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1 LRH: Trethowan *et al.*

2 RRH: Floristics across Sulawesi

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

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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-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

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

Here we present analyses of ten 0.25 ha forest plots across Sulawesi. We explore (1) diversity, endemism and species dominance at sites and (2) the edaphic and spatial effects upon the difference between communities across sites.

2. METHODS

2.1 Field sites, sample collection and species identification

Ten lowland 0.25 ha permanent forest plots were established during 2016 (Figure 1, Table S1). Two plots were located on ultramafic soils in Morowali Nature Reserve. Four plots were located on the Bualemo peninsula, two were on mafic soils and two on limestone. Four plots were located on Wawonii island, two were on sand and two on ultramafic soils.

Based upon the spatial structure of genetic data from animal populations, seven areas of endemism have been drawn in Sulawesi (Evans *et al.* 2003). Wawonii is part of the Southeast area of endemism, Bualemo part of East Central and Morowali is at the boundary between East and West Central. Sites also differ in their geological history (Nugraha & Hall 2018): Wawonii emerged above sea level within the last 4 million years; Morowali uplifted as part of a proto-island c. 20 million years ago, and the continued uplift of this proto-island led to the emergence of Bualemo c. 3 million years ago. These dates are based upon palaeontological, petrological and heavy mineral studies, U-Pb dating of detrital zircons and analysis of sedimentary rocks in the field; there is an understandable degree of error in these

dates with greater likelihood of error the further back in time the date in question (Nugraha & Hall 2018).

Following published protocols, trees with stems ≥ 10 cm diameter at breast height (dbh; 1.3 m) were measured and permanently tagged (Phillips *et al.* 2009). Specimens for all species were collected and deposited at Royal Botanic Gardens, Kew and Herbarium Bogoriense. The top set and a set for Palu are stored at Bogor. The Tropical Plant Families Identification Handbook (Utteridge & Bramley 2015) was used for preliminary field-based family level specimen identification with final identification of specimens undertaken at Kew. All individuals were assigned to genera. Specimens that could not be confidently assigned to a named species were assigned as having an affinity to another species (10 % of stems) or as a morphospecies within the assigned genus (42 %). Specimens were compared among sites, so that even where a species name could not be confidently assigned to a species, we were confident that a taxon occurring at more than one site was given the same morphospecies code.

2.2 Soil data

Soil samples were collected from each of the 10 x 10 m subplots within each plot and pooled to form a single sample per plot. Total C measurement used the Walkley and Black method and total N the Kjeldahl method. Total soil Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn was quantified via digestion of 0.5 g soil in 5 ml HNO₃ and 1 ml HClO₄ at 100 to 200 ° C by ramping over a 7 hour period then diluted to 25 ml with deionized water and analysis on an Agilent Technologies 4100 microwave plasma atomic emission spectrometer (Co, Cr and Ni) or an Agilent Technologies 200 Series atomic absorption spectrometer (all other elements). Soil metal concentrations were first scaled (z-scores) and then reduced to five principal component (PC) axes that accounted for > 90 % variability in the full dataset. Axes 1 and 3

accounted for variability in micronutrients and soil trace elements Co, Cr, Cu, Fe, Mn, Ni and Zn, axis 2: Al, C and phytonutrients Ca, N and P, axis 4: Co and Mg, and axis 5: K. Full loadings can be found in the supplementary material (Table S2).

2.3 Diversity, endemism and dominance

We calculated Hill number conversions of species richness, Shannon and Simpson diversities for each site (Chao *et al.* 2014). The use of Hill numbers overcomes the lack of a linear relationship between abundance-weighted diversity measures and increasing species richness when partitioning diversity between assemblages (Chiu *et al.* 2014). Species richness, Shannon and Simpson diversity equivalents are defined by a weighting parameter q with values 0, 1 and 2 respectively (Hill 1973). To deal with the issue of diversity scaling with sample size, we also calculated interpolated (rarefied) diversity values. This gave us diversity values equal to those calculated if all plots had the same number of individuals as the plot with fewest individuals. To identify the effect of region and soil PC axes upon diversity measures we used a general linear model. We also calculated Fisher's alpha diversity for comparison with regional datasets.

To identify how many species at our sites are endemic to Sulawesi we first consulted the Plants of the World Online database (POWO 2019). For those families in POWO not reviewed by taxonomic experts we checked Flora Malesiana (van Steenis 1951). If there was also no Flora Malesiana treatment, we reviewed relevant literature (Merrill 1922, Sleumer 1969, Hartley 1979, Stevens 1980, Turner 1995, Weerasooriya & Saunders 2002, Wiriadinata *et al.* 2013, de Kok 2016, Ganesan *et al.* 2020).

We also carried out an indicator species analyses (Dufrêne & Legendre 1997). We identified indicator species for regions and soil types. Species that represent at least ten percent of stems across at least ten percent of plots were designated as dominant (Arellano *et al.* 2014).

2.4 Difference in community species composition

The difference in community composition between sites was calculated with Jaccard (incidence based) and Bray Curtis (abundance weighted) beta diversity measures. We calculated the components of Jaccard similarity known as nestedness and turnover. This shows if differences between sites are caused by one community being a subset of the other (nestedness) or by the presence of species unique to each assemblage (turnover) (Baselga 2010). Bray-Curtis component equivalents were also calculated (Baselga 2017). Mantel tests were used to test for effects of spatial, edaphic and climatic distance upon beta diversity measures. We fitted linear models of beta diversity measure as the response and each of spatial, edaphic and climatic distance as predictors and took the adjusted R^2 values as a measure of how much each predictor explained variance in beta diversity. Edaphic distance was defined as the Euclidean distance in 5-dimensional (5 PCA axes) space between plots. Nineteen climatic variables from WorldClim were scaled (z-scores) and reduced to 3 principal component axes (that explained > 90 % variation in the data). Climatic distances were the Euclidean distances between plots in the 3 PCA axes-based multivariate space. Climatic variables used were annual mean temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month,

precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter.

We performed non-metric dimensional scaling (NMDS) ordination and ran permutation tests (999 permutations) to quantify the significance of soil axes and region upon community composition. We also carried out UPMGA cluster analysis of the Jaccard dissimilarity matrix.

All analyses were performed in R version 3.4.1 (R Core Team 2017). Hill numbers were calculated with *iNext* (Hsieh *et al.* 2016). Indicator species analysis was performed with *indicspecies*. Beta diversity and components calculated with *betapart* (Baselga 2010) and visualised using ternary plots in *ggtern* (Hamilton & Ferry 2018). The dissimilarity measures calculated in *betapart* were converted to similarity measures (1 – dissimilarity) to conform with ternary plot requirement for variables to sum to a constant. NMDS ordination and permutation tests for effects of environment was carried out with *vegan*. Code for analysis is in online supporting information.

3. RESULTS

3.1 General floristics

In total, 1434 trees from 283 species were recorded across all ten plots (Table S3 and S4). Burseraceae (140 individuals), Myristicaceae (108), Sapotaceae (108) and Myrtaceae (100) were the most commonly encountered families. *Girardinia subaequalis* (Cannabaceae; 75) and *Castanopsis acuminatissima* (Fagaceae; 48) were the two most common species.

Myristicaceae, Myrtaceae and Sapotaceae were the most diverse families with 20, 19 and 18 species/morphospecies respectively. Only seven species were found in all three regions, these were *Cerbera odollum* (Apocynaceae), *Endiandra sulavesiana* (Lauraceae), *Garcinia celebica* (Clusiaceae), a morphospecies of *Garcinia*, *Gnetum gnemon* (Gnetaceae) *Myristica koordersii* (Myristicaceae) and a morphospecies of *Syzygium* (Myrtaceae). Five species were present in both Bualemo and Morowali, six in both Bualemo and Wawonii and 13 in both Morowali and Bualemo. Fifty-five species were found on more than one soil type.

3.2 Diversity, endemism and dominance

We found no effect of region and weak effects of soil PC axes upon Hill value diversity (Fig. 2). This was consistent across measures increasingly weighted by species abundance and interpolated measures (Fig. 2). Fisher's alpha shows greater diversity across our plot series compared to Seram (Edwards *et al.* 1990). However, greater diversity was seen in Borneo and Sumatra (e.g. Potts *et al.* 2002, Sambas and Siregar 2004).

We found 20 species endemic to Sulawesi across our plots. We found three indicator species on sand; on sand and ultramafic we found a single indicator, and a single indicator species was found on mafic and limestone (Table 1). There was a single indicator species for Bualemo only, 14 for Morowali only, seven for Wawonii only and two indicator species for both Morowali and Wawonii (Table 2).

We identified nine dominant species (Arellano *et al.* 2014). These were *Gironniera subaequalis* (Cannabaceae), *Microcos* aff. *paniculata* (Malvaceae) and *Palaquium maliliense* (Sapotaceae), two morphospecies of *Canarium* (Burseraceae) and a morphospecies each of *Aglaia* (Meliaceae), *Dacryodes* (Burseraceae), *Mallotus* (Euphorbiaceae) and *Platea*

(Metteniusaceae, recently moved from Icacinaceae). These species accounted for 10 % of stems in at least one plot and, generally, this frequency was only reached in a single plot. There was no overlap with the seven taxa that are found in all three regions. These species only ever dominated in one region and generally on one soil type.

3.3 Difference in community species composition

Results from incidence based (Jaccard) and abundance based (Bray Curtis) differences in community composition were consistent across analyses. For simplicity, we present Jaccard dissimilarity results here (Bray Curtis component equivalents can be found in supporting information, Figure S1). Jaccard dissimilarity results were caused by species turnover between communities rather than nestedness (Figure 3). We found no significant effects of space, soil or climate upon Jaccard dissimilarity according to Mantel tests (all $p > 0.1$). A greater amount of variation in Jaccard dissimilarity was explained by space (adjusted $R^2 = 0.006$) than soil however (adjusted $R^2 = 0.002$), and climate lacked a relationship with Jaccard dissimilarity (adjusted $R^2 = -0.014$). Overall, this reflected large differences in community composition between regions and greater similarity within regions; there was still low similarity between plots in Bualemo, however.

The NMDS ordination (Figure 4a) and permutation tests showed no impact of soil variables (all axes $p > 0.05$) but a significant impact of region ($p = 0.001$) upon community species composition. The UPMGA clustering of the Jaccard dissimilarity results showed clear regional groups (Fig. 3b). Within each regional cluster, communities on the same soil type tended to group together. The only exception being the limestone plots in Bualemo - these two plots were on a limestone hill and in a limestone valley respectively.

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.*

2015, Draper *et al.* 2017). In Sulawesi, we find that edaphic difference between sites correlates with community composition far less than spatial separation. So why could we find a low effect of soil in Sulawesi? The main difference between our sites and many studied elsewhere is that we mostly sampled soils considered stressful for plants. Large compositional differences in tree communities tend to be seen between a benign and harsh soil type because species adapted to benign environments cannot tolerate the stressful areas, and species that tolerate stressful areas are outcompeted in benign environments (Grime 1977). If the flora of Sulawesi is generally tolerant of the stressful soils, perhaps the boundary from one soil to the next is not as great as that between benign and stressful soil - meaning stress tolerant species are able to persist across soil types.

The results here are preliminary, the ten sites presented above need to be complemented with data from other areas of endemism and more fertile soil types. Only with this data will it be possible to test how stress tolerance and the legacy of proto-islands joining influences Sulawesi's flora. A future dataset could begin by combining those sites presented here alongside those from Lore Lindu National Park. An initial comparison suggests that the Celestrales, Oxalidales, Malpighiales (COM) clade that often dominate ultramafic floras (Pillon *et al.* 2019) account for 17 % of stems at our sites, whereas, in Lore Lindu (albeit at higher elevations than our sites), COM species account for < 10 % of stems (Brambach *et al.* 2017). Unpacking how the stressful soils of Sulawesi differentially affect clades should be possible with a larger dataset (Fernandez-Going *et al.* 2013).

Recently there has been a re-emphasis on the effects of geological variability upon biodiversity (Alahuhta *et al.* 2020, Read *et al.* 2020). Sulawesi not only has many types of geology (i.e. those underlying the soil types studied here), but it also has an ontogeny with

the potential to influence biogeography irrespective of geological similarity or dissimilarity. In addition, Sulawesi is mountainous with large areas of mafic and ultramafic soils. This combination has been linked to particularly high diversity in the tropics (Rahbek *et al.* 2019). How species richness and turnover across space is affected by both island/mountain formation and geology in Sulawesi requires substantial future research.

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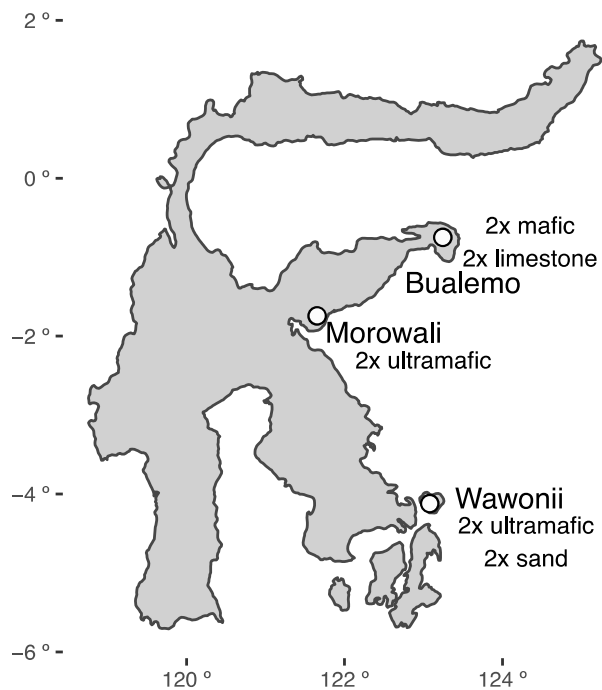
Table 1 Indicator tree species for communities on contrasting soil types in forest plots across three regions in Sulawesi, Indonesia.

| Family | Species | Indicator value | P value |
|---------------------|--|-----------------|---------|
| Sand | | | |
| Stemonuraceae | <i>Stemonurus celebicus</i> | 0.981 | 0.020 |
| Burseraceae | <i>Canarium</i> sp. 5 | 0.972 | 0.025 |
| Pentaphylacaceae | <i>Ternstroemia</i> aff. <i>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 |

Table 2 Indicator tree species for communities in forest plots across three regions of Sulawesi, Indonesia.

| 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</i> aff. <i>longifolia</i> | 1 | 0.025 |
| Meliaceae | <i>Dysoxylum</i> aff. <i>alliaceum</i> | 1 | 0.025 |
| Moraceae | <i>Ficus subulata</i> | 1 | 0.025 |
| Cardiopteridaceae | <i>Gonocaryum littorale</i> | 1 | 0.025 |
| Chrysobalanaceae | <i>Kostermanthus</i> sp. 1 | 1 | 0.025 |
| Rutaceae | <i>Melicope</i> aff. <i>latifolia</i> | 1 | 0.025 |
| Myristicaceae | <i>Myristica</i> sp. 1 | 1 | 0.025 |
| Sapotaceae | <i>Planchonella</i> aff. <i>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</i> sp. 5 | 0.935 | 0.050 |
| Annonaceae | <i>Monoon</i> aff. <i>coriaceum</i> | 0.913 | 0.030 |
| Wawonii | | | |
| Moraceae | <i>Artocarpus integer</i> | 1 | 0.010 |
| Clusiaceae | <i>Garcinia</i> sp. 7 | 1 | 0.010 |
| Myristicaceae | <i>Horsfieldia lancifolia</i> | 1 | 0.010 |
| Myristicaceae | <i>Knema</i> sp. 1 | 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 |

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

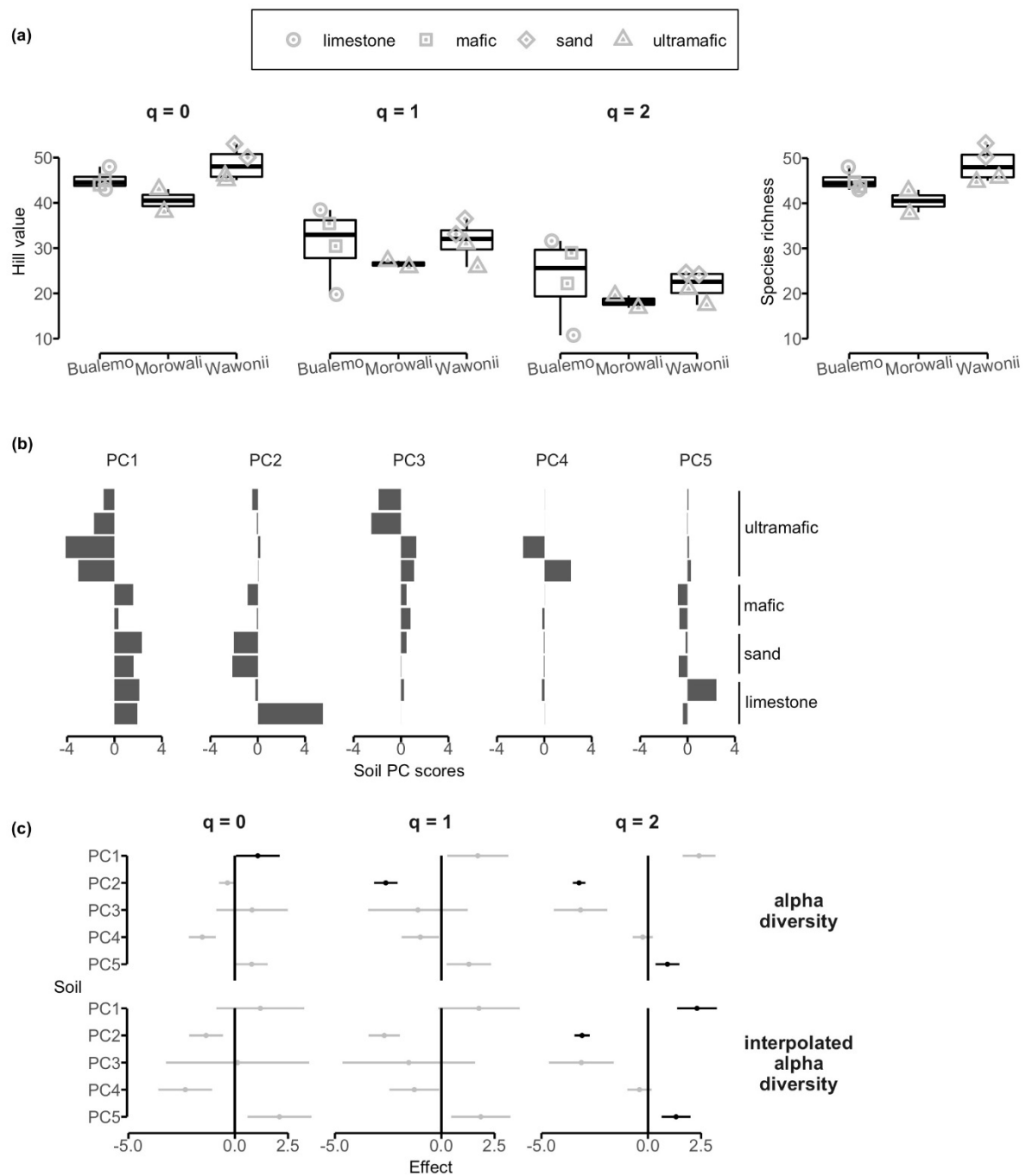


Figure 3 Ternary plots of the Jaccard similarity measure of tree community beta diversity and turnover and nestedness components across permanent forest plots (a) within and (b) between regions of Sulawesi, Indonesia.

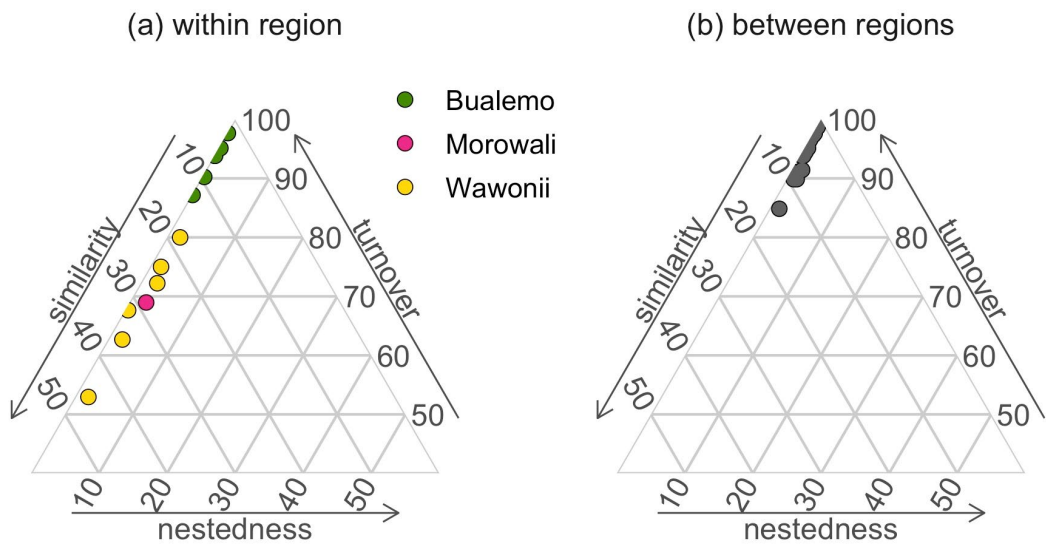
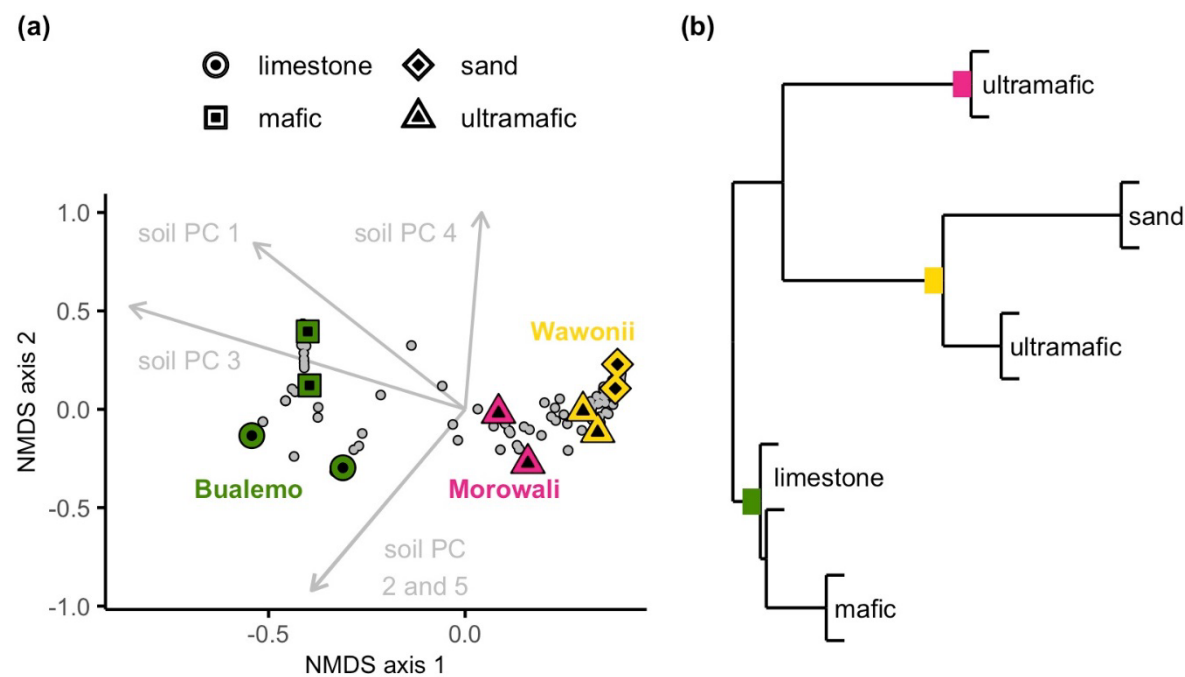


Figure 4 (a) Ordination of tree communities in Sulawesi (Indonesia) forest plots by non-metric multidimensional scaling. Region is indicated with point colours. Soil types are denoted by point shape. Arrows show soil principal component (PC) axes. Grey points indicate species position in ordination space. (b) Clustergram from UPMGA scaling of Jaccard dissimilarity between communities. Colours show the region.



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