3

4

5

6   **Floristics of forests across low nutrient soils in Sulawesi, Indonesia**

7

8

9

10   **Liam A. Trethowan [1,2], Wolf L. Eiserhardt [2,3], Deden Girmansyah [4], Endang Kintamani**

11   **[4], Timothy M. A. Utteridge [2], Francis Q. Brearley [1]**

12   [1] Manchester Metropolitan University, Manchester, United Kingdom.

13   [2] Royal Botanic Gardens Kew, London, United Kingdom.

14   [3] Aarhus University, Aarhus, Denmark.

15   [4] Herbarium Bogoriense, Indonesian Institute of Sciences, Cibinong, Indonesia.

16   **Correspondence:** Liam Trethowan, Herbarium, Royal Botanic Gardens Kew, London,

17   United Kingdom. Email: l.trethowan@kew.org

18

19

20

21

22

24 **Abstract**

25 The island of Sulawesi formed from the joining of proto-islands roughly three million years

26 ago. Regions of zoological endemism, corresponding to the proto-islands, have been

27 reported. Sulawesi's tree communities, however, remain poorly documented. In better-

28 studied tropical regions, soil types similar to those found in Sulawesi often have distinctive

29 tree communities. To gather data on Sulawesi's tree communities we established ten (0.25

30 ha) plots on four soil types across three regions. We documented diversity, endemism,

31 dominance and species composition. Linear models of species composition showed greater

32 influence of geographic distance rather than soil, and no relationship with climate. This

33 suggests that the legacy of Sulawesi's formation may have influenced tree communities more

34 so than the soil types we sampled. Most of our plots were on stressful soil types making it

35 difficult to conclude on the importance of edaphic specialization in the Sulawesi tree flora.

36 The lack of climatic effects reflects Sulawesi's position within the wet tropics where the

37 small climatic differences are unlikely to have large influence on tree communities.

38

39 *Key words*: biogeography; Indonesia; macroecology; serpentine; ultramafic; Wallacea.

40

41 The data in this study are openly available at

42 https://figshare.com/authors/Liam_Trethowan/8268603

1. INTRODUCTION

The bioregion of Wallacea is made up of the islands between Borneo and New Guinea. It has high species richness and endemism, and its forests are threatened by human land-use change (Myers *et al.* 2000). Wallacean islands are key to the dispersal and diversification of the few well-studied taxa (Moyle *et al.* 2016, Tänzler *et al.* 2016, Rowe *et al.* 2019), yet most taxa in Wallacea are poorly studied. Wallacea's largest island is Sulawesi, and its diversity is of such interest that it was described by Alfred Russell Wallace as

'wonderfully rich in peculiar forms; many of which are singular or beautiful, and are in some cases absolutely unique' (Wallace 1869).

Discovery of the 'peculiar', 'beautiful' and 'unique' flora continues (Cámara-Leret & Veldkamp 2011, Bramley 2012, Low 2013, Brambach *et al.* 2016, Rugayah & Sunarti 2017, Rustiami & Henderson 2017, Kartonegoro *et al.* 2018). Knowledge of floristics across much of the island is still lacking, however, with low density of botanical collections and forest monitoring plots (Kessler *et al.* 2002, Brearley *et al.* 2019). One of the only places where the flora has been examined thoroughly is the Lore Lindu National Park (Culmsee *et al.* 2010, 2011, Culmsee & Leuschner 2013, Brambach *et al.* 2017, 2020), a site that covers only a few of the soil types found in Sulawesi (Cannon *et al.* 2007). The island has many soil types including limestone and ultramafic soils that possess a chemistry that many plants are ill-equipped to tolerate (Nie *et al.* 2011, Galey *et al.* 2017, Kong *et al.* 2017, Pillon *et al.* 2019). Limestone soils have high pH and high magnesium and calcium concentrations (Nie *et al.* 2011), whilst ultramafic soils are rich in many often toxic metals and low in phosphorus (Proctor 2003). On Sulawesi there are also nitrogen-poor sandy soils and mafic soils that are metal rich but less so than ultramafics (Cannon *et al.* 2007, Whitten *et al.* 2012). In

69   combination, these soils create a mosaic of varying stressors. The tree communities across

70   this mosaic are the subject of this paper.

71

72   Specialization of plants to a particular soil type occurs often (Cowling *et al.* 1994).

73   Species traits tend to be adapted to specific ranges of environmental variables (Parker &

74   Maynard Smith 1990). Species do not, therefore, occupy environments where their traits do

75   not offer sufficient fitness (Fernandez-Going *et al.* 2013). The result is species that are

76   restricted to a single environment. In other parts of the world, the stressful soil types found in

77   Sulawesi harbour many endemic species (Cowling & Holmes 1992, Anacker 2011, Fine &

78   Baraloto 2016). Furthermore, zoological endemism in Sulawesi has a marked spatial

79   influence (Evans *et al.* 2003), that most obviously correlates with the formation of the island

80   (Frantz *et al.* 2018). Sulawesi formed from an agglomeration of a number of different proto-

81   islands within the last 20 million years (Nugraha & Hall 2018). The proto-islands largely

82   overlap with the identified areas of endemism (Fooden 1969, Evans *et al.* 2003). To what

83   degree island formation and soils have shaped endemism in Sulawesi's tree flora is unclear.

84

85   In most communities, a few common species tend to be found together with many

86   rarer species (Preston 1948). Tree species become common in very specific local

87   environmental conditions (Umaña *et al.* 2017) and, as a result, do not generally dominate

88   across different environments (Pitman *et al.* 2013) although there are, of course, exceptions

89   to the rule (Draper *et al.* 2019). Exceptions occur when contrast in the environment is not too

90   great (Fine & Baraloto 2016). For instance, in the western Amazon there is a large contrast

91   between infertile white sands and more fertile terra firme soils and the dominant species

92   differ (Fine & Baraloto 2016). Whereas, in the Upper Rio Negro of Brazil terra firme soils

93   are less fertile, the contrast with white sand is less and dominants occur across the divide

94   (Stropp *et al.* 2011). Tree species dominance across the soils of Sulawesi is completely

95   unknown.

96

97   Here we present analyses of ten 0.25 ha forest plots across Sulawesi. We explore (1)

98   diversity, endemism and species dominance at sites and (2) the edaphic and spatial effects

99   upon the difference between communities across sites.

100

101 **2. METHODS**

102

103 **2.1 Field sites, sample collection and species identification**

104 Ten lowland 0.25 ha permanent forest plots were established during 2016 (Figure 1, Table

105 S1). Two plots were located on ultramafic soils in Morowali Nature Reserve. Four plots were

106 located on the Bualemo peninsula, two were on mafic soils and two on limestone. Four plots

107 were located on Wawonii island, two were on sand and two on ultramafic soils.

108

109   Based upon the spatial structure of genetic data from animal populations, seven areas

110 of endemism have been drawn in Sulawesi (Evans *et al.* 2003). Wawonii is part of the

111 Southeast area of endemism, Bualemo part of East Central and Morowali is at the boundary

112 between East and West Central. Sites also differ in their geological history (Nugraha & Hall

113 2018): Wawonii emerged above sea level within the last 4 million years; Morowali uplifted

114 as part of a proto-island c. 20 million years ago, and the continued uplift of this proto-island

115 led to the emergence of Bualemo c. 3 million years ago. These dates are based upon

116 palaeontological, petrological and heavy mineral studies, U-Pb dating of detrital zircons and

117 analysis of sedimentary rocks in the field; there is an understandable degree of error in these

118   dates with greater likelihood of error the further back in time the date in question (Nugraha &

119   Hall 2018).

120

121   Following published protocols, trees with stems ≥ 10 cm diameter at breast height (dbh;

122   1.3 m) were measured and permanently tagged (Phillips *et al.* 2009). Specimens for all species

123   were collected and deposited at Royal Botanic Gardens, Kew and Herbarium Bogoriense. The

124   top set and a set for Palu are stored at Bogor. The Tropical Plant Families Identification

125   Handbook (Utteridge & Bramley 2015) was used for preliminary field-based family level

126   specimen identification with final identification of specimens undertaken at Kew. All

127   individuals were assigned to genera. Specimens that could not be confidently assigned to a

128   named species were assigned as having an affinity to another species (10 % of stems) or as a

129   morphospecies within the assigned genus (42 %). Specimens were compared among sites, so

130   that even where a species name could not be confidently assigned to a species, we were

131   confident that a taxon occurring at more than one site was given the same morphospecies code.

132

133   **2.2 Soil data**

134   Soil samples were collected from each of the 10 x 10 m subplots within each plot and pooled

135   to form a single sample per plot. Total C measurement used the Walkley and Black method

136   and total N the Kjeldahl method. Total soil Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn

137   was quantified via digestion of 0.5 g soil in 5 ml HNO_3 and 1 ml $HClO_4$ at 100 to 200 ° C by

138   ramping over a 7 hour period then diluted to 25 ml with deionized water and analysis on an

139   Agilent Technologies 4100 microwave plasma atomic emission spectrometer (Co, Cr and Ni)

140   or an Agilent Technologies 200 Series atomic absorption spectrometer (all other elements).

141   Soil metal concentrations were first scaled (z-scores) and then reduced to five principal

142   component (PC) axes that accounted for > 90 % variability in the full dataset. Axes 1 and 3

143 accounted for variability in micronutrients and soil trace elements Co, Cr, Cu, Fe, Mn, Ni and

144 Zn, axis 2: Al, C and phytonutrients Ca, N and P, axis 4: Co and Mg, and axis 5: K. Full

145 loadings can be found in the supplementary material (Table S2).

146

147 **2.3 Diversity, endemism and dominance**

148 We calculated Hill number conversions of species richness, Shannon and Simpson diversities

149 for each site (Chao *et al.* 2014). The use of Hill numbers overcomes the lack of a linear

150 relationship between abundance-weighted diversity measures and increasing species richness

151 when partitioning diversity between assemblages (Chiu *et al.* 2014). Species richness,

152 Shannon and Simpson diversity equivalents are defined by a weighting parameter q with

153 values 0, 1 and 2 respectively (Hill 1973). To deal with the issue of diversity scaling with

154 sample size, we also calculated interpolated (rarefied) diversity values. This gave us diversity

155 values equal to those calculated if all plots had the same number of individuals as the plot

156 with fewest individuals. To identify the effect of region and soil PC axes upon diversity

157 measures we used a general linear model. We also calculated Fisher's alpha diversity for

158 comparison with regional datasets.

159

160   To identify how many species at our sites are endemic to Sulawesi we first consulted

161 the Plants of the World Online database (POWO 2019). For those families in POWO not

162 reviewed by taxonomic experts we checked Flora Malesiana (van Steenis 1951). If there was

163 also no Flora Malesiana treatment, we reviewed relevant literature (Merrill 1922, Sleumer

164 1969, Hartley 1979, Stevens 1980, Turner 1995, Weerasooriya & Saunders 2002, Wiriadinata

165 *et al.* 2013, de Kok 2016, Ganesan *et al.* 2020).

166

167   We also carried out an indicator species analyses (Dufrêne & Legendre 1997). We

168   identified indicator species for regions and soil types. Species that represent at least ten

169   percent of stems across at least ten percent of plots were designated as dominant (Arellano *et*

170   *al.* 2014).

171

172   **2.4 Difference in community species composition**

173   The difference in community composition between sites was calculated with Jaccard

174   (incidence based) and Bray Curtis (abundance weighted) beta diversity measures. We

175   calculated the components of Jaccard similarity known as nestedness and turnover. This

176   shows if differences between sites are caused by one community being a subset of the other

177   (nestedness) or by the presence of species unique to each assemblage (turnover) (Baselga

178   2010). Bray-Curtis component equivalents were also calculated (Baselga 2017). Mantel tests

179   were used to test for effects of spatial, edaphic and climatic distance upon beta diversity

180   measures. We fitted linear models of beta diversity measure as the response and each of

181   spatial, edaphic and climatic distance as predictors and took the adjusted R^2 values as a

182   measure of how much each predictor explained variance in beta diversity. Edaphic distance

183   was defined as the Euclidean distance in 5-dimensional (5 PCA axes) space between plots.

184   Nineteen climatic variables from WorldClim were scaled (z-scores) and reduced to 3

185   principal component axes (that explained > 90 % variation in the data). Climatic distances

186   were the Euclidean distances between plots in the 3 PCA axes-based multivariate space.

187   Climatic variables used were annual mean temperature, mean diurnal temperature range,

188   isothermality, temperature seasonality, maximum temperature of warmest month, minimum

189   temperature of coldest month, temperature annual range, mean temperature of wettest

190   quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean

191   temperature of coldest quarter, annual precipitation, precipitation of wettest month,

192   precipitation of driest month, precipitation seasonality, precipitation of wettest quarter,

193   precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest

194   quarter.

195

196   We performed non-metric dimensional scaling (NMDS) ordination and ran

197   permutation tests (999 permutations) to quantify the significance of soil axes and region upon

198   community composition. We also carried out UPMGA cluster analysis of the Jaccard

199   dissimilarity matrix.

200

201   All analyses were performed in R version 3.4.1 (R Core Team 2017). Hill numbers

202   were calculated with *iNext* (Hsieh *et al.* 2016). Indicator species analysis was performed with

203   *indicspecies*. Beta diversity and components calculated with *betapart* (Baselga 2010) and

204   visualised using ternary plots in *ggtern* (Hamilton & Ferry 2018). The dissimilarity measures

205   calculated in *betapart* were converted to similarity measures (1 – dissimilarity) to conform

206   with ternary plot requirement for variables to sum to a constant. NMDS ordination and

207   permutation tests for effects of environment was carried out with *vegan*. Code for analysis is

208   in online supporting information.

209

210   **3. RESULTS**

211

212   **3.1 General floristics**

213   In total, 1434 trees from 283 species were recorded across all ten plots (Table S3 and S4).

214   Burseraceae (140 individuals), Myristicaceae (108), Sapotaceae (108) and Myrtaceae (100)

215   were the most commonly encountered families. *Gironniera subaequalis* (Cannabaceae; 75)

216   and *Castanopsis acuminatissima* (Fagaceae; 48) were the two most common species.

217   Myristicaceae, Myrtaceae and Sapotaceae were the most diverse families with 20, 19 and 18

218   species/morphospecies respectively. Only seven species were found in all three regions, these

219   were *Cerbera odollum* (Apocynaceae), *Endiandra sulavesiana* (Lauraceae), *Garcinia*

220   *celebica* (Clusiaceae), a morphospecies of *Garcinia*, *Gnetum gnemon* (Gnetaceae) *Myristica*

221   *koordersii* (Myristicaceae) and a morphospecies of *Syzygium* (Myrtaceae). Five species were

222   present in both Bualemo and Morowali, six in both Bualemo and Wawonii and 13 in both

223   Morowali and Bualemo. Fifty-five species were found on more than one soil type.

224

225   **3.2 Diversity, endemism and dominance**

226   We found no effect of region and weak effects of soil PC axes upon Hill value diversity (Fig.

227   2). This was consistent across measures increasingly weighted by species abundance and

228   interpolated measures (Fig. 2). Fisher's alpha shows greater diversity across our plot series

229   compared to Seram (Edwards *et al.* 1990). However, greater diversity was seen in Borneo

230   and Sumatra (e.g. Potts et al. 2002, Sambas and Siregar 2004).

231

232   We found 20 species endemic to Sulawesi across our plots. We found three indicator

233   species on sand; on sand and ultramafic we found a single indicator, and a single indicator

234   species was found on mafic and limestone (Table 1). There was a single indicator species for

235   Bualemo only, 14 for Morowali only, seven for Wawonii only and two indicator species for

236   both Morowali and Wawonii (Table 2).

237

238   We identified nine dominant species (Arellano *et al.* 2014). These were *Gironniera*

239   *subaequalis* (Cannabaceae)*, Microcos* aff. *paniculata* (Malvaceae) and *Palaquium maliliense*

240   (Sapotaceae), two morphospecies of *Canarium* (Burseraceae) and a morphospecies each of

241   *Aglaia* (Meliaceae)*, Dacryodes* (Burseraceae)*, Mallotus* (Euphorbiaceae) and *Platea*

242 (Metteniusaceae, recently moved from Icacinaceae). These species accounted for 10 % of

243 stems in at least one plot and, generally, this frequency was only reached in a single plot.

244 There was no overlap with the seven taxa that are found in all three regions. These species

245 only ever dominated in one region and generally on one soil type.

246

247 **3.3 Difference in community species composition**

248 Results from incidence based (Jaccard) and abundance based (Bray Curtis) differences in

249 community composition were consistent across analyses. For simplicity, we present Jaccard

250 dissimilarity results here (Bray Curtis component equivalents can be found in supporting

251 information, Figure S1). Jaccard dissimilarity results were caused by species turnover

252 between communities rather than nestedness (Figure 3). We found no significant effects of

253 space, soil or climate upon Jaccard dissimilarity according to Mantel tests (all $p > 0.1$). A

254 greater amount of variation in Jaccard dissimilarity was explained by space (adjusted R^2 =

255 0.006) than soil however (adjusted R^2 = 0.002), and climate lacked a relationship with

256 Jaccard dissimilarity (adjusted R^2 = -0.014). Overall, this reflected large differences in

257 community composition between regions and greater similarity within regions; there was still

258 low similarity between plots in Bualemo, however.

259

260　　　The NMDS ordination (Figure 4a) and permutation tests showed no impact of soil

261 variables (all axes $p > 0.05$) but a significant impact of region ($p = 0.001$) upon community

262 species composition. The UPMGA clustering of the Jaccard dissimilarity results showed

263 clear regional groups (Fig. 3b). Within each regional cluster, communities on the same soil

264 type tended to group together. The only exception being the limestone plots in Bualemo -

265 these two plots were on a limestone hill and in a limestone valley respectively.

266

4. DISCUSSION

Results tentatively show spatial structuring of tree communities in Sulawesi. If this is the case, could it be a legacy of Sulawesi's island formation? The current landmass formed c. 3 million years ago. Since that time, it appears that the tree flora between the three regions we sampled have remained very different. This could simply be a result of species lacking traits that promote dispersal between regions (Nekola & White 1999). This seems unlikely in Sulawesi where the requirement to occupy the newly formed proto-islands should promote a flora with high dispersal capacity (Arjona *et al.* 2018). There could also be climatic barriers to dispersal between the three study regions (Garg *et al.* 2018, Giarla *et al.* 2018). However, Sulawesi belongs to the wet tropical biome (Metzger *et al.* 2013). This is important because biome boundaries tend to limit plant dispersal (Crisp *et al.* 2009). Therefore, because Sulawesi does not have sharp biome boundaries, there are unlikely to be large climatic effects upon dispersal between regions - this is reflected in the lack of climatic covariation with beta diversity seen here. So, could the uplift and formation of Sulawesi shape the tree communities? Island uplift creates newly available land area (Borregaard *et al.* 2017). There should be a lag in time before this area is colonised (Svenning *et al.* 2015). Could the time lag be increased if the newly available land area is a result of proto-islands becoming a single island? Initially, regional floras would reflect the floras of the proto-islands. This should limit dispersal between regions because of limits imposed by the competing species of the flora already present (Foster 1999).

The second result of note is the small effect of soil upon tree communities. Across both the Amazon and Borneo, soils shape tree communities (Potts *et al.* 2002, Fine & Kembel 2011, Eiserhardt *et al.* 2013, Cámara-Leret *et al.* 2017). This results in marked turnover of species at edaphic boundaries (Paoli *et al.* 2006, Fine *et al.* 2010, Aiba *et al.*

292 2015, Draper *et al.* 2017). In Sulawesi, we find that edaphic difference between sites

293 correlates with community composition far less than spatial separation. So why could we find

294 a low effect of soil in Sulawesi? The main difference between our sites and many studied

295 elsewhere is that we mostly sampled soils considered stressful for plants. Large

296 compositional differences in tree communities tend to be seen between a benign and harsh

297 soil type because species adapted to benign environments cannot tolerate the stressful areas,

298 and species that tolerate stressful areas are outcompeted in benign environments (Grime

299 1977). If the flora of Sulawesi is generally tolerant of the stressful soils, perhaps the boundary

300 from one soil to the next is not as great as that between benign and stressful soil - meaning

301 stress tolerant species are able to persist across soil types.

302

303   The results here are preliminary, the ten sites presented above need to be

304 complemented with data from other areas of endemism and more fertile soil types. Only with

305 this data will it be possible to test how stress tolerance and the legacy of proto-islands joining

306 influences Sulawesi's flora. A future dataset could begin by combining those sites presented

307 here alongside those from Lore Lindu National Park. An initial comparison suggests that the

308 Celestrales, Oxalidales, Malphigiales (COM) clade that often dominate ultramafic floras

309 (Pillon *et al.* 2019) account for 17 % of stems at our sites, whereas, in Lore Lindu (albeit at

310 higher elevations than our sites), COM species account for < 10 % of stems (Brambach *et al.*

311 2017). Unpacking how the stressful soils of Sulawesi differentially affect clades should be

312 possible with a larger dataset (Fernandez-Going *et al.* 2013).

313

314   Recently there has been a re-emphasis on the effects of geological variability upon

315 biodiversity (Alahuhta *et al.* 2020, Read *et al.* 2020). Sulawesi not only has many types of

316 geology (i.e. those underlying the soil types studied here), but it also has an ontogeny with

317   the potential to influence biogeography irrespective of geological similarity or dissimilarity.

318   In addition, Sulawesi is mountainous with large areas of mafic and ultramafic soils. This

319   combination has been linked to particularly high diversity in the tropics (Rahbek *et al.* 2019).

320   How species richness and turnover across space is affected by both island/mountain

321   formation and geology in Sulawesi requires substantial future research.

322
323
324   **REFERENCES**
325

326   AIBA, S., Y. SAWADA, M. TAKYU, T. SEINO, K. KITAYAMA, and R. REPIN. 2015. Structure, floristics and
327   diversity of tropical montane rain forests over ultramafic soils on Mount Kinabalu
328   (Borneo) compared with those on non-ultramafic soils. Aust. J. Bot. 63: 191–203.

329   ALAHUHTA, J., M. TOIVANEN, and J. HJORT. 2020. Geodiversity–biodiversity relationship needs
330   more empirical evidence. Nat. Ecol. Ecol. 4: 2–3.

331   ANACKER, B. L. 2011. Phylogenetic patterns of endemism and diversity. *In* Harrison, S., and N.
332   Rajakaruna (Eds.). Serpentine: the evolution and ecology of a model system.
333   University of California Press, Berkeley, USA. pp. 49–70.

334   ARELLANO, G., L. CAYOLA, I. LOZA, V. TORREZ, and M. J. MACÍA. 2014. Commonness patterns and
335   the size of the species pool along a tropical elevational gradient: insights using a new
336   quantitative tool. Ecography 37: 536–543.

337   ARJONA, Y., M. NOGALES, R. HELENO, and P. VARGAS. 2018. Long-distance dispersal syndromes
338   matter: diaspore–trait effect on shaping plant distribution across the Canary Islands.
339   Ecography 41: 805–814.

340   BASELGA, A. 2010. Partitioning the turnover and nestedness components of beta diversity.
341   Global Ecol. Biogeogr. 19: 134–143.

342   BASELGA, A. 2017. Partitioning abundance-based multiple-site dissimilarity into components:
343   balanced variation in abundance and abundance gradients. Methods Ecol. Evol. 8:
344   799–808.

345   BORREGAARD, M. K., I. R. AMORIM, P. A. BORGES, J. S. CABRAL, J. M. FERNÁNDEZ-PALACIOS, R. FIELD, L.
346   R. HEANEY, H. KREFT, T. J. MATTHEWS, and J. M. OLESEN. 2017. Oceanic island
347   biogeography through the lens of the general dynamic model: assessment and
348   prospect. Biol. Rev. 92: 830–853.

349   BRAMBACH, F., M. COODE, S. BIAGIONI, and H. CULMSEE. 2016. *Elaeocarpus firdausii*
350   (Elaeocarpaceae), a new species from tropical mountain forests of Sulawesi.
351   PhytoKeys 62: 1–14.

352 BRAMBACH, F., C. LEUSCHNER, A. TJOA, and H. CULMSEE. 2017. Diversity, endemism, and
353   composition of tropical mountain forest communities in Sulawesi, Indonesia, in
354   relation to elevation and soil properties. Perspect. Plant Ecol. Evol. Syst. 27: 68–79.

355 BRAMBACH, F., C. LEUSCHNER, A. TJOA, and H. CULMSEE. 2020. Predominant colonization of
356   Malesian mountains by Australian tree lineages. J. Biogeogr. 47: 355–370.

357 BRAMLEY, G. L. 2012. Three new species of *Callicarpa* (Lamiaceae) from Sulawesi. Kew Bull.
358   67: 213–223.

359 BREARLEY, F. Q. ET AL. 2019. Opportunities and challenges for an Indonesian forest monitoring
360   network. Ann. For. Sci. 76: 54.

361 CÁMARA-LERET, R., H. TUOMISTO, K. RUOKOLAINEN, H. BALSLEV, and S. MUNCH KRISTIANSEN. 2017.
362   Modelling responses of western Amazonian palms to soil nutrients. J. Ecol. 105: 367–
363   381.

364 CÁMARA-LERET, R., and J. F. VELDKAMP. 2011. A remarkable new *Medinilla* (Melastomataceae)
365   from Celebes (Sulawesi), Indonesia. Gard. Bull. Singapore 62: 213-221.

366 CANNON, C. H., M. SUMMERS, J. R. HARTING, and P. J. KESSLER. 2007. Developing conservation
367   priorities based on forest type, condition, and threats in a poorly known ecoregion:
368   Sulawesi, Indonesia. Biotropica 39: 747–759.

369 CHAO, A., C.-H. CHIU, and L. JOST. 2014. Unifying species diversity, phylogenetic diversity,
370   functional diversity, and related similarity and differentiation measures through Hill
371   numbers. Annu. Rev. Ecol. Evol. Syst. 45: 297–324.

372 CHIU, C.-H., L. JOST, and A. CHAO. 2014. Phylogenetic beta diversity, similarity, and
373   differentiation measures based on Hill numbers. Ecol. Monogr. 84: 21–44.

374 COWLING, R. M., and P. M. HOLMES. 1992. Endemism and speciation in a lowland flora from
375   the Cape Floristic Region. Biol. J. Linn. Soc. 47: 367–383.

376 COWLING, R. M., E. T. F. WITKOWSKI, A. V. MILEWSKI, and K. R. NEWBEY. 1994. Taxonomic, edaphic
377   and biological aspects of narrow plant endemism on matched sites in mediterranean
378   South Africa and Australia. J. Biogeogr. 21: 651–664.

379 CRISP, M. D., M. T. ARROYO, L. G. COOK, M. A. GANDOLFO, G. J. JORDAN, M. S. MCGLONE, P. H.
380   WESTON, M. WESTOBY, P. WILF, and H. P. LINDER. 2009. Phylogenetic biome
381   conservatism on a global scale. Nature 458: 754–756.

382 CULMSEE, H., and C. LEUSCHNER. 2013. Consistent patterns of elevational change in tree
383   taxonomic and phylogenetic diversity across Malesian mountain forests. J. Biogeogr.
384   40: 1997–2010.

385 CULMSEE, H., C. LEUSCHNER, G. MOSER, and R. PITOPANG. 2010. Forest aboveground biomass
386   along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in
387   tropical montane rain forests. J. Biogeogr. 37: 960–974.

388   CULMSEE, H., R. PITOPANG, H. MANGOPO, and S. SABIR. 2011. Tree diversity and
389   phytogeographical patterns of tropical high mountain rain forests in Central
390   Sulawesi, Indonesia. Biodiv. Conserv. 20: 1103–1123.

391   DE KOK, R. P. J. 2016. A revision of *Cryptocarya* R. Br.(Lauraceae) of peninsular Malaysia. Kew
392   Bull. 71: 7.

393   DRAPER, F. C., ET AL. 2019. Dominant tree species drive beta diversity patterns in western
394   Amazonia. Ecology 100: e02636.

395   DRAPER, F. C., ET AL. 2017. Peatland forests are the least diverse tree communities
396   documented in Amazonia, but contribute to high regional beta-diversity. Ecography
397   41: 1256–1269.

398   DUFRÊNE, M., and P. LEGENDRE. 1997. Species assemblages and indicator species: the need for
399   a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

400   EDWARDS, I. D., R. W. PAYTON, J. PROCTOR, and S. RISWAN. 1990. Altitudinal zonation of the rain
401   forests in the Manusela National Park, Seram, Maluku, Indonesia. *In* P. Baas, K.
402   Kalkman, and R. Geesink (Eds.). The plant diversity of Malesia. Kluwer Academic
403   Publishers, Dordrecht, The Netherlands. pp. 161–175.

404   EISERHARDT, W. L., J.-C. SVENNING, W. J. BAKER, T. L. COUVREUR, and H. BALSLEV. 2013. Dispersal
405   and niche evolution jointly shape the geographic turnover of phylogenetic clades
406   across continents. Sci. Rep. 3: 1164.

407   EVANS, B. J., J. SUPRIATNA, N. ANDAYANI, M. I. SETIADI, D. C. CANNATELLA, and D. J. MELNICK. 2003.
408   Monkeys and toads define areas of endemism on Sulawesi. Evolution 57: 1436–
409   1443.

410   FERNANDEZ-GOING, B. M., S. P. HARRISON, B. L. ANACKER, and H. D. SAFFORD. 2013. Climate
411   interacts with soil to produce beta diversity in Californian plant communities.
412   Ecology 94: 2007–2018.

413   FINE, P. V. A., and C. BARALOTO. 2016. Habitat endemism in white-sand forests: insights into
414   the mechanisms of lineage diversification and community assembly of the
415   Neotropical flora. Biotropica 48: 24–33.

416   FINE, P. V. A., R. GARCÍA-VILLACORTA, N. C. A. PITMAN, I. MESONES, and S. W. KEMBEL. 2010. A
417   floristic study of the white-sand forests of Peru. Ann. MO Bot. Gard. 97: 283–305.

418   FINE, P. V. A., and S. W. KEMBEL. 2011. Phylogenetic community structure and phylogenetic
419   turnover across space and edaphic gradients in western Amazonian tree
420   communities. Ecography 34: 552–565.

421   FOODEN, J. 1969. Taxonomy and evolution of the monkeys of Celebes. S. Karger, Basel,
422   Switzerland.

423   FOSTER, B. L. 1999. Establishment, competition and the distribution of native grasses among
424   Michigan old-fields. J. Ecol. 87: 476–489.

425   FRANTZ, L. A., A. RUDZINSKI, A. M. S. NUGRAHA, A. EVIN, J. BURTON, A. HULME-BEAMAN, A.
426   LINDERHOLM, R. BARNETT, R. VEGA, and E. K. IRVING-PEASE. 2018. Synchronous
427   diversification of Sulawesi's iconic artiodactyls driven by recent geological events.
428   Proc. R. Soc. B 285: 20172566.

429   GALEY, M. L., A. VAN DER ENT, M. C. M. IQBAL, and N. RAJAKARUNA. 2017. Ultramafic geoecology of
430   South and Southeast Asia. Bot. Stud. 58: 18.

431   GANESAN, S. K., D. J. MIDDLETON, and P. WILKIE. 2020. A revision of *Pterospermum* (Malvaceae:
432   Dombeyoideae) in Malesia. Edin. J. Bot. in press.

433   GARG, K. M., B. CHATTOPADHYAY, P. R. WILTON, D. M. PRAWIRADILAGA, and F. E. RHEINDT. 2018.
434   Pleistocene land bridges act as semipermeable agents of avian gene flow in
435   Wallacea. Mol. Phylogenet. Evol. 125: 196–203.

436   GIARLA, T. C., S. P. MAHER, A. S. ACHMADI, M. K. MOORE, M. T. SWANSON, K. C. ROWE, and J. A.
437   ESSELSTYN. 2018. Isolation by marine barriers and climate explain areas of endemism
438   in an island rodent. J. Biogeogr. 45: 2053–2066.

439   GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its
440   relevance to ecological and evolutionary theory. Am. Nat. 111: 1169–1194.

441   HAMILTON, N. E., and M. FERRY. 2018. ggtern: ternary diagrams using ggplot2. J. Stat. Softw.
442   87: c03.

443   HARTLEY, T. G. 1979. A revision of the genus *Tetractomia* (Rutaceae). J. Arnold Arbor. 60:
444   127–153.

445   HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology
446   54: 427–432.

447   HSIEH, T. C., K. H. MA, and A. CHAO. 2016. iNEXT: an R package for rarefaction and
448   extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7: 1451–1456.

449   KARTONEGORO, A., R. E. BONE, and H. J. ATKINS. 2018. Eleven new species of *Cyrtandra*
450   (Gesneriaceae) from Sulawesi, Indonesia. Edin. J. Bot. 75: 173-204.

451   KESSLER, P. J., M. M. BOS, S. S. DAZA, A. KOP, L. P. M. WILLEMSE, R. PITOPANG, and S. R. GRADSTEIN.
452   2002. Checklist of woody plants of Sulawesi, Indonesia. Blumea. Supplement 14: 1–
453   160.

454   KONG, H., F. L. CONDAMINE, A. J. HARRIS, J. CHEN, B. PAN, M. MÖLLER, V. S. HOANG, and M. KANG.
455   2017. Both temperature fluctuations and East Asian monsoons have driven plant
456   diversification in the karst ecosystems from southern China. Mol. Ecol. 26: 6414–
457   6429.

458   LOW, Y. W. 2013. Two new species of Sulawesi *Gardenia* (Rubiaceae) and notes on *G.
459   mutabilis*. Syst. Bot. 38: 235–241.

460   MERRILL, E. D. 1922. New or noteworthy Philippine plants XVII. Philipp. J. Sci. 20: 367–476.

461 METZGER, M. J., R. G. BUNCE, R. H. JONGMAN, R. SAYRE, A. TRABUCCO, and R. ZOMER. 2013. A high-
462   resolution bioclimate map of the world: a unifying framework for global biodiversity
463   research and monitoring. Global Ecol. Biogeogr. 22: 630–638.

464 MOYLE, R. G., C. H. OLIVEROS, M. J. ANDERSEN, P. A. HOSNER, B. W. BENZ, J. D. MANTHEY, S. L.
465   TRAVERS, R. M. BROWN, and B. C. FAIRCLOTH. 2016. Tectonic collision and uplift of
466   Wallacea triggered the global songbird radiation. Nat. Commun. 7: 12709.

467 MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. DA FONSECA, and J. KENT. 2000.
468   Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

469 NEKOLA, J. C., and P. S. WHITE. 1999. The distance decay of similarity in biogeography and
470   ecology. J. Biogeogr. 26: 867–878.

471 NIE, Y., H. CHEN, K. WANG, W. TAN, P. DENG, and J. YANG. 2011. Seasonal water use patterns of
472   woody species growing on the continuous dolostone outcrops and nearby thin soils
473   in subtropical China. Plant Soil 341: 399–412.

474 NUGRAHA, A. M. S., and R. HALL. 2018. Late Cenozoic palaeogeography of Sulawesi, Indonesia.
475   Palaeogeogr. Palaeoclimatol. Palaeoecol. 490: 191–209.

476 PAOLI, G. D., L. M. CURRAN, and D. R. ZAK. 2006. Soil nutrients and beta diversity in the Bornean
477   Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. J.
478   Ecol. 94: 157–170.

479 PARKER, G. A., and J. MAYNARD SMITH. 1990. Optimality theory in evolutionary biology. Nature
480   348: 27-33.

481 PHILLIPS, O. L., T. R. BAKER, T. R. FELDPAUSCH, and R. J. BRIENEN. 2009. RAINFOR: field manual for
482   plot establishment and remeasurement. Available at:
483   www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_June_200
484   9_ENG.pdf.

485 PILLON, Y., D. A. GONZÁLEZ, H. RANDRIAMBANONA, P. P. LOWRY, T. JAFFRÉ, and S. MERLOT. 2019.
486   Parallel ecological filtering of ultramafic soils in three distant island floras. J.
487   Biogeogr. 46: 2457–2465.

488 PITMAN, N. C. A., M. R. SILMAN, and J. W. TERBORGH. 2013. Oligarchies in Amazonian tree
489   communities: a ten-year review. Ecography 36: 114–123.

490 POTTS, M. D., P. S. ASHTON, L. S. KAUFMAN, and J. B. PLOTKIN. 2002. Habitat patterns in tropical
491   rain forests: a comparison of 105 plots in northwest Borneo. Ecology 83: 2782–2797.

492 POWO. 2019. Plants of the World Online. Available at:
493   http://www.plantsoftheworldonline.org/.

494 PRESTON, F. W. 1948. The commonness, and rarity, of species. Ecology 29: 254–283.

495 PROCTOR, J. 2003. Vegetation and soil and plant chemistry on ultramafic rocks in the tropical
496   Far East. Perspect. Plant Ecol. Syst. 6: 105–124.

497 RAHBEK, C., M. K. BORREGAARD, A. ANTONELLI, R. K. COLWELL, B. G. HOLT, D. NOGUES-BRAVO, C. M. Ø.
498   RASMUSSEN, K. RICHARDSON, M. T. ROSING, R. J. WHITTAKER, and J. FJELDSÅ. 2019. Building
499   mountain biodiversity: geological and evolutionary processes. Science 365: 1114–
500   1119.

501 READ, Q. D., P. L. ZARNETSKE, S. RECORD, K. M. DAHLIN, J. K. COSTANZA, A. O. FINLEY, K. D. GADDIS, J.
502   M. GRADY, M. L. HOBI, A. M. LATIMER, S. L. MALONE, S. V. OLLINGER, S. PAU, and A. M.
503   WILSON. 2020. Beyond counts and averages: relating geodiversity to dimensions of
504   biodiversity. Glob. Ecol. Biogeogr. 29: 696–710

505 ROWE, K. C., A. S. ACHMADI, P.-H. FABRE, J. J. SCHENK, S. J. STEPPAN, and J. A. ESSELSTYN. 2019.
506   Oceanic islands of Wallacea as a source for dispersal and diversification of murine
507   rodents. J. Biogeogr. 46: 2752–2768.

508 RUGAYAH, T. R., and S. SUNARTI. 2017. The genus *Lasianthus* (Rubiaceae) in Wawonii island,
509   Southeast Sulawesi, Indonesia. Reinwardtia 16: 97–101.

510 RUSTIAMI, H., and A. HENDERSON. 2017. A synopsis of *Calamus* (Arecaceae) in Sulawesi.
511   Reinwardtia 16: 49–63.

512 SAMBAS, E. N., and M. SIREGAR. 2004. Flora of Alas river bank, Ketambe, Gunung Leuser
513   National Park. BioSMART 6: 33–38.

514 SLEUMER, H. 1969. Materials towards the knowledge of the Icacinaceae of Asia, Malesia, and
515   adjacent areas. Blumea 17: 181–264.

516 VAN STEENIS, C. G. G. J. 1951. Flora Malesiana:present and prospects. Taxon 1: 21–24.

517 STEVENS, P. F. 1980. A revision of the Old World species of *Calophyllum* (Guttiferae). J. Arnold
518   Arbor. 61: 117–424.

519 STROPP, J., P. VAN DER SLEEN, P. A. ASSUNÇÃO, A. L. DA SILVA, and H. TER STEEGE. 2011. Tree
520   communities of white-sand and terra-firme forests of the upper Rio Negro. Acta
521   Amaz. 41: 521–544.

522 SVENNING, J.-C., W. L. EISERHARDT, S. NORMAND, A. ORDONEZ, and B. SANDEL. 2015. The influence
523   of paleoclimate on present-day patterns in biodiversity and ecosystems. Annu. Rev.
524   Ecol. Evol. Syst. 46: 551–572.

525 TÄNZLER, R., M. H. VAN DAM, E. F. TOUSSAINT, Y. R. SUHARDJONO, M. BALKE, and A. RIEDEL. 2016.
526   Macroevolution of hyperdiverse flightless beetles reflects the complex geological
527   history of the Sunda Arc. Sci. Rep. 6: 18793.

528 TURNER, I. M. 1995. A catalogue of the vascular plants of Malaya. Gard. Bull. Singapore 47. 1–
529   5.

530 UMAÑA, M. N., C. ZHANG, M. CAO, L. LIN, and N. G. SWENSON. 2017. A core-transient framework
531   for trait-based community ecology: an example from a tropical tree seedling
532   community. Ecol. Lett. 20: 619–628.

533   UTTERIDGE, T. M. A., and G. BRAMLEY. 2015. Tropical plant families identification handbook, 2nd
534   Edition. Royal Botanic Gardens, Kew, UK.

535   WALLACE, A. R. 1869. The Malay archipelago. Macmillan and Co, London, UK.

536   WEERASOORIYA, A. D., and R. M. SAUNDERS. 2002. (1521-1522) Proposals to reject the names
537   *Mitrephora teysmannii* and *Orophea macrocarpa* (Annonaceae). Taxon 51: 191–192.

538   WHITTEN, T., G. S. HENDERSON, and M. MUSTAFA. 2012. The ecology of Sulawesi. Tuttle
539   Publishing, Clarendon, USA.

540   WIRIADINATA, H., D. GIRMANSYAH, J. HUNTER, W. S. HOOVER, and K. KARTAWINATA. 2013. Floristic
541   study of West Sumbawa, Indonesia. Reinwardtia 13: 391–404.

542

543

544   Table 1 Indicator tree species for communities on contrasting soil types in forest plots across

545   three regions in Sulawesi, Indonesia.

546

Family	Species	Indicator value	P value
Sand			
Stemonuraceae	*Stemonurus celebicus*	0.981	0.020
Burseraceae	*Canarium* sp. 5	0.972	0.025
Pentaphylacaceae	*Ternstroemia* aff. *penangiana*	0.943	0.020
Limestone and mafic			
Sapindaceae	*Pometia pinnata*	1	0.010
Sand and ultramafic			
Cannabaceae	*Gironniera subaequalis*	1	0.010

547
548
549
550
551
552
553
554
555
556
557
558

559 Table 2 Indicator tree species for communities in forest plots across three regions of

560 Sulawesi, Indonesia.

561
562

Family	Species	Indicator value	P value
Bualemo			
Sapindaceae	*Pometia pinnata*	1	0.015
Morowali			
Araucariaceae	*Agathis dammara*	1	0.025
Phyllanthaceae	*Baccaurea celebica*	1	0.025
Putranjivaceae	*Drypetes* aff. *longifolia*	1	0.025
Meliaceae	*Dysoxylum* aff. *alliaceum*	1	0.025
Moraceae	*Ficus subulata*	1	0.025
Cardiopteridaceae	*Gonocaryum littorale*	1	0.025
Chrysobalanaceae	*Kostermanthus* sp. 1	1	0.025
Rutaceae	*Melicope* aff. *latifolia*	1	0.025
Myristicaceae	*Myristica* sp. 1	1	0.025
Sapotaceae	*Planchonella* aff. *malaccensis*	1	0.025
Oxalidaceae	*Sarcotheca celebica*	1	0.025
Myristicaceae	*Knema stellata*	0.949	0.050
Sapotaceae	*Palaquium* sp. 5	0.935	0.050
Annonaceae	*Monoon* aff. *coriaceum*	0.913	0.030
Wawonii			
Moraceae	*Artocarpus integer*	1	0.010
Clusiaceae	*Garcinia* sp. 7	1	0.010
Myristicaceae	*Horsfieldia lancifolia*	1	0.010
Myristicaceae	*Knema* sp. 1	1	0.010
Dipterocarpaceae	*Vatica flavovirens*	1	0.010
Fagaceae	*Castanopsis acuminatissima*	0.990	0.010
Sapotaceae	*Planchonella firma*	0.922	0.025
Morowali and Wawonii			
Cannabaceae	*Gironniera subaequalis*	1	0.015
Myrtaceae	*Kjellbergiodendron celebicum*	0.913	0.05

563
564
565
566
567
568
569
570
571
572

573

574

575

576   Figure 1 Localities of permanent forest plots in Sulawesi, Indonesia. Bualemo has two mafic

577   and two limestone plots, Morowali has two ultramafic plots, and Wawonii has two ultramafic

578   and two sand plots.
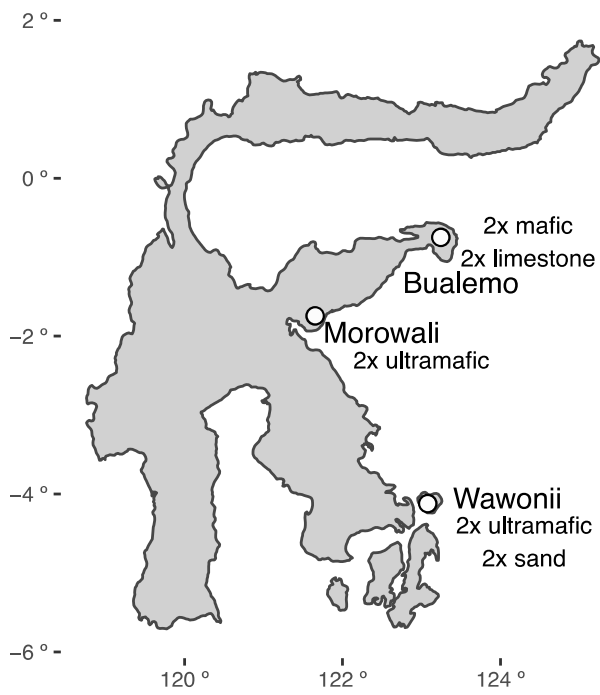
580

581   Figure 2 (a) Abundance unweighted (q = 0) and abundance weighted (q = 1 and 2) Hill

582   number values and species richness of tree communities across permanent forest plots in

583   three regions of Sulawesi, Indonesia. q = 0,1,2 are species richness, Shannon and Simpson

584   diversity equivalent Hill numbers, respectively. (b) Edaphic principal component axes scores

585   for all plots in Sulawesi. (c) Effects of edaphic principal components upon Sulawesi tree

586   community Hill number and interpolated Hill number measures (rows) with increasing

587   abundance weighting defined by parameter q (columns). Significant effects ($p < 0.05$) are

588   denoted by black symbols. Points represent coefficient estimates and whiskers the standard

589   error for the estimates.

590

(a)

(b)

(c)

591
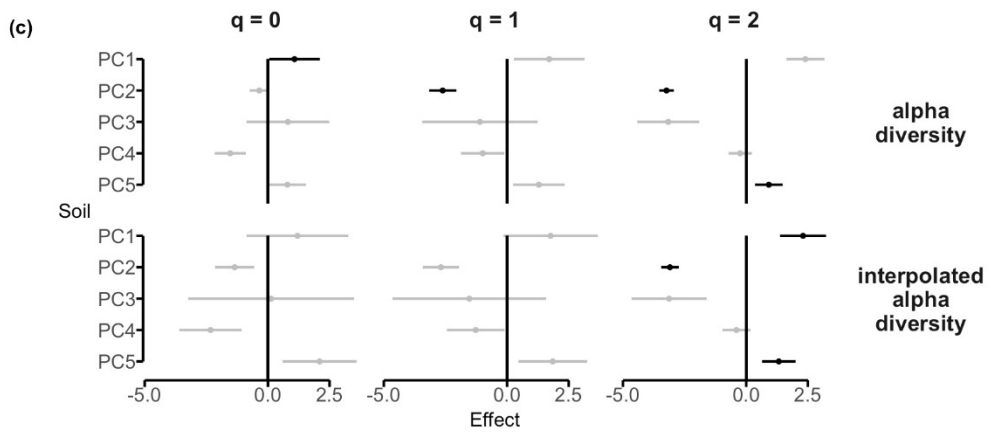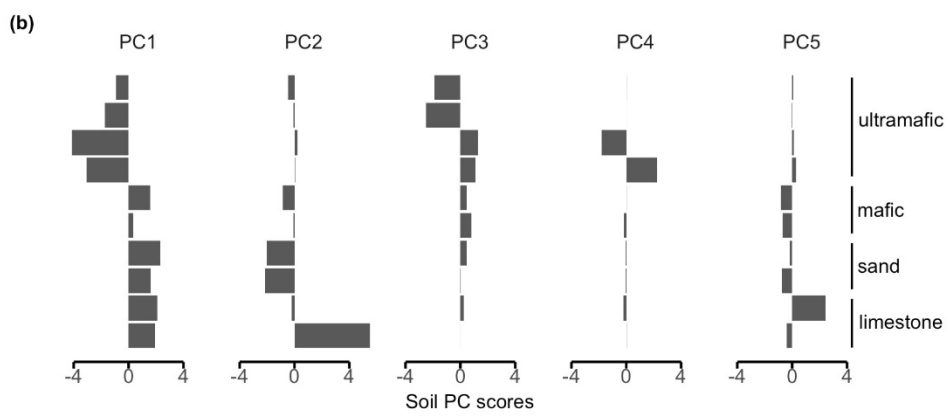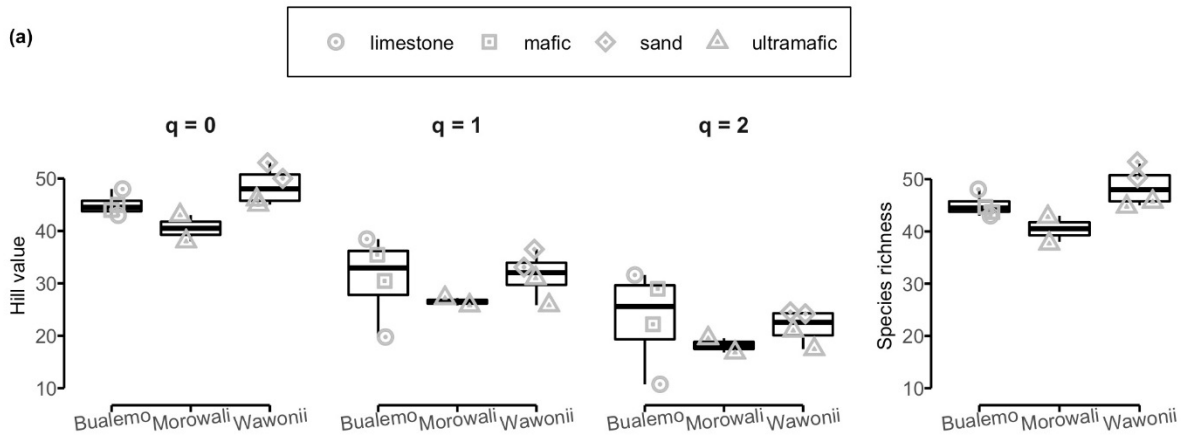
592   Figure 3 Ternary plots of the Jaccard similarity measure of tree community beta diversity and

593   turnover and nestedness components across permanent forest plots (a) within and (b) between

594   regions of Sulawesi, Indonesia.

595

596

597
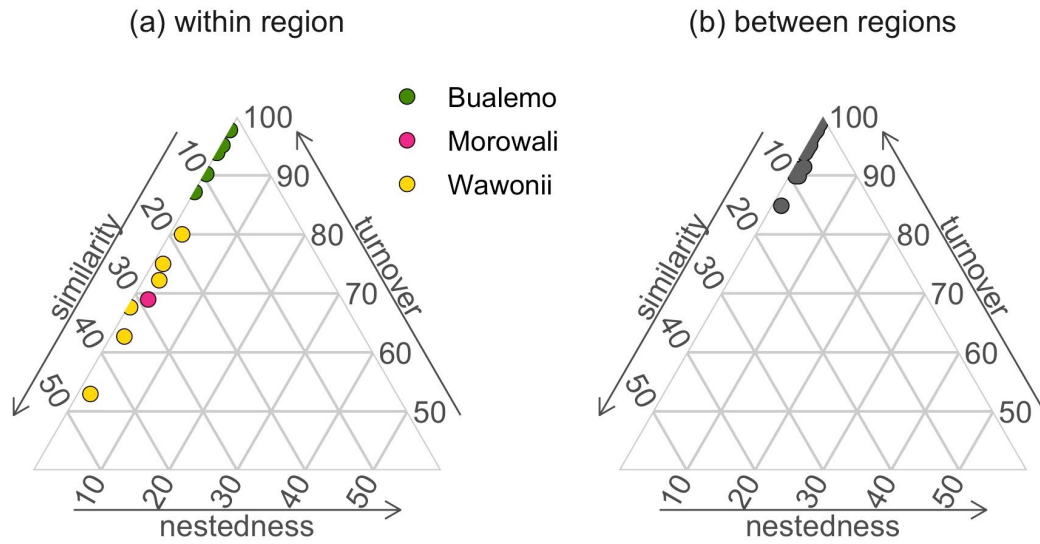
Figure 4 (a) Ordination of tree communities in Sulawesi (Indonesia) forest plots by non-

599 metric multidimensional scaling. Region is indicated with point colours. Soil types are

600 denoted by point shape. Arrows show soil principal component (PC) axes. Grey points

601 indicate species position in ordination space. (b) Clustergram from UPMGA scaling of

602 Jaccard dissimilarity between communities. Colours show the region.

603

604

605