

1 LRH: Trethowan *et al.*

2 RRH: Floristics across Sulawesi

3

4

5

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

7

8

9

10 **Liam A. Trethowan**<sup>1,2</sup>, **Wolf L. Eiserhardt**<sup>2,3</sup>, **Deden Girmansyah**<sup>4</sup>, **Endang Kintamani**  
11 **<sup>4</sup>, Timothy M. A. Utteridge**<sup>2</sup>, **Francis Q. Brearley**<sup>1</sup>

12 <sup>1</sup> Manchester Metropolitan University, Manchester, United Kingdom.

13 <sup>2</sup> Royal Botanic Gardens Kew, London, United Kingdom.

14 <sup>3</sup> Aarhus University, Aarhus, Denmark.

15 <sup>4</sup> 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

23 Received \_\_\_\_; revision accepted \_\_\_\_.

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](https://figshare.com/authors/Liam_Trethowan/8268603)

## 43 1. INTRODUCTION

44  
45 The bioregion of Wallacea is made up of the islands between Borneo and New Guinea. It has  
46 high species richness and endemism, and its forests are threatened by human land-use change  
47 (Myers *et al.* 2000). Wallacean islands are key to the dispersal and diversification of the few  
48 well-studied taxa (Moyle *et al.* 2016, Tänzler *et al.* 2016, Rowe *et al.* 2019), yet most taxa in  
49 Wallacea are poorly studied. Wallacea's largest island is Sulawesi, and its diversity is of such  
50 interest that it was described by Alfred Russell Wallace as

51  
52 *'wonderfully rich in peculiar forms; many of which are singular or beautiful, and are in some*  
53 *cases absolutely unique'* (Wallace 1869).

54  
55 Discovery of the 'peculiar', 'beautiful' and 'unique' flora continues (Cámara-Leret &  
56 Veldkamp 2011, Bramley 2012, Low 2013, Brambach *et al.* 2016, Rugayah & Sunarti 2017,  
57 Rustiami & Henderson 2017, Kartonegoro *et al.* 2018). Knowledge of floristics across much  
58 of the island is still lacking, however, with low density of botanical collections and forest  
59 monitoring plots (Kessler *et al.* 2002, Brearley *et al.* 2019). One of the only places where the  
60 flora has been examined thoroughly is the Lore Lindu National Park (Culmsee *et al.* 2010,  
61 2011, Culmsee & Leuschner 2013, Brambach *et al.* 2017, 2020), a site that covers only a few  
62 of the soil types found in Sulawesi (Cannon *et al.* 2007). The island has many soil types  
63 including limestone and ultramafic soils that possess a chemistry that many plants are ill-  
64 equipped to tolerate (Nie *et al.* 2011, Galey *et al.* 2017, Kong *et al.* 2017, Pillon *et al.* 2019).  
65 Limestone soils have high pH and high magnesium and calcium concentrations (Nie *et al.*  
66 2011), whilst ultramafic soils are rich in many often toxic metals and low in phosphorus  
67 (Proctor 2003). On Sulawesi there are also nitrogen-poor sandy soils and mafic soils that are  
68 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-Goñi *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  $\geq 10$  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<sub>3</sub> and 1 ml HClO<sub>4</sub> 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

#### 267 4. DISCUSSION

268 Results tentatively show spatial structuring of tree communities in Sulawesi. If this is  
269 the case, could it be a legacy of Sulawesi's island formation? The current landmass formed c.  
270 3 million years ago. Since that time, it appears that the tree flora between the three regions we  
271 sampled have remained very different. This could simply be a result of species lacking traits  
272 that promote dispersal between regions (Nekola & White 1999). This seems unlikely in  
273 Sulawesi where the requirement to occupy the newly formed proto-islands should promote a  
274 flora with high dispersal capacity (Arjona *et al.* 2018). There could also be climatic barriers  
275 to dispersal between the three study regions (Garg *et al.* 2018, Giarla *et al.* 2018). However,  
276 Sulawesi belongs to the wet tropical biome (Metzger *et al.* 2013). This is important because  
277 biome boundaries tend to limit plant dispersal (Crisp *et al.* 2009). Therefore, because  
278 Sulawesi does not have sharp biome boundaries, there are unlikely to be large climatic effects  
279 upon dispersal between regions - this is reflected in the lack of climatic covariation with beta  
280 diversity seen here. So, could the uplift and formation of Sulawesi shape the tree  
281 communities? Island uplift creates newly available land area (Borregaard *et al.* 2017). There  
282 should be a lag in time before this area is colonised (Svenning *et al.* 2015). Could the time  
283 lag be increased if the newly available land area is a result of proto-islands becoming a single  
284 island? Initially, regional floras would reflect the floras of the proto-islands. This should limit  
285 dispersal between regions because of limits imposed by the competing species of the flora  
286 already present (Foster 1999).

287

288 The second result of note is the small effect of soil upon tree communities. Across  
289 both the Amazon and Borneo, soils shape tree communities (Potts *et al.* 2002, Fine &  
290 Kembel 2011, Eiserhardt *et al.* 2013, Cámara-Leret *et al.* 2017). This results in marked  
291 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 geocology 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\\_2009\\_ENG.pdf](http://www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_June_2009_ENG.pdf).  
484
- 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. ZARNETSKY, 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, 2<sup>nd</sup>  
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	<i>Stemonurus celebicus</i>	0.981	0.020
Burseraceae	<i>Canarium sp. 5</i>	0.972	0.025
Pentaphylacaceae	<i>Ternstroemia aff. penangiana</i>	0.943	0.020
Limestone and mafic			
Sapindaceae	<i>Pometia pinnata</i>	1	0.010
Sand and ultramafic			
Cannabaceae	<i>Gironniera subaequalis</i>	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	<i>Pometia pinnata</i>	1	0.015
Morowali			
Araucariaceae	<i>Agathis dammara</i>	1	0.025
Phyllanthaceae	<i>Baccaurea celebica</i>	1	0.025
Putranjivaceae	<i>Drypetes aff. longifolia</i>	1	0.025
Meliaceae	<i>Dysoxylum aff. alliaceum</i>	1	0.025
Moraceae	<i>Ficus subulata</i>	1	0.025
Cardiopteridaceae	<i>Gonocaryum littorale</i>	1	0.025
Chrysobalanaceae	<i>Kostermanthus sp. 1</i>	1	0.025
Rutaceae	<i>Melicope aff. latifolia</i>	1	0.025
Myristicaceae	<i>Myristica sp. 1</i>	1	0.025
Sapotaceae	<i>Planchonella aff. malaccensis</i>	1	0.025
Oxalidaceae	<i>Sarcotheca celebica</i>	1	0.025
Myristicaceae	<i>Knema stellata</i>	0.949	0.050
Sapotaceae	<i>Palaquium sp. 5</i>	0.935	0.050
Annonaceae	<i>Monoon aff. coriaceum</i>	0.913	0.030
Wawonii			
Moraceae	<i>Artocarpus integer</i>	1	0.010
Clusiaceae	<i>Garcinia sp. 7</i>	1	0.010
Myristicaceae	<i>Horsfieldia lancifolia</i>	1	0.010
Myristicaceae	<i>Knema sp. 1</i>	1	0.010
Dipterocarpaceae	<i>Vatica flavovirens</i>	1	0.010
Fagaceae	<i>Castanopsis acuminatissima</i>	0.990	0.010
Sapotaceae	<i>Planchonella firma</i>	0.922	0.025
Morowali and Wawonii			
Cannabaceae	<i>Gironniera subaequalis</i>	1	0.015
Myrtaceae	<i>Kjellbergiodendron celebicum</i>	0.913	0.05

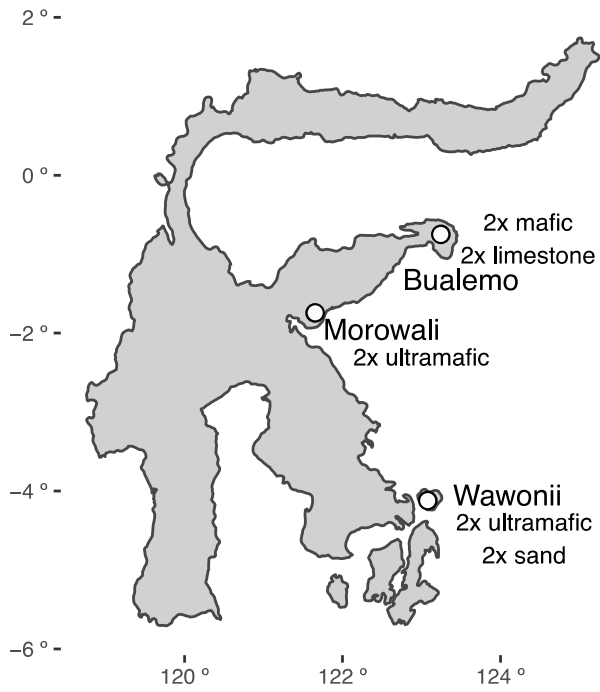
563  
 564  
 565  
 566  
 567  
 568  
 569  
 570  
 571  
 572

573

574

575

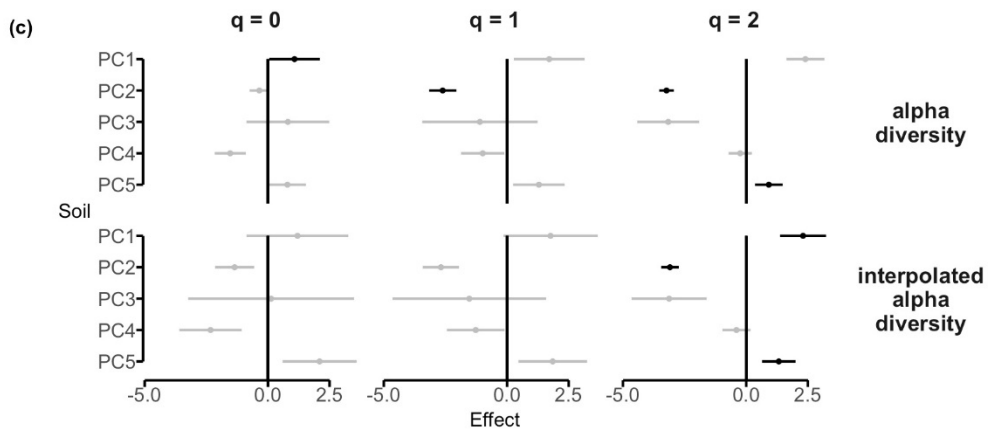
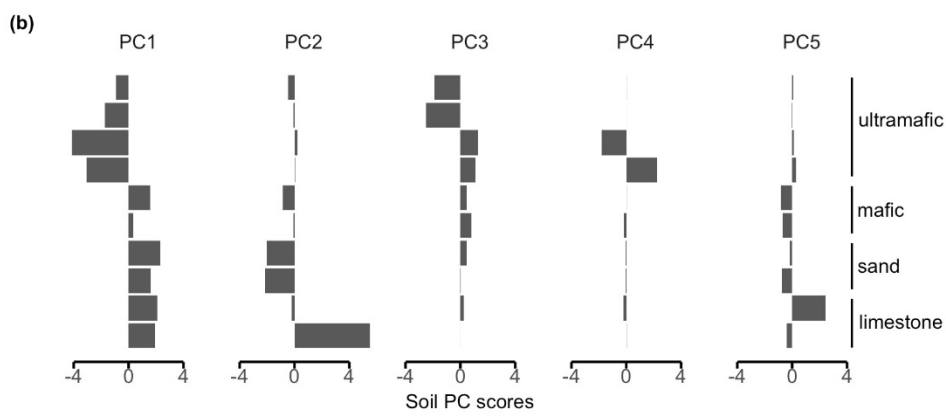
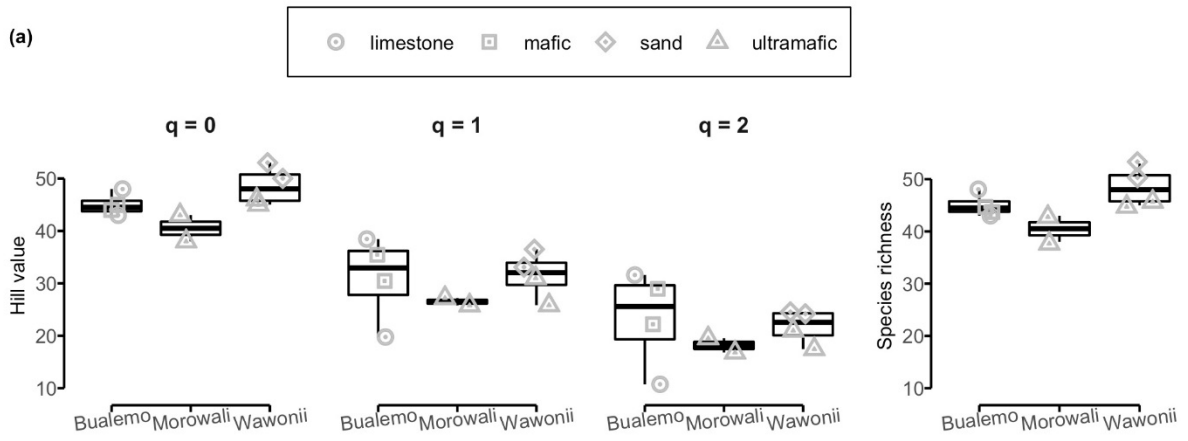
576 Figure 1 Localities of permanent forest plots in Sulawesi, Indonesia. Bualemo has two mafic  
577 and two limestone plots, Morowali has two ultramafic plots, and Wawonii has two ultramafic  
578 and two sand plots.



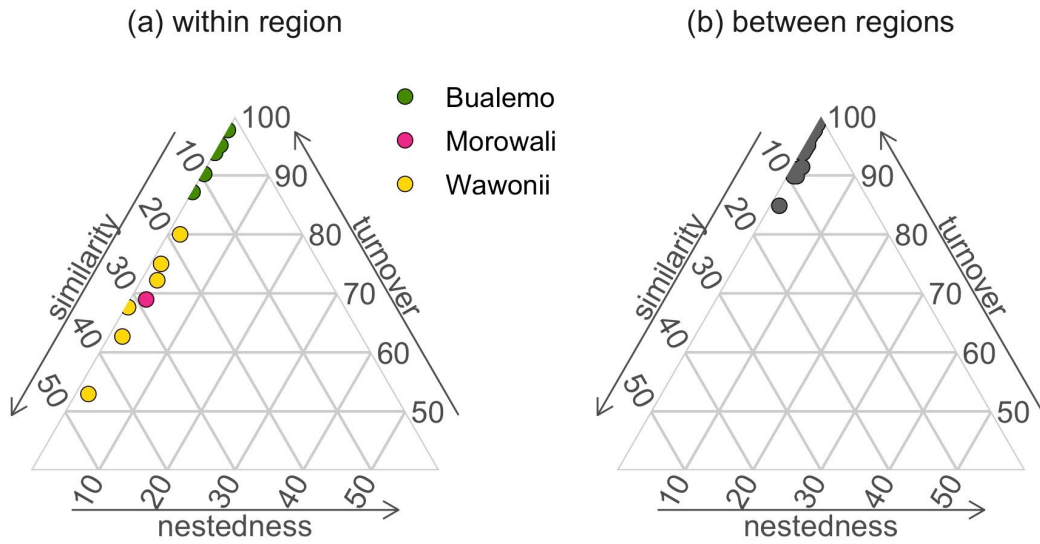
580

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





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.

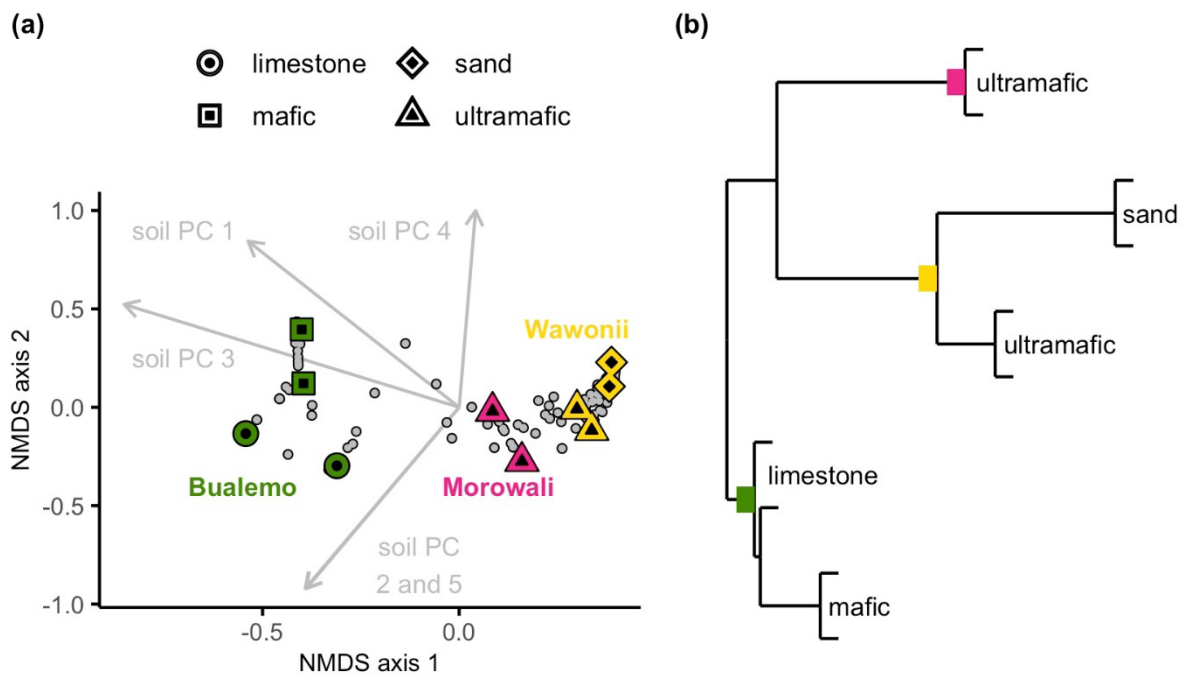


595

596

597

598 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

606 **ACKNOWLEDGEMENTS**

607

608 We acknowledge the Indonesian Ministry of Research and Technology (RisTek) for  
609 permission to perform fieldwork. Also, Herbarium Bogoriense (BO) for the Memorandum of  
610 Understanding and Material Transfer Agreement. We thank Indonesian forestry offices and  
611 staff at Aliansi Konservasi Tompotika for support in the field. Fieldwork was only possible  
612 due to the help of guides: Aga, Yes, Amin, Muksin, Sumardin, Dado, Hanya, Ete, Asrion,  
613 Lendo, Manto and Peno. LAT's funding was provided by the Bentham Moxon Trust,  
614 Coalbourn Trust, Botanical Research Fund, an MMU postgraduate studentship and Emily  
615 Holmes awards. We thank the Indonesian Agricultural Research Agency (Badan Litbang  
616 Kementerian Pertanian) for carrying out soil analyses. FQB thanks NERC for funding a trip  
617 to Sulawesi. WLE's contribution was supported by a research grant (00025354) from  
618 VILLUM FONDEN. We thank taxonomic experts for their assistance identifying the  
619 collections: Terry Pennington, Ian Turner, Marie Briggs, Laura Pearce, Eve Lucas, Yee Wen  
620 Low, Alex Munro, David Middleton, Willem de Wilde, Brigitta de Wilde-Duyfjes, Peter  
621 Ashton, Gwilym Lewis, Gemma Bramley, Jess Rickenback and Caroline Pannell. LAT is  
622 grateful to Robert Hall and Robert Whittaker for discussions. We thank Jennifer Rowntree,  
623 Gwilym Lewis, Giacomo Sellan, Toby Pennington, Tim Baker, Paul Fine, Cam Webb, Jim  
624 McGuire, Jennifer Powers and an anonymous reviewer for comments that much improved the  
625 manuscript.

626