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1   **Soil characteristics influence species composition and forest structure**

2   **differentially among tree size classes in a Bornean heath forest**.

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25 **Abstract:**

26 *Background and aims*: Whilst several studies have shown that edaphic variability influences

27 species composition in nutrient-poor tropical forests, the determinants of local species

28 distributions and, in particular, how these change from younger to mature individuals in such

29 forests are still under debate, and have been poorly explored in tropical heath forests that are

30 among the least fertile tropical forest ecosystems.

31 *Methods*: We investigated the influence of soil fertility and topography on a Bornean heath

32 forest species composition, α-, β-diversity and tree size structure among size classes by

33 recording all trees ≥ 1 cm DBH in 16 forest plots totalling 0.36 ha.

34 *Results:* Tree species distributions generally followed gradients in available Al and soil depth;

35 α- and β-diversity were linked to soil depth, and to some extent also to pH and the H:Al ratio.

36 In contrast, forest structural attributes (basal area and stem density) were negatively correlated

37 with both available and total P and a wider suite of soil nutrients, although trees ≥ 10 cm DBH

38 were positively correlated with total P.

39 *Conclusion:* Our study shows that heath forest species distribution, richness and structure is

40 related to both edaphic and topographic characteristics and that soil acidity might have a strong

41 influence in shaping these forests' features. Among size classes, small trees are less influenced

42 by soil and topography, whereas the sensitivity to these variables increases with tree size. We

43 thus highlight that multiple edaphic factors influence different aspects of tropical forest

44 structure, including different tree life stages, and species composition.

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

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48   **INTRODUCTION:**

49   Tropical forests have the highest tree species diversity in the world (Gentry 1988; Ghazoul and

50   Sheil 2010; Whitmore 1990) but we still strive to understand how such diversity is created and

51   maintained. Several theories have been proposed to address this question such as the Janzen–

52   Connell hypothesis (Janzen 1970, Connell 1971), neutral theory (Hubbell 2001) and

53   environmental filtering (Baldeck et al. 2013). Although the drivers explained by different

54   hypotheses might operate simultaneously and might have divergent controlling factors among

55   sites, environmental factors influence tree species distribution and community composition in

56   a considerable number of studies (Wright 2002, Legendre et al. 2005). In particular, climatic

57   factors are important at continental scales (ter Steege et al. 2006, Zhang et al. 2016), whereas

58   at smaller scales, topography and soil chemistry (Clark et al. 1998, Phillips et al. 2003) have a

59   greater influence on species distributions (Condit et al. 2013, Jucker et al. 2018).

60   Most broad-scale studies of tree distribution only consider trees with a stem diameter at breast

61   height (1.3 m; DBH) greater than 5 cm or 10 cm (e.g. Slik et al. 2015), so younger trees with

62   smaller DBH (i.e. saplings) are often overlooked. In Borneo, for example, Paoli et al. (2006)

63   and Sukri et al. (2012) reported small DBH trees to be distributed irrespectively of soil nutrient

64   concentrations, whereas the distributions of larger DBH individuals were significantly

65   influenced by edaphic variables. This implies that through tree ontogeny, individuals become

66   more susceptible to the selective pressure of soil fertility so only the species adapted to

67   particular soil conditions survive and grow (Russo et al. 2005). It is noteworthy that many

68   experimental studies of forest nutrient limitation focus on seedlings and saplings grown in pots

69   with different nutrient additions (e.g. Brearley et al. 2007, Nilus et al. 2011). If selective *in situ*

70   response to soil fertility differ among size classes, then conclusions from pot bioassays must

71   be taken with caution. It is thus paramount to consider trees from smaller size classes when

72   conducting *in situ* studies of soil influences on species distribution and forest structure.

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73   Heath forests occur throughout the tropics on nutrient-poor sandy soil (podzols), with

74 vegetation physiognomy characterised by a generally stunted appearance, sclerophyllous

75 leaves and short, untapered stems (Richards 1936, Janzen 1974, Peace & Macdonald 1981,

76 Turner 1994, Becker et al. 1999, Proctor 1999, Turner et al. 2000, Kenzo et al. 2014). These

77 forests also have a high density of understorey trees, low species diversity (Anderson 1981,

78 Frasier et al. 2008), and a high degree of endemism (Garcia 2016). Heath forest distributions

79 and the characteristic features of their trees have been ascribed to low soil pH (Luizao et al.

80 2007), deficient soil nitrogen (Luizao 1994, Proctor 1999, Proctor et al. 1983, Brearley et al.

81 2011) or the interaction of these two factors (Luizao 1996). A number of studies (Brünig 1974,

82 Newbery 1991, Newbery et al. 1986) classified several typologies of Bornean heath forests

83 (known as *kerangas* locally) but few have linked heath forest species distribution to either soil

84 chemical or topographic variables. Nonetheless, these valuable studies draw some notable

85 conclusions. At Gunung Mulu (Sarawak, Malaysia), Newbery & Proctor (1984) focussed on

86 differences in soil chemistry and found species distribution to be associated with differences in

87 soil organic C and CEC, whilst Miyamoto et al. (2003) found the most abundant tree species

88 to be weakly associated with humus depth in a Central Kalimantan (Indonesia) heath forest.

89 Din et al. (2015), instead, ascribed variation in a Bruneian heath forest community to soil N

90 concentration but highlighted that other topographic and edaphic variables, not considered in

91 their study, might also have an effect on species distributions.

92   In this study, we used sixteen small plots in heath forest situated in north-east Malaysian

93 Borneo. All plots were in close proximity to one another (within an area c. 0.05 km^2) to limit

94 potential differences in bedrock and rainfall patterns and their influence on tree species

95 distribution and forest structure. In particular, in this study we asked: (1) which soil chemical

96 and topographic factors significantly influenced forest tree species composition and structure,

97 and (2) how the influence of these factors varied among tree-size classes?

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99   **METHODS**:

100   Our experimental site is the Kabili-Sepilok Forest Reserve (KSFR), located in the

101   Malaysian state of Sabah on the island of Borneo (5° 51' N, 117° 58' E) (Figures 1a & 1b in

102   Supplementary information). Local bedrock consists of sandstone interbedded with occasional

103   mudstone inclusions. The climate is equatorial with an annual precipitation of c. 3000 mm;

104   only one month (April) receives less than 100 mm on average (Fox 1973, Nilus 2003).

105   We installed sixteen 15 m x 15 m plots within the *kerangas* forest of the KSFR, all at

106   least 30 m apart from one another (Figure 1c in Supplementary information) over podzol

107   (USDA soil classification) soils. The plots were located on a gently sloping (c. 15 °), north-

108   facing hillside. Plot slope was determined as the mean value of four measurements of the angle

109   from the top to the bottom of each plot using a hypsometer (Vertex IV, Haglöf, Långsele,

110   Sweden). Plot elevation was determined with a GPS (Garmin Etrex 10, Garmin Ltd, Kansas

111   City, KS, USA). Within all plots, trees and lianas ≥1 cm diameter at breast height (DBH;

112   diameter measured at 1.3 m from the ground) were permanently tagged and their DBH recorded.

113   Furthermore, we recorded the height of 25 randomly selected trees per plot spanning the tallest

114   to the shortest tree with a hypsometer (Vertex IV, Haglöf, Långsele, Sweden) to relate the DBH

115   to position in the canopy. Lianas were measured at 1.3 metres from their last rooting point. We

116   then binned trees with DBH: ≥1-<2 cm, ≥2-<5 cm, ≥5-<10 cm and ≥10 cm (from now on

117   referred as <2, 2-5, 5-10, and >10 cm DBH). Species identification was carried out by staff

118   from Kabili-Sepilok Forest Research Centre Herbarium.

119   SOIL SAMPLING AND SOIL CHEMICAL ANALYSIS- Within every plot, a single soil pit of

120   approximately 30 cm x 30 cm was dug to compare soil depths across the plots. Each plot was

121   divided into four subplots (7.5 m x 7. 5 m) and a soil sample from the top 5 cm was collected

122   in each subplot following removal of roots and coarse undecomposed leaves by digging a hole

123   of approximately 10 cm x 10 cm using a knife; we collected 64 samples from the 16 plots in

124   total. Each soil sample was split in two subsamples. The first subsample (approximately 2 g)

125   was added to 30 ml of 1 M KCl and shaken for one hour in the field, allowed to equilibrate in

126   a refrigerator for 18 hours, then filtered and analysed for NH_4^+ and NO_3^- on a segmented flow

127   analyser (Astoria-Pacific A2, Clackamas, OR, USA). On the second subsample, we measured

128   moisture content, pH, available and total nutrients, C and N as well as exchangeable acidity

129   and Al. Soil moisture content was determined gravimetrically after drying 3 g of soil to a

130   constant weight at 105ºC. To measure pH, 5 g of fresh soil was shaken in 12.5 ml of distilled

131   water overnight and pH recorded with a Corning 240 pH meter. We then oven dried at 50°C

132   and ground the remaining soil for use in macro and micro-nutrient analysis. Samples (0.25 g)

133   were microwave-digested (Mars Xpress 5, CEM Corporation, Matthews, NC, USA) for total

134   Al and P analysis with a solution of 8 ml HNO_3 and 2 ml deionised H_2O. Extractable soil P, Fe

135   and Mn were extracted with a Mehlich I solution (2 g of soil shaken with 20 ml of Mehlich I

136   solution for 5 minutes on a reciprocating shaker at 120 oscillations per minute ;Wuenscher et

137   al. 2015). For soil exchangeable Ca, Na, Mg and K, we added 2 g of soil to 20 ml of 1 M

138   ammonium acetate and shook for two hours using a reciprocating shaker at 120 oscillations per

139   minute (modified from Van Reeuwijk 2002). We determined exchangeable acidity (H^+ and Al)

140   through titration of a 1 M KCl extraction (5 g soil and 50 ml KCl shaken for one hour) with

141   0.02 M NaOH and 0.01 % phenolphthalein (modified from Van Reeuwijk 2002). We also

142   measured exchangeable Al on the 1 M KCl extracts. Cation and metal concentrations were

143   quantified using an iCAP Duo 6300 inductively coupled plasma optical emission spectrometer

144   (Thermo Scientific, Waltham, MA, USA). Cation exchange capacity was calculated as sum of

145   bases and exchangeable acidity. Total C and N concentrations were determined by combusting

146   0.15 g of soil in a Leco TruSpec CN analyser (St Joseph, MI, USA).

147   STATISTICAL ANALYSIS- For the ordinations, we used the package *vegan* (Oksanen

148   2015) in R 3.5.1 (R Development Core Team 2009). We visualised soil differences among

149   plots by performing a redundancy analysis (RDA; significance checked with 999 permutations)

150   of soil chemistry variables constrained by topography where all the variables were centred and

151   scaled. We determined collinearity and selected the main variables that accounted for edaphic

152   variation amongst plots for the canonical correspondence (CCA) analysis with a principal

153   component analysis (PCA) following the approach of Abdi & Williams (2010). This consisted

154   of selecting the variables that exceeded the expected average contribution to the two first

155   principal components. Selected variables were then used as explanatory variables alongside

156   topographical data for CCA ordination of our tree community dataset.

157   We calculated α-diversity with the Shannon-Wiener (*H'*) index, whereas for β-diversity

158   we calculated a matrix of total dissimilarity between plots with Jaccard dissimilarity index

159   (function *beta.pair()* of the R package *betapart*; Baselga & Orme 2012). A preliminary

160   exploration of community composition across our plots was carried out using a detrended

161   correspondence analysis (DCA). We then identified associations of selected species to soil

162   variables following Shenbrot et al. (1991) who considered the position of the species centroids

163   with respect to the standard error of the CCA ordination main centroid. If a species' centroid

164   was located within the triplot main centroid's standard deviation, the species was labelled as a

165   "generalist", whereas species that had a positive or negative position along an axis were

166   considered a "specialist" (Table S3). The criterion to select species were a) their abundance

167   among the plots using Shannon-Wiener diversity index and b) their score on the first two CCA

168   axes. We centred and scaled the chemical, topographic variables as well as the absolute species

169   abundances before the CCA, down-weighted the importance of rare species with the

170   "*downweight()*" function in R package *vegan* (Oksanen 2015) and visualised the results using

171   a CCA triplot. The significance of edaphic and topographic variables was obtained with a

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172   permutational ANOVA (999 permutations; Oksanen 2015) by terms that also report a *pseudo*

173   *F* test (i.e. the ratio of constrained and unconstrained total inertia, each divided by their

174   respective degrees of freedom). We performed a non- parametric Spearman correlation to

175   determine correlations among α-diversity, stem density and basal area with the same chemical

176   and topographical variables used in the CCA, whereas we performed a Mantel test (9999

177   permutations) to assess whether β-diversity correlated with soil or topographic variables

178   selected with PCA. We used a Mantel test because β-diversity is presented as a dissimilarity

179   matrix. The CCA, Spearman correlations and Mantel test were performed with all trees

180   combined and then re-run with the four tree size classes (<2, 2-5, 5-10 and >10 cm DBH).

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182   **RESULTS:**

183   The forest plots were characterized by a typical short-statured heath forest with a canopy height

184   of approximately 28 m. In total, we tagged 3336 living individuals ≥ 1cm DBH. The

185   understorey was dense with a mean of 0.73 trees 1-5 cm DBH per m^2 and 0.19 trees ≥ 5 cm

186   DBH per m^2; lianas were scarce (a mean across 16 plots of 217 individuals per ha). Trees < 2

187   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

188   m (± 1.7), trees 5-10 cm DBH had a mean height of 11.4 m (± 2.8) and trees > 10 cm DBH had

189   a mean height of 21.0 m (± 5.3). Throughout our plots, there was a mean of 199.7 (± 30.1)

190   stems $plot^{-1}$ whereas basal area had a mean of 36.3 (±10.9) $m^2 ha^{-1}$. Relative basal area and stem

191   density for the 20 most abundant species is shown in Table 1.

192   TREE DIVERSITY - In total we identified 2398 trees and shrubs to species level and 784

193   trees to genus, 12 to family with 142 not identified. We found 124 species within 48 families

194   of which Myrtaceae (19 %) and Rubiaceae (14%) were most abundant. Myrtaceae had the

195   greatest basal area (31 %), followed by Dipterocarpaceae (19 %), Clusiaceae (11 %),

196   Euphorbiaceae (10 %) and Sapotaceae (5 %). Alpha diversity (H') throughout the plots had a

197   mean of 3.48 (±0.23 SD). The DCA (Figure S2, Supplementary information) revealed three

198   main plot groupings that reflected plot position on the hillslope, with strong floristic similarity

199   between plot I, J and L near the ridge crest, A, F, G, H, K and M in the middle of the hill and

200   B, C, D, E, N, O and P at the base (Figure S1c, Supplementary information).

201   TOPOGRAPHY, SOIL CHEMISTRY AND PCA GRADIENT - The plots lay on a gently sloping

202   hill with an elevation spanning 50 m between the highest and the lowest plot. Plots at the top

203   of the slope had deeper (i.e. > 90 cm in plot I) podzolised soil than lower elevation plots (i.e.

204   24 cm in plot D). Generally, all plots were acidic (pH < 4) with a high concentration of total

205   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

206   to the high exchangeable acidity. Soil C:N ratio was high (mean 22.9 ± 0.7). Low soil N was

207   reflected by low ammonium (mean 8.5 ± 1.1 $\mu g\ g^{-1}$) and nitrate (mean 0.59 ± 0.1 $\mu g\ g^{-1}$)

208   concentrations (Table S1). The RDA first axis was characterised by a plot slope gradient

209   (loading on the first axis: 0.99, $p<0.05$) showing that flatter plots to have less acidic pH, and

210   lower exchangeable acidity and CEC. The second RDA axis was characterised by plot

211   elevation (loading on the second axis: 0.99, $p<0.01$) and, to a lesser extent, by soil depth

212   (loading on the second axis: 0.83, $p<0.05$) showing that higher elevation plots had deeper soil

213   with high available aluminium, low H:Al ratio and total as well as available P (Figure 1). The

214   PCA found seven variables exhibited collinearity (total Al, exchangeable acidity and available

215   Fe, Na, K, Mg and Ca) so these were removed along with variables with non-significant

216   loadings. The PCA first and second axes explained 40.8 % and 28.8 % of the variability in soil

217   properties, respectively. The first axis was related to CEC, total and available P, pH and NH_4^+

218   whereas the second axis was linked to the H:Al ratio, available Al and Mn and the C:N ratio.

219   The variables that exceeded the expected average contribution to the two first principal

220   components were CEC, total P, available Al and P, H:Al ratio and pH (Table S2,

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221   Supplementary information); these were retained for the CCA, Spearman and Mantel analyses

222   along with topographic variables (elevation, slope) and soil depth.

223   SPECIES DISTRIBUTION RELATED TO ENVIRONMENTAL VARIABLES - From the CCA, we

224   can see that species followed the first two axes of the ordination in agreement with topography

225   and soil chemistry (Figure 2). Among the different tree DBH classes, soil chemistry and

226   topography together explained between 68 % and 76 % of the floristic variation. In particular,

227   soil depth and available Al were important for most size classes of trees but were less important

228   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

229   depth, respectively). Floristic variation in trees 5 - 10 cm DBH was influenced by CEC (X^2 =

230   0.21, p < 0.05) and total soil P (X^2 = 0.23, p < 0.05; Table 2). From the CCA ordination, we

231   therefore identified two soil gradients along which species appear to be distributed. The first

232   was the H:Al ratio-soil depth gradient and the second was the CEC-pH gradient (Figure 2).

233   Although the CCA triplot's first axis was mainly driven by the H:Al ratio and soil depth

234   gradients, available Al achieved high loadings on both the first (0.44; Table 2) and second axes

235   (0.44) stressing the importance that Al retains in influencing species distributions.

236   SPECIES EDAPHIC ASSOCIATIONS AND SOIL GRADIENTS - From the CCA analyses, 51

237   species retained both high importance for among-plot diversity and high scores on the first two

238   ordination axes. Of these species, 19 were associated with a low H:Al ratio and deep soil,

239   whereas no species was associated with shallow soil and a high H:Al ratio (CCA first axis,

240   Table S3). Furthermore, we identified another 18 species as generalists, but their association

241   changed among the DBH classes considered. The only species that maintained a generalist

242   species distribution among all DBH classes was *Cotylolebium melanoxylon* (Dipterocarpaceae).

243   *Garcinia gaudichaudii* (Clusiaceae), *Gaertnera junghuhniana* (Rubiaceae), *Dracaena elliptica*

244   (Asparagaceae), *Syzygium cauditilimbum* (Myrtaceae) and *Syzygium* sp. were generalists in at

245   least two size classes (Table S3).

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246   FOREST STRUCTURE, ALPHA- AND BETA- DIVERSITY - Soil heterogeneity clearly

247   influence forest structure although the Spearman and Mantel tests, consistent with the CCA,

248   showed different influences of soil and topographic variables among DBH classes (Tables 3 &

249   4). In particular, stem density and basal area decreased with high soil P. Density of all trees,

250   and particularly those <2 cm DBH ($p<0.01$) were negatively correlated with available Mn and

251   density and basal area of trees 5-10 cm DBH was negatively correlated with CEC, available Al

252   and pH in addition to slope and soil depth (all $p < 0.05$).

253   A similar suite of elements also influenced α-diversity but correlations with soil

254   chemistry and topography were mostly found in trees 5-10 cm DBH (CEC and pH: $p <0.01$;

255   total P, slope and depth: $p <0.05$) whereas in trees > 10 cm DBH α-diversity correlated only

256   with available Al and pH ($p <0.05$).

257   The results of the Mantel test for β-diversity (Table 4) showed topography to be

258   consistently significant among size classes, although at different degrees and with different

259   variables. In particular, soil depth was most significant for trees 2-5 cm DBH ($p <0.01$) and 5-

260   10 cm DBH ($p <0.001$) along with plot elevation for trees 5-10 cm DBH ($p <0.01$). Soil

261   chemistry was only correlated with β-diversity for trees 2-5 cm DBH (H:Al ratio at $p <0.05$)

262   and 5-10 cm DBH (pH and H:Al ratio at $p <0.05$ and $p <0.01$).

263

264   **DISCUSSION:**

265   Nutrient-poor tropical forests support high tree species diversity but the relative

266   influence of environmental factors on these forests' floristic variability still needs further

267   research. Our study site showed a typical heath forest floristic diversity, forest structure, and

268   soil chemistry. We showed that soil acidity, topography and nutrient limitation act in concert

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269   to shape species distribution, structure and diversity of the Kabili-Sepilok heath forest

270   ecosystem. The influences of these topo-edaphic factors change among size classes.

271   The heath forest in our study site had a basal area of trees > 5 cm DBH (34.4 m^2 ha^{-1})

272   and stem density of trees > 5 cm DBH (1997 stems ha^{-1}), similar to other Bornean heath forests

273   (e.g. Proctor et al. 1983; Davies & Becker 1991; Miyamoto et al. 2007). When compared to

274   the adjacent lowland evergreen rain forest, stem density was approximately doubled (1002

275   stems ha^{-1}; Nilus 2003) whilst basal area was very similar (35 m^2 ha^{-1}; Nilus 2003). The most

276   abundant families were rather different to other Bornean tropical heath forests. In comparison

277   to the extensive study undertaken by Newbery (1991) in Brunei and Sarawak heath forests, our

278   site lacked Myrsinaceae, Annonaceae and Chrysobalanaceae. This might be due to the limited

279   area of our study (0.36 ha), requiring caution when comparing with results from other studies

280   because such a small area might not be sufficient to exhaustively capture forest structure and

281   biodiversity indices that are sample size dependent (Condit et al. 1996).

282   The soil (podzol) underlying our plots had a greater concentration of available P and a

283   lower concentration of Al compared with the heath forest plots (acrisol) of Nilus (2003) in the

284   same KSFR, suggesting that the soils in our plots had likely gone through a longer or more

285   intense podzolisation process. During podzolisation, the soil is weathered and clay is eluviated

286   (Bravard & Righi 1989) so Al and Fe are deposited in deeper layers of the mineral soil

287   (Andriesse 1975), which often forms an indurated hardpan (Andriesse 1968). Usually, in

288   tropical soils, available P is bound to Fe and Al, but the low concentration of these cations in

289   podzols increases P availability in the soil solution (as also seen by Medina & Cuevas 1989,

290   Coomes 1997, Metali et al. 2015).

291   INFLUENCE OF SOIL AND TOPOGRAPHY ON FLORISTIC DISTRIBUTION, DIVERSITY AND

292   FOREST STRUCTURE - Our results show that topography and soil chemistry have a strong

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293   influence on floristic distribution. Generally, it appears that, within our heath forest, the

294   variation in species composition is driven by both edaphic and topographic variables, in

295   particular available Al concentration and soil depth. On the other hand, soil nutrients (CEC and

296   total P) along with soil pH play a major role only for tree (5 - 10 cm DBH) α- diversity, whereas

297   an interaction of soil acidity, Al and topographic factors influences β-diversity. As Al is an

298   important constituent of soil acidity, we argue that, in combination with its ratio with H^+, is

299   important in shaping heath forest species composition as hypothesised by Proctor (1999). It is

300   noteworthy that available Al covaries with soil depth and elevation and is directly linked to a

301   decrease in the H:Al ratio. In Brazilian cerrado ecosystems, a similar pattern of increasing Al

302   with elevation was observed to underpin species composition (Guidão et al. 2002, Abreu et al.

303   2012, Soares et al. 2015, Silva et al. 2016). Aluminium is abundant in clay-rich acidic soils and,

304   together with H^+, is toxic for plants. Along a soil gradient with different clay content (e.g.

305   ultisol to podzol) Al is likely to create a species distribution gradient based on species' Al

306   tolerance (Kidd & Proctor, 2001). On the other hand, within our sandy podzol, the lack of Al-

307   rich clay means low soil Al concentrations (as seen in the plots at the base of the slope). In such

308   cases, a beneficial role of soil Al would be to reduce H^+ toxicity through its buffering action

309   (Proctor 1999, Luizao 1996, Luizao et al. 2007). Hydrogen is more detrimental to plants than

310   Al - experimental Al addition, for instance, enhanced growth of temperate (Kinraide 1993,

311   Kidd & Proctor 2000) and tropical plants (Osaki et al., 1997) adapted to an extremely acidic

312   Al-poor soil. In some acidic and sandy soils, it could be argued that plants accumulate Al in

313   leaves to buffer H^+ toxicity through their litterfall with Al accumulators composing more than

314   30 % of the biomass in e.g. Brazilian cerrado (Goodland & Pollard 1973, Haridasan 1982,

315   2008). In our plots, *Gaertnera junghuhniana* (Rubiaceae) the most common species with a

316   generalist distribution, is an Al accumulator (i.e. has a leaf Al concentration higher than 1000

317    $\mu g\ g^{-1}$; Sellan 2019). This further supports the importance of soil acidity, and Al, as a driver of

318   species distribution in our study site. On the other hand, considering the emphasis given to low

319   N availability in some studies as a theory to explain heath forest characters (e.g. see Vernimmen

320   et al. 2013), N was too low to significantly explain differences among plots and thus was

321   excluded from the analysis post PCA variable selection.

322   Soil P (available and total) influenced species richness of our plots for trees 5 - 10 cm

323   DBH and structure (i.e. basal area and stem density) of trees > 5 cm DBH. Surprisingly, plots

324   with high soil P concentrations had lower basal area and stem density (although this was largely

325   driven by smaller trees < 10 cm DBH). We would have expected the contrary as P is often

326   considered to be limiting in lowland rain forest (Cleveland et al. 2011; LeBauer and Treseder

327   2008), and evidence suggests that it might also be limiting in heath forest (Dent et al., 2006).

328   High available P concentrations are found in plots with low exchangeable Al (as discussed

329   above) where soil acidity is likely dominated by H^+ rather than Al (Proctor 1999). So, the

330   negative relationship among soil P and forest structure is possibly due to H^+ toxicity rather than

331   to soil P *per se*.

332   Interestingly, soil depth is a strong selective force for the distribution of trees 5 - 10 cm

333   DBH with species as *Madhuca pallida* (Sapotaceae), *Shorea multiflora* (Dipterocarpaceae) and

334   *Gluta oba* (Anacardiaceae) associated with deeper soil. This result seems to agree with the

335   hypothesis proposed by Newbery (1991), and supported by Grainger & Becker (2001), that

336   heath forests are composed of two ecophysiological and structural guilds: one with dominant

337   deep-rooted trees and one with small shallow-rooted trees. Alternatively, soil depth is possibly

338   important because a deeper soil has a greater volume and thus holds more nutrients per area

339   unit.

340   DIFFERENT INFLUENCES OF EDAPHIC AND TOPOGRAPHIC VARIABLES AMONG SIZE CLASSES - The

341   diverse influence of nutrients and topography on tree species distribution, plot α- and β-

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342 diversity as well as community structure clearly changes among size classes. In particular, trees

343 <5 cm DBH showed weak correlations among structure, floristic variation and diversity with

344 edaphic and topographic variables when compared to individuals > 5 cm DBH. This differential

345 effect among size classes was documented elsewhere in Asian forests (e.g. Paoli et al. 2008,

346 Sukri et al. 2012, Xu et al. 2016, Yang et al. 2016) and we propose this dissimilarity to be the

347 effect of light competition. Small understorey trees are primarily limited by light availability

348 as they are growing below the forest canopy (Coomes & Allen 2007, Cai et al. 2008) and only

349 secondarily from other resources. Despite heath forest's low leaf area index (Vernimmen et al.

350 2007) and high light availability at ground level (Richards 1936), leaves of understorey

351 saplings (Cao 2000, Cao and Booth 2001) had adaptations to low light availability when

352 compared to leaves of the same species growing in brighter environments. Based on our results,

353 indeed, the smallest size classes had a mean height of 2.9 m (< 2 cm DBH) and 5.7 m (2-5 cm

354 DBH), well below the canopy height of 28 m, whereas trees 5-10 cm DBH had a mean height

355 of c. 11 m, which might be sufficient to free them from light limitation. In this case, nutrient

356 availability would have a greater influence on the distribution of trees >5 cm DBH. The poor

357 correlation of tree species distribution with topo-edaphic factors for trees > 10 cm DBH might

358 be explained by the dynamic nature of soil chemistry. In both tropical (Bauters et al. 2017) and

359 temperate (Mueller et al. 2012; Vesterdal et al. 2008) forest plantations, changes in topsoil

360 nutrient content and acidity have been recorded after just a few decades. Tropical trees can be

361 as old as 1000 years (Chambers et al. 1998; Kurokawa et al. 2003) and in heath forests trees,

362 diameter growth is slow compared to lowland evergreen forest (Nilus 2003; Brearley et al.

363 unpublished data). Although we have no information on tree age in our forest, it is likely that

364 trees > 10 cm DBH developed in a soil with different nutrient characteristics from the ones we

365 see today. Alternatively, the lack of correlation between trees > 10 cm DBH species distribution

366 and topo-edaphic variables might be due to the random mortality of big trees in our plots. It is

367   also interesting to note that trees > 10 cm DBH show an opposite correlation of basal area with

368   soil total P and of α-diversity with soil pH if compared to trees 5-10 cm DBH. This might

369   highlight different strategies to overcome soil acidity and absorb nutrients between different

370   tree life stages.

371

372   SOIL-SPECIES ASSOCIATIONS - We acknowledge that our study plots are small but,

373   comparing our results with existing literature, we found them to be consistent with other studies.

374   For example, Baltzer et al. (2005) found *Shorea multiflora* to be a sandstone forest (humult

375   ultisol) specialist in the same Kabili-Sepilok Forest Reserve. Our results thus agree with Baltzer

376   et al. (2005) because sandstone soil is higher in Al than heath forest and we found *S. multiflora*

377   to be more common in soil with low H:Al ratio, i.e. a soil with high available Al. The same is

378   applicable to the results of Potts et al. (2002) who found *Pimelodendron griffithianum*

379   (Euphorbiaceae) to be a generalist, *Vatica micrantha* (Dipterocarpaceae) and *Mangifera* sp.

380   (Anacardiaceae) to favour Al- rich humult ultisols and two *Diospyros* (Ebenaceae) species to

381   be specialists in udult ultisols (more nutrient rich soil). The dispersion of species around the

382   ordination centroid in our analysis revealed that more than half of the species considered in this

383   analysis followed a soil gradient (i.e. 16 species out of 23, considering all size classes grouped

384   together).

385   The cumulative number of species following the soil depth- H:Al gradient through the

386   split size classes (18 species) instead of the CEC-pH gradient (19 species) was very similar.

387   However, the higher score of the first CCA axis gives us a further reasonable criterion to

388   suggest a greater influence of the depth-H:Al gradient rather than the CEC-pH gradient on

389   species distribution. A secondary result is that, among the heath forest generalist species, we

390   found *Gaertnera junghuhniana*, which is an Al accumulator. This characteristic might allow

16

391   *G. junghuhniana* to succeed throughout our heath forest site because of its capacity of attenuate

392   H^+ toxicity through Al-rich leaf litterfall.

393

394   Our study demonstrated that there are complex interactions among topography, nutrient

395   limitation and soil acidity that influence different aspects of forest tree species distributions

396   and forest structure in this Bornean heath forest. These variables showed a greater importance

397   for trees 5- 10 cm DBH, confirming a recently developed hypothesis suggesting that

398   environmental filtering is almost absent in the early stages of plant development and become

399   cumulative with age (Jabot et al. 2008). Generally, we suggest soil acidity to be a factor of

400   primary importance in shaping this heath forest's floristic variation and structure. Given the

401   high conservation value of this fragile forest type (Oktavia et al. 2015; Whitmore 1984) we

402   underscore its susceptibility to changes in soil pH and encourage careful management and

403   protection of heath forests.

412

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

414

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631　　　　　*FIGURE 1. Redundancy analysis (RDA) biplot with the main soil chemical variables*

632　　*(grey) constrained by plot topography (blue) in the heath forest of the Kabili-Sepilok Forest*

633　　*Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA*

634　　*ordination.*
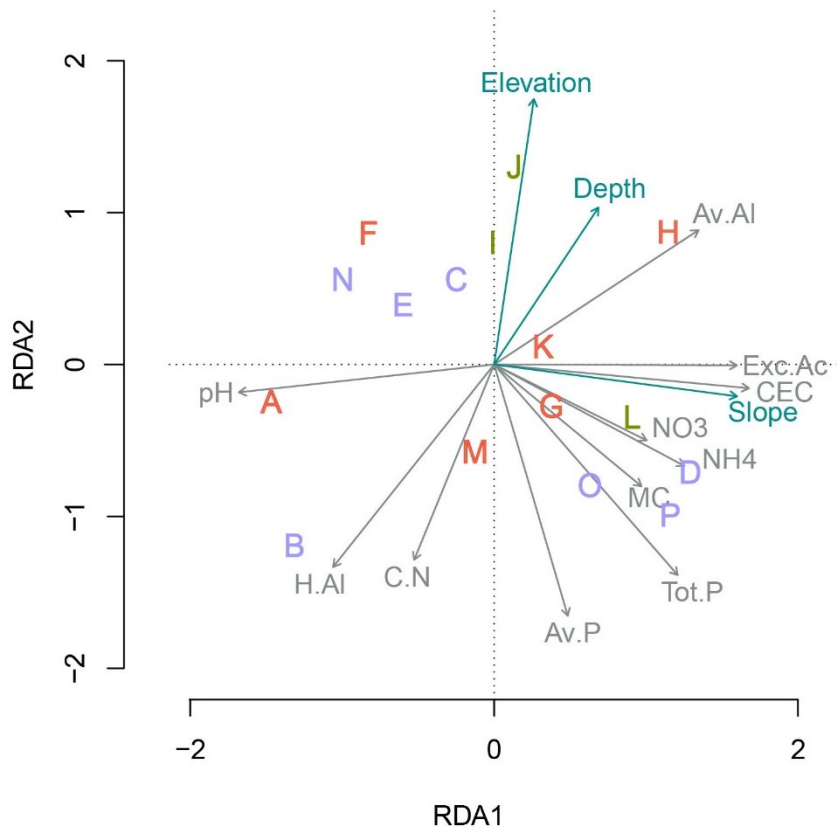
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637   *FIGURE 2. Canonical correspondence analysis (CCA) triplot with the tree species*

638   *(represented as crosses) of all size classes in study plots (represented as letters) in the heath*

639   *forest of the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. The species whose names are*

640   *written in full are the most abundant following the Shannon-Wiener diversity index and have*

641   *a significant loading on the first two ordination axes. The red circle represents the standard*

642   *deviation of the ordination centroid and the colour of the name of plot reflects their grouping*

643   *on the DCA ordination.*
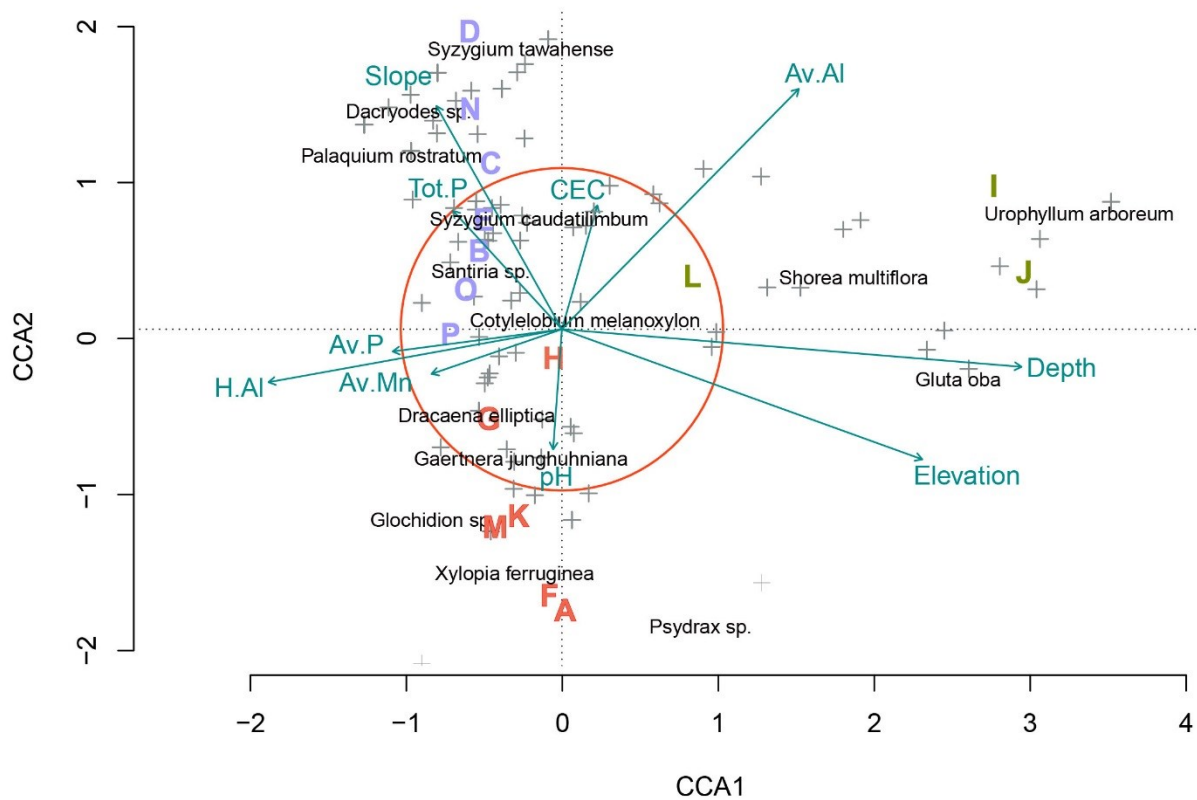
644

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.
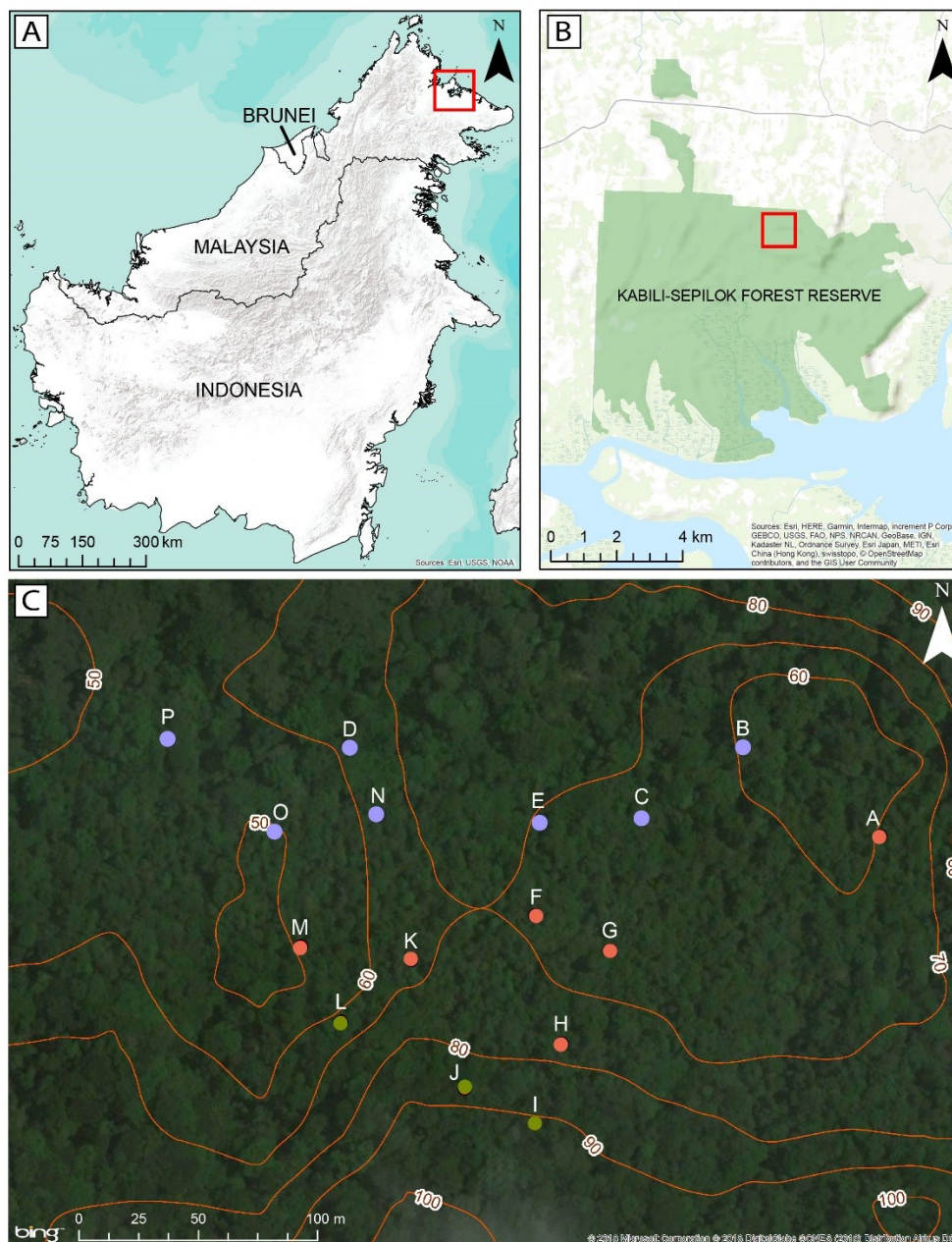
FIGURE S2. Detrended correspondence analysis (DCA) using the absolute density of the 126 species found in 16 heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Colour of the name of plots reflects their grouping on the DCA ordination.
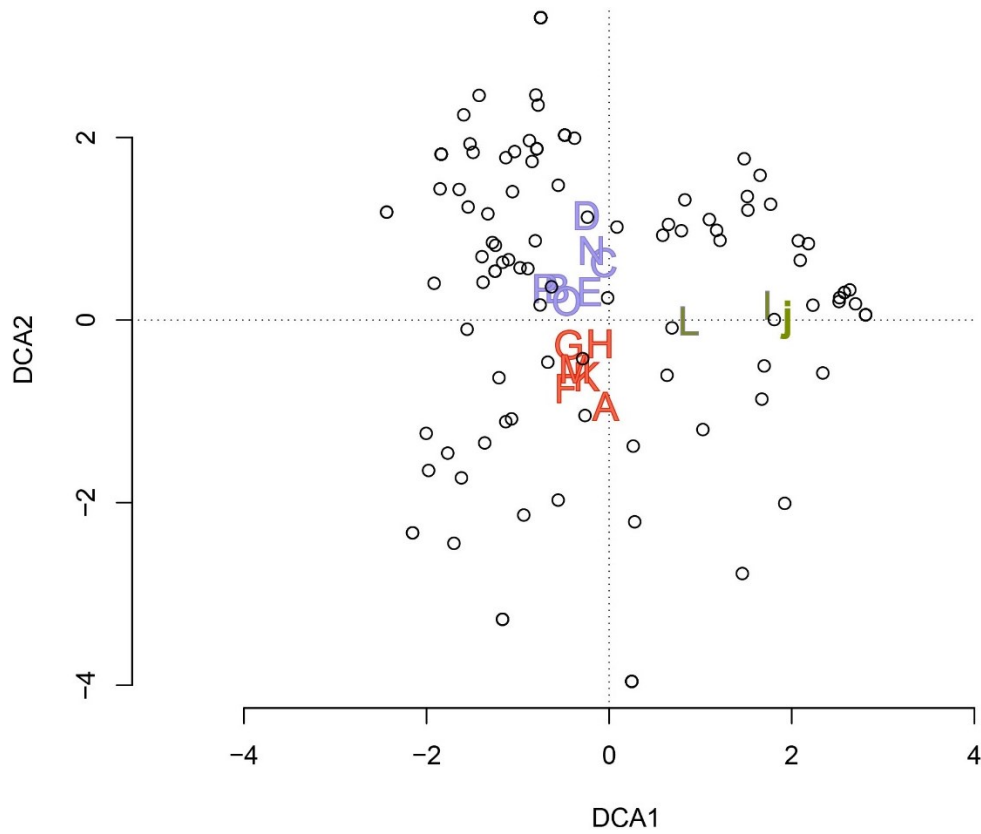
TABLE S1. Soil chemical and topographical characteristics of heath forest plots in the Kabili-Sepilok Forest Reserve, Sabah, Malaysia. Values

of chemical variables are means of four measurements whereas topographic variables consist of only one measurement per plot (excepting

slope).

Plot	pH (H$_2$O)	Moisture Content (%)	Exchangeable Acidity	Aluminium	H:Al Ratio	Total Al	P	Available P	Mn	Fe
			cmol$_c$ kg^{-1}					µg g^{-1}		
A	3.89	5.37	1.51	0.18	7.7	178.7	40.8	10.7	2.4	20.2
B	4.05	8.74	2.02	0.32	9.1	148.6	61.1	21.5	6.3	18.1
C	3.75	5.79	2.42	0.55	3.5	216.8	42.5	10.7	0.9	33.1
D	3.56	13.90	4.26	0.76	4.7	271.8	70.2	16.6	2.3	29.7
E	3.68	6.67	2.10	0.37	5.2	153.0	36.7	8.2	0.9	17.8
F	3.82	4.00	1.47	0.26	4.6	106.5	28.2	8.6	0.7	14.4
G	3.63	9.40	2.77	0.42	3.4	287.9	59.3	15.4	4.2	42.8
H	3.56	6.49	4.31	1.13	2.8	365.1	56.9	12.4	1.1	33.7
I	3.80	6.11	2.18	0.68	2.2	402.5	42.8	10.7	1.1	44.6
J	3.72	7.02	2.53	0.80	2.8	535.0	38.8	9.5	1.2	42.3
K	3.68	5.80	2.36	0.63	2.9	260.4	57.6	15.4	1.0	22.5
L	3.43	13.60	3.74	0.60	5.3	285.9	70.1	15.2	1.3	21.5
M	3.74	4.62	2.50	0.40	5.2	173.7	54.2	19.8	2.7	18.2
N	3.82	6.20	1.64	0.31	4.7	133.8	38.1	9.4	0.7	15.5
O	3.64	7.04	2.28	0.39	4.9	209.0	65.6	18.1	3.0	22.7
P	3.58	8.43	2.77	0.47	5.2	236.3	76.2	22.9	6.2	28.8

Table 1. Continued.

Plot	Exchangeable				CEC	NH$_4^+$	NO$_3^-$	C:N Ratio	Plot ASL	Plot Slope	Soil Depth
	Ca	K	Mg	Na							
	cmol$_c$ kg^{-1}					µg g^{-1}			m	%	cm
A	0.30	0.20	0.61	0.12	2.37	4.9	0.0	26.6	55	9.5	23
B	0.13	0.07	0.11	0.03	3.59	4.2	0.0	26.3	49	12.3	19
C	0.16	0.12	0.37	0.07	3.36	9.6	0.2	24.5	69	13.7	23
D	0.14	0.19	0.44	0.08	6.03	11.7	1.1	25.2	53	14.6	24
E	0.14	0.13	0.32	0.05	2.59	6.4	0.4	23.7	50	14.8	27
F	0.16	0.10	0.21	0.04	2.00	6.2	0.6	17.7	73	13.3	29
G	0.19	0.20	0.38	0.09	4.68	10.0	0.8	26.0	66	13.1	32
H	0.21	0.17	0.82	0.23	5.67	5.4	0.5	19.5	64	14.1	39
I	0.16	0.13	0.35	0.07	2.64	7.8	0.8	21.7	83	13.3	100
J	0.13	0.20	0.33	0.12	3.11	7.6	0.2	16.7	74	12.8	49
K	0.19	0.18	0.50	0.07	3.47	11.6	0.7	24.6	61	14.3	39
L	0.17	0.37	0.75	0.09	6.00	9.8	0.0	21.9	64	14.8	48
M	0.34	0.17	0.58	0.06	3.96	8.9	0.8	27.0	60	14.9	32
N	0.12	0.12	0.23	0.05	2.25	1.6	0.3	21.7	51	14.1	21
O	0.49	0.20	0.65	0.07	3.66	9.0	2.0	22.7	42	15.8	27
P	0.51	0.20	0.78	0.07	4.62	20.8	1.1	21.5	48	15.4	33

TABLE 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.	+						+		+	

Species										
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		-						-		