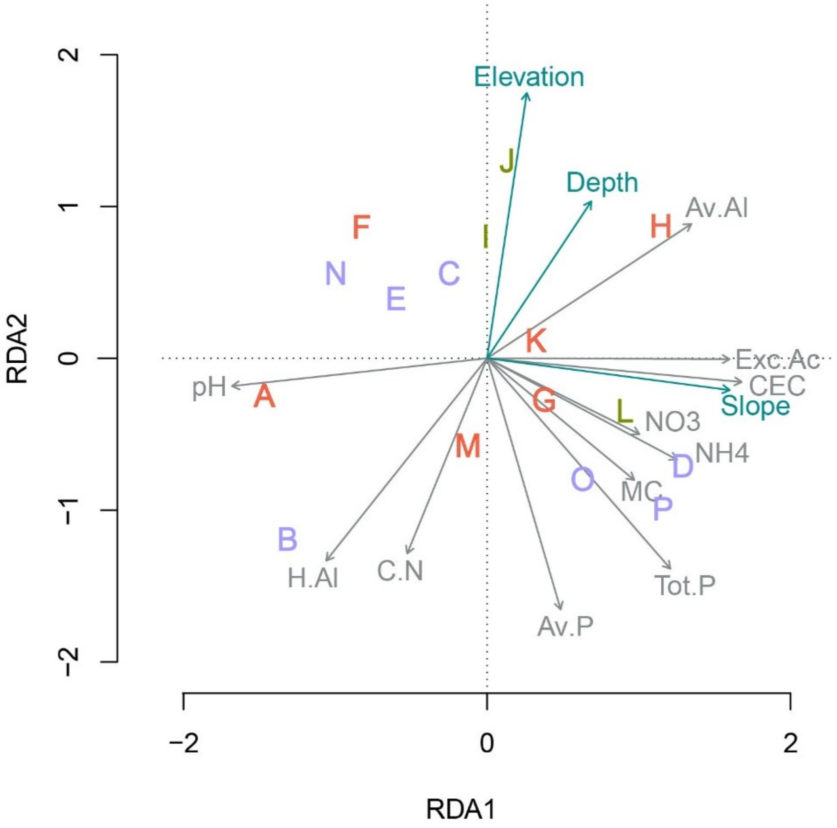

FIGURE 2. Canonical correspondence analysis (CCA) triplot with the tree species (represented as crosses) of all size classes in study plots (represented as letters) in the heath forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The species whose names are written in full are the most abundant following the Shannon-Wiener diversity index and have a significant loading on the first two ordination axes. The red circle represents the standard deviation of the ordination centroid and the colour of the name of plot reflects their grouping on the DCA ordination.

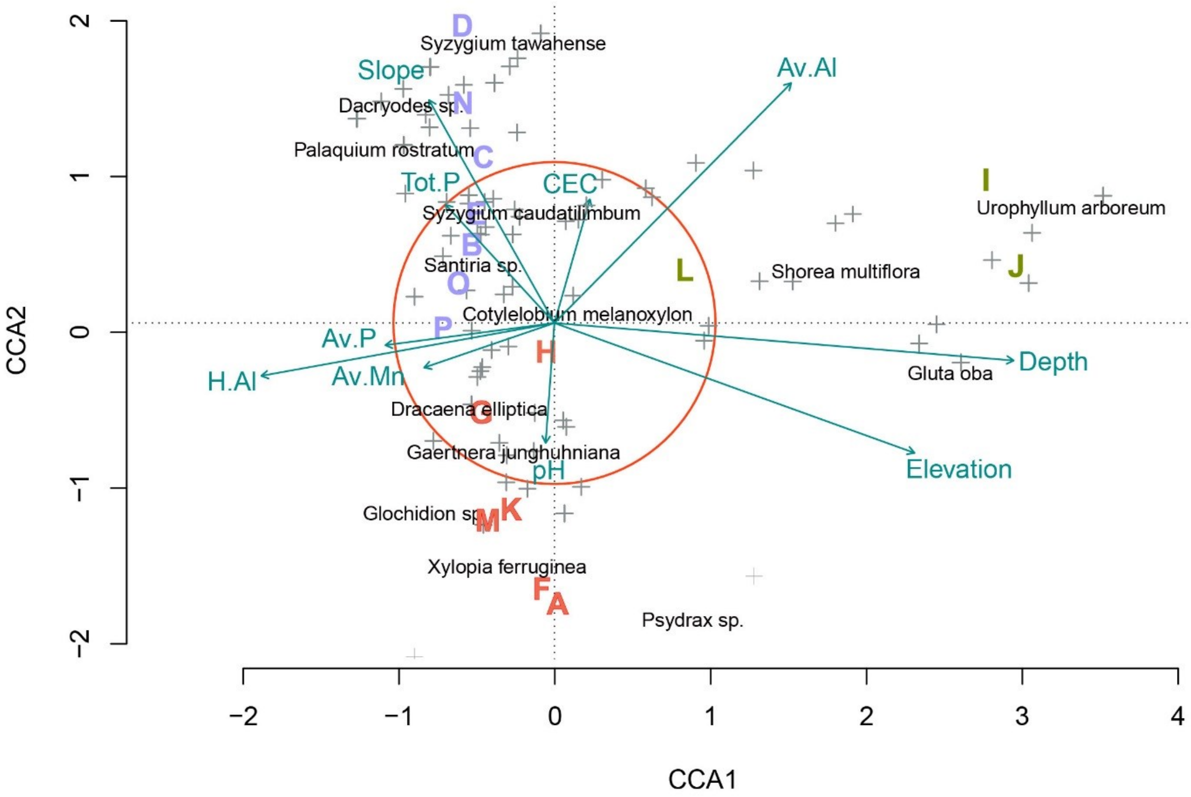

Table 1 Stem density and basal area of the 20 most common species in heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia.

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

*TABLE 2. Scores of soil and topographic variables on the first CCA axes in four tree size classes heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant values (‘***’ < 0.001, ‘**’ <0.01, ‘*’ < 0.05, ‘+’ < 0.1) are in bold.*

Size class (cm)		Available Mn	CEC	Available Al	Total P	Available P	pH	H:Al ratio	Plot slope	Soil depth	Plot elevation	Number of individuals
All	Axis1 score	-0.24	0.07	**0.44***	-0.20	-0.31	-0.02	-0.54	**-0.23**$^{+}$	**0.85***	0.67	3194
	F-stat	0.99	1.08	2.19	1.43	1.27	0.85	1.07	1.68	2.51	0.89	
<2	Axis1 score	0.21	-0.01	**-0.43***	0.25	0.34	-0.08	0.58	0.35	**-0.83***	-0.67	1413
	F-stat	0.86	0.92	2.11	1.16	1.30	0.95	1.21	1.43	1.89	0.78	
2-5	Axis1 score	-0.25	0.13	**0.41**$^{+}$	-0.10	-0.22	-0.13	-0.52	-0.11	**0.92***	0.67	1087
	F-stat	0.90	1.11	1.50	1.08	1.06	0.89	0.92	1.39	2.36	0.90	
5-10	Axis1 score	0.09	**-0.14***	**-0.35***	**0.07***	0.15	0.06	0.41	**0.19**$^{+}$	**-0.86****	**-0.63**$^{+}$	353
	F-stat	1.30	1.59	1.94	1.75	1.00	1.34	1.42	1.50	2.61	1.14	
>10	Axis1 score	-0.30	0.09	**0.53**$^{+}$	-0.19	-0.35	-0.08	-0.58	-0.06	0.83	0.64	341
	F-stat	1.05	1.06	1.69	1.05	0.80	0.71	0.86	0.97	1.74	0.73	

TABLE 3. Results of the Spearman correlation test among forest structure (i.e. basal area and stem density) and α-diversity (calculated with Shannon-Wiener diversity index) with edaphic and topographic variables in heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant values (‘***’ < 0.001, ‘**’ <0.01, ‘*’ < 0.05) are in bold.

Size classes (cm)	Variable	Available Mn	CEC	Available Al	Total P	Available P	pH	H:Al ratio	Plot slope	Soil depth	Plot elevation
All	Basal area	0.30	0.15	-0.05	**0.61***	0.37	-0.19	0.33	0.10	-0.18	-0.25
	Stem density	**-0.70****	-0.35	0.003	**-0.54***	**-0.60***	0.08	-0.28	-0.17	-0.01	0.42
	α-diversity	-0.34	-0.20	0.01	0.01	-0.19	-0.02	0.08	-0.02	-0.40	-0.02
<2	Basal area	-0.57	-0.21	0.18	-0.38	-0.42	0.01	-0.37	-0.15	0.01	0.42
	Stem density	**-0.64****	-0.15	0.26	-0.37	-0.49	-0.06	-0.45	-0.08	0.14	0.46
	α-diversity	-0.31	-0.22	0.04	-0.06	-0.13	0.01	0.08	0.05	-0.38	-0.15
2-5	Basal area	-0.27	-0.19	-0.18	-0.25	-0.20	0.03	0.09	-0.11	-0.02	0.08
	Stem density	-0.33	-0.07	-0.12	-0.09	-0.14	-0.15	0.21	0.18	-0.15	0.01
	α-diversity	-0.36	-0.17	0.06	0.03	-0.06	0.03	0.06	0.10	-0.39	-0.08
5-10	Basal area	**-0.50***	**-0.70****	**-0.49***	**-0.74*****	**-0.62****	**0.53***	-0.09	**-0.51***	-0.40	0.26
	Stem density	-0.45	**-0.82*****	**-0.65****	**-0.73****	**-0.54***	**0.69****	0.11	**-0.51***	**-0.58***	0.10
	α-diversity	-0.47	**-0.69****	-0.37	**-0.56***	-0.46	**0.66****	0.14	**-0.54***	**-0.61***	0.09
>10	Basal area	0.36	0.32	0.13	**0.69****	0.45	-0.29	0.19	0.10	-0.05	-0.15
	Stem density	0.10	0.19	-0.11	0.12	0.06	-0.09	0.05	-0.06	0.19	0.17
	α-diversity	0.02	0.44	**0.49***	0.28	-0.05	**-0.54***	-0.02	0.03	0.30	0.16

*Table 4. Results of the Mantel test between β-diversity (calculated as total dissimilarity matrix with Jaccard index) and edaphic and topographic variables in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Significant values (‘***’ < 0.001, ‘**’ <0.01, ‘*’ < 0.05) are in bold.*

Size class (cm)	Available Mn	CEC	Available Al	Total P	Available P	pH	H:Al ratio	Plot slope	Soil depth	Plot elevation
All	-0.08	-0.27	0.03	-0.10	-0.06	-0.03	0.25	0.22	0.47	**0.30***
<2	-0.09	-0.23	0.01	-0.05	-0.04	-0.01	0.20	0.21	**0.39***	**0.29***
2-5	-0.09	-0.17	0.10	-0.05	-0.09	0.09	**0.34***	**0.39***	**0.48****	0.23
5-10	-0.01	-0.03	0.14	-0.06	-0.09	**0.25***	**0.32****	**0.27***	**0.45*****	**0.32****
>10	-0.11	-0.12	0.06	-0.02	-0.07	-0.07	0.06	-0.09	0.38	**0.35***

SUPPORTING INFORMATION:

FIGURE S1. Location of the study site. A) The island of Borneo with the approximate position of the Kabili-Sepilok Forest Reserve (Sabah, Malaysia) highlighted in red. B) The Kabili-Sepilok Forest Reserve with the approximate location of the study plots highlighted and C) the study plot positions in the forest. Colour of the name of plots reflects their grouping on the DCA ordination.

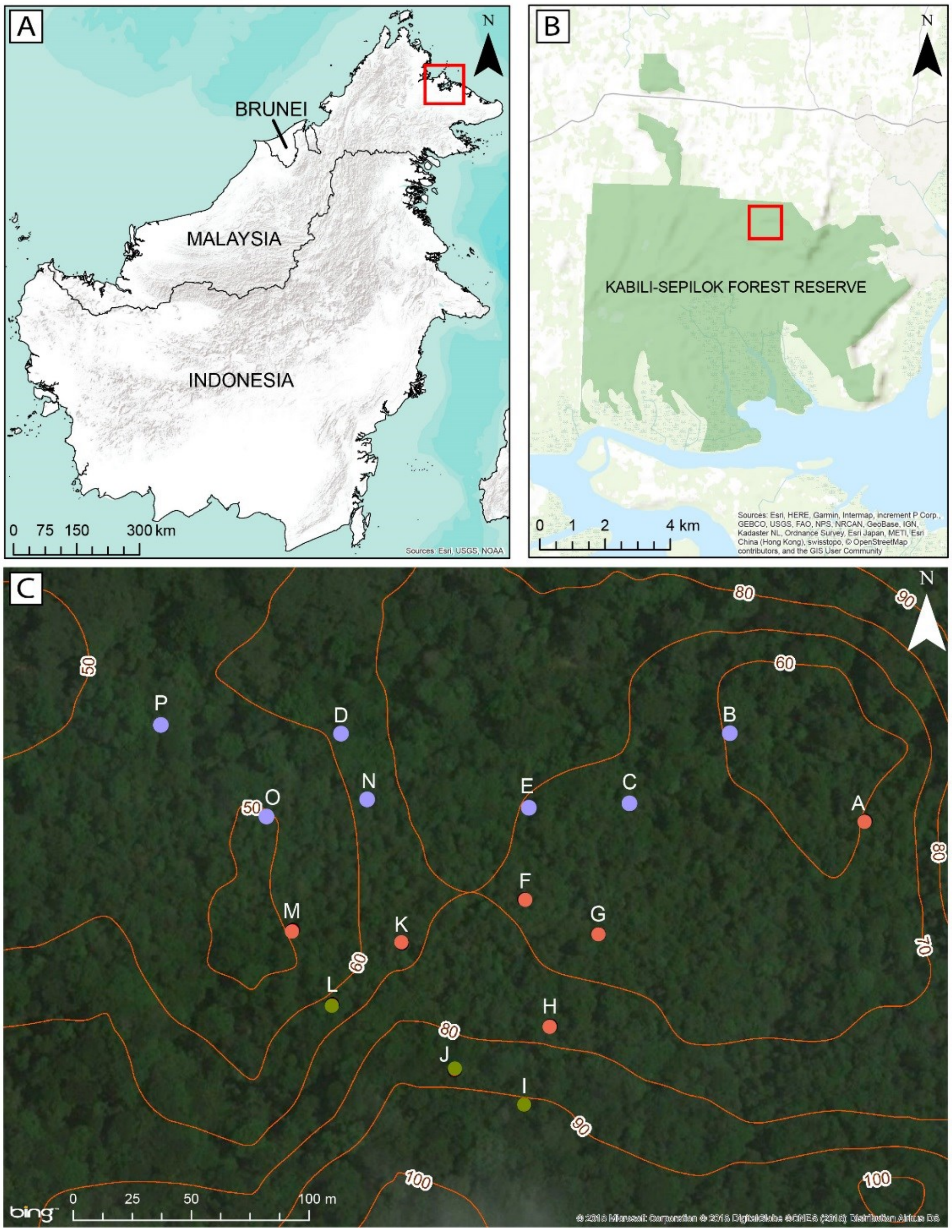

FIGURE S2. Detrended correspondence analysis (DCA) using the absolute density of the 126 species found in 16 heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA ordination.

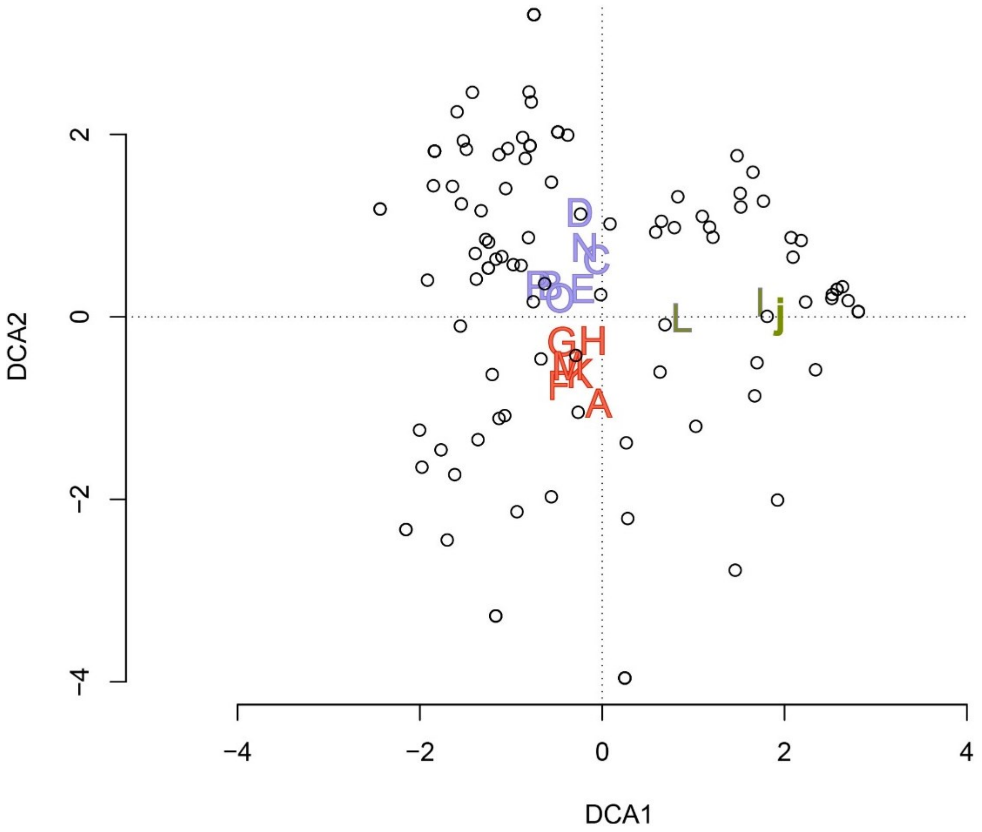

TABLE S1. Soil chemical and topographical characteristics of heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Values of chemical variables are means of four measurements whereas topographic variables consist of only one measurement per plot (excepting slope).

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

Table 1. Continued.

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

TABLE S2. Contribution on principal component analysis (PCA) first and second axis of soil chemical parameters from heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The variables that scored a contribution higher than the expected one for both dimensions are noted in bold.

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

TABLE S3. Association of the 52 most important tree species with the first (H:Al ratio-soil depth) or second (CEC-pH) CCA axes ordination of heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Columns are divided per size-class and axis considered. The species whose centroid was located within the triplot main centroid standard deviation have been called "generalists" (g in the table), whereas the species that had a positive or negative correlation with the indicated axis have been designated with a "+" or a "-", respectively. If a cell is empty it means that the individuals from that species in that size class were not important in determining inter-plot variation.

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

Memecylon sp.			+							
Mezzettia sp.			+							
Myristica sp.				+						
Myristica malaccensis					+					
Myrsine sp.		-		-						-
Palaquium rostratum		+		+		+				+
Parinari sp.		+								
Parishia insignis					+				+	
Pimeleodendron griffithianum									g	g
Psydrax sp.		-	+		+					
Rothmannia sp.	+		+							
Santiria sp.	g	g				+				
Shorea falciferoides				-						
Shorea multiflora	+						+			
Stemonurus sp.								+		
Syzygium cauditilmbum	g	g			g	g	g	g		+
Syzygium sp.	g	g			g	g			g	g
Syzygium tawahense						+				
Ternstroemia aneura					g	g				
Timonius flavescens			g	g		-				
Tristaniopsis obovata				-					g	g
Urophylum arboreum	+									
Vatica micrantha					+		+			
Xanthophyllum flavescens							+			
Xylopia ferruginea		-						-		