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Floristics of forests across low nutrient soils in Sulawesi, Indonesia

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Abstract

The island of Sulawesi formed from the joining of proto-islands roughly three million years ago. Regions of zoological endemism, corresponding to the proto-islands, have been reported. Sulawesi's tree communities, however, remain poorly documented. In better-studied tropical regions, soil types similar to those found in Sulawesi often have distinctive tree communities. To gather data on Sulawesi's tree communities, we established ten (0.25 ha) plots on four soil types across three regions. We documented diversity, endemism, dominance, and species composition. Linear models of species composition showed greater influence of geographic distance rather than soil, and no relationship with climate. This suggests that the legacy of Sulawesi's formation may have influenced tree communities more so than the soil types we sampled. Most of our plots were on stressful soil types making it difficult to conclude on the importance of edaphic specialization in the Sulawesi tree flora. The lack of climatic effects reflects Sulawesi's position within the wet tropics where the small climatic differences are unlikely to have large influence on tree communities.

Abstract in Indonesian is available with online material.

KEYWORDS
biogeography, Indonesia, macroecology, serpentine, ultramafic, Wallacea

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, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Wallacean islands are key to the dispersal and diversification of the few well-studied taxa (Moyle et al., 2016; Rowe et al., 2019; Tänzler et al., 2016), 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 (Brambach, Coode, Biagioni, & Culmsee, 2016; Bramley, 2012; Cámara-Leret & Veldkamp, 2011; Kartonegoro, Bone, & Atkins, 2018; Low, 2013; Rugayah & Sunarti, 2017; Rustiami & Henderson, 2017). Knowledge of floristics across much of the island is still lacking, however, with low density of botanical collections and forest monitoring plots (Brearley et al., 2019; Kessler et al., 2002). One of the only

places where the flora has been examined thoroughly is the Lore Lindu National Park (Brambach, Leuschner, Tjoa, & Culmsee, 2017, 2020; Culmsee & Leuschner, 2013; Culmsee, Leuschner, Moser, & Pitopang, 2010; Culmsee, Pitopang, Mangopo, & Sabir, 2011), a site that covers only a few of the soil types found in Sulawesi (Cannon, Summers, Harting, & Kessler, 2007). The island has many soil types including limestone and ultramafic soils that possess a chemistry that many plants are ill-equipped to tolerate (Galey, van der Ent, Iqbal, & Rajakaruna, 2017; Kong et al., 2017; Nie et al., 2011; 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, Henderson, & Mustafa, 2012). In combination, these soils create a mosaic of varying stressors. The tree communities across this mosaic are the subject of this paper.

Specialization of plants to a particular soil type occurs often (Cowling, Witkowski, Milewski, & Newbey, 1994). Species traits tend to be adapted to specific ranges of environmental variables (Parker & Maynard Smith, 1990). Species do not, therefore, occupy environments where their traits do not offer sufficient fitness (Fernandez-Going, Harrison, Anacker, & Safford, 2013). The result is species that are restricted to a single environment. In other parts of the world, the stressful soil types found in Sulawesi harbor many endemic species (Anacker, 2011; Cowling & Holmes, 1992; Fine & Baraloto, 2016). Furthermore, zoological endemism in Sulawesi has a marked spatial influence (Evans et al., 2003), that most obviously correlates with the formation of the island (Frantz et al., 2018). Sulawesi formed from an agglomeration of a number of different proto-islands within the last 20 million years (Nugraha & Hall, 2018). The proto-islands largely overlap with the identified areas of endemism (Evans et al., 2003; Fooden, 1969). To what degree island formation and soils have shaped endemism in Sulawesi's tree flora is unclear.

In most communities, a few common species tend to be found together with many rarer species (Preston, 1948). Tree species become common in very specific local environmental conditions (Umaña, Zhang, Cao, Lin, & Swenson, 2017) and, as a result, do not generally dominate across different environments (Pitman, Silman, & Terborgh, 2013) although there are, of course, exceptions to the rule (Draper et al., 2019). Exceptions occur when contrast in the environment is not too great (Fine & Baraloto, 2016). For instance, in the western Amazon, there is a large contrast between infertile white sands and more fertile terra firme soils and the dominant species differ (Fine & Baraloto, 2016). Whereas, in the Upper Rio Negro of Brazil terra firme soils are less fertile, the contrast with white sand is less and dominants occur across the divide (Stropp, Van Der Sleen, Assunção, da Silva, & ter Steege, 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 (a) diversity, endemism, and species dominance at sites and (b) 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).
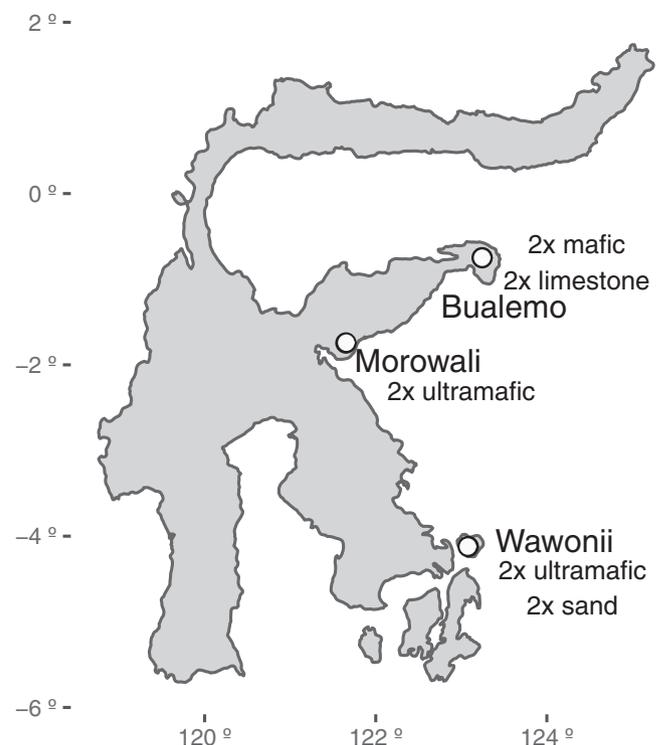
FIGURE 1 Localities of permanent forest plots in Sulawesi, Indonesia. Bualemo has two mafic and two limestone plots, Morowali has two ultramafic plots, and Wawonii has two ultramafic and two sand plots

Following published protocols, trees with stems ≥10 cm diameter at breast height (dbh; 1.3 m) were measured and permanently tagged (Phillips, Baker, Feldpausch, & Brienen, 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 × 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 HNO_3 and 1 ml $HClO_4$ at 100 to 200°C by ramping over a 7-hr 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, Chiu, & Jost, 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, Jost, & Chao, 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 (Ganesan, Middleton, & Wilkie, 2020; Hartley, 1979; de Kok, 2016; Merrill, 1922; Sleumer, 1969; Stevens, 1980; Turner, 1995; Weerasooriya & Saunders, 2002; Wiriadinata, Girmansyah, Hunter, Hoover, & Kartawinata, 2013).

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 10% of plots were designated as dominant (Arellano, Cayola, Loza, Torrez, & Macía, 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
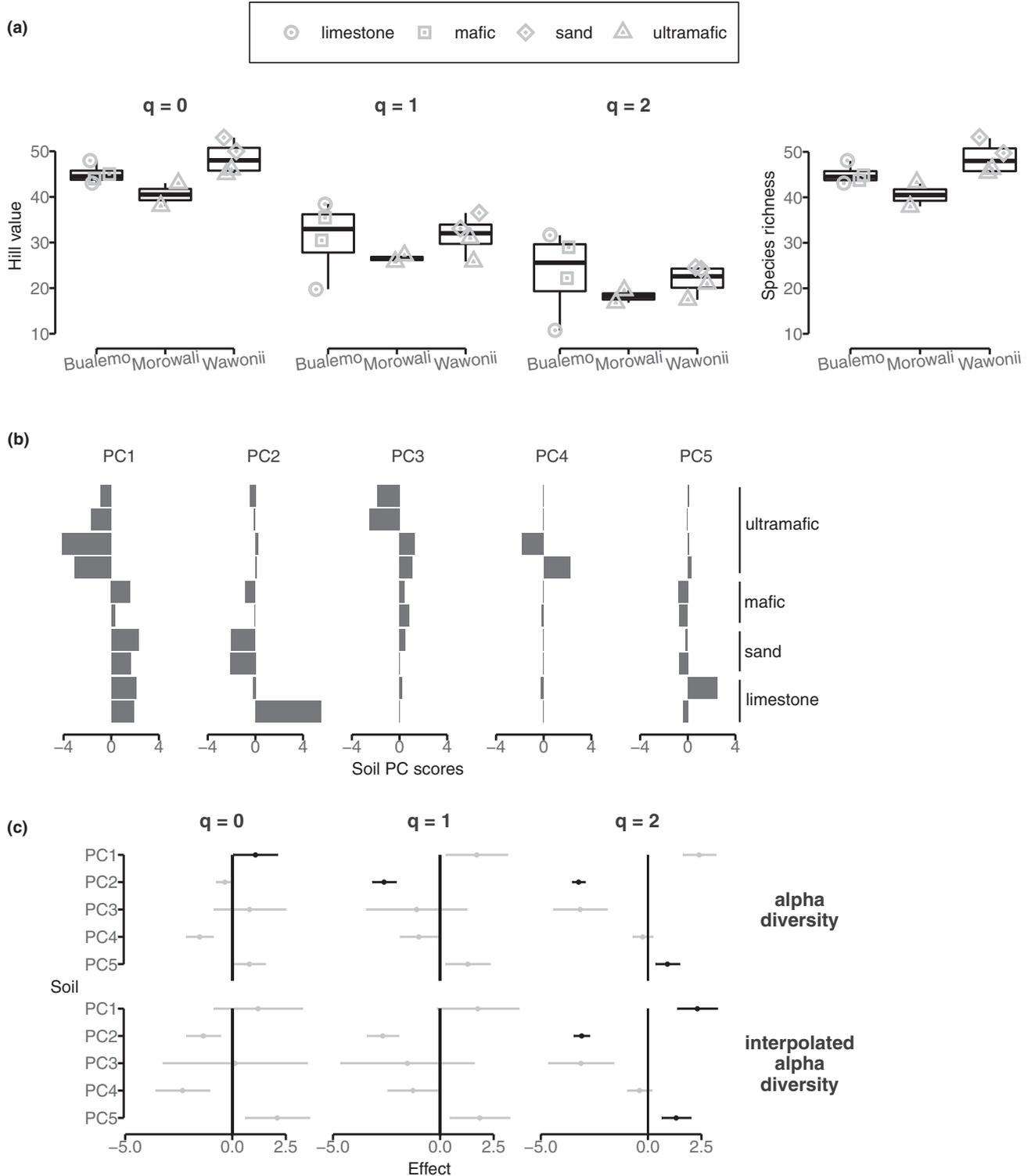
FIGURE 2 (a) Abundance unweighted ($q = 0$) and abundance-weighted ($q = 1$ and 2) Hill number values and species richness of tree communities across permanent forest plots in three regions of Sulawesi, Indonesia. $q = 0,1,2$ are species richness, Shannon and Simpson diversity equivalent Hill numbers, respectively. (b) Edaphic principal component axes scores for all plots in Sulawesi. (c) Effects of edaphic principal components upon Sulawesi tree community Hill number and interpolated Hill number measures (rows) with increasing abundance weighting defined by parameter q (columns). Significant effects ($p < 0.05$) are denoted by black symbols. Points represent coefficient estimates and whiskers the standard error for the estimates.

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, Ma, & Chao, 2016). Indicator species analysis was performed with *indicspecies*.

Beta diversity and components calculated with *betapart* (Baselga, 2010) and visualized 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 were carried out with *vegan*. Code for analysis is in online supporting information.

3 | RESULTS

3.1 | General floristics

In total, 1,434 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. *Gironniera 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 (Figure 2). This was consistent across measures increasingly weighted by species abundance and interpolated measures (Figure 2). Fisher's alpha shows greater diversity across our plot series compared to Seram (Edwards, Payton, Proctor, & Riswan, 1990). However, greater diversity was seen in Borneo and Sumatra (e.g., Potts, Ashton, Kaufman, & Plotkin, 2002; Sambas & 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),

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	*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

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 $p > .05$) but a significant impact of region ($p = .001$) upon community species composition. The UPMGA clustering of the Jaccard dissimilarity results showed clear regional groups (Figure 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.

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

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

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, Nogales, Heleno, & Vargas, 2018). There could also be climatic barriers to dispersal between the three study regions (Garg, Chattopadhyay, Wilton,

Prawiradilaga, & Rheindt, 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 colonized (Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 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 (Cámara-Leret, Tuomisto, Ruokolainen, Balslev, & Munch Kristiansen, 2017; Eiserhardt, Svenning, Baker, Couvreur, & Balslev, 2013; Fine & Kembel, 2011; Potts et al., 2002). This results in marked turnover of species at edaphic boundaries (Aiba et al., 2015; Draper et al., 2017; Fine, García-Villacorta, Pitman, Mesones, & Kembel, 2010; Paoli, Curran, & Zak, 2006). 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, Malphigiales (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, Toivanen, & Hjort, 2020; Read et al., 2020). Sulawesi not only has many types of geology (i.e.,

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.

(a) within region

(b) between regions

● Bualemo
● Morowali
● Wawonii
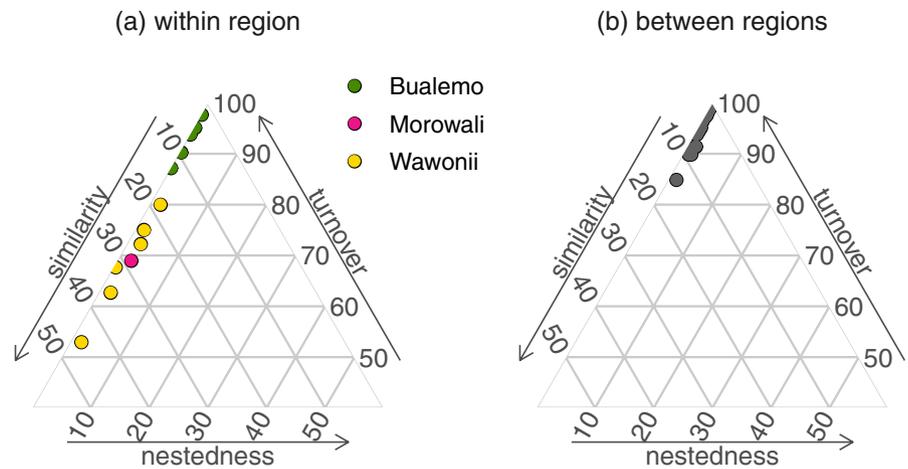
FIGURE 4 (a) Ordination of tree communities in Sulawesi (Indonesia) forest plots by non-metric multidimensional scaling. Region is indicated with point colors. Soil types are denoted by point shape. Arrows show soil principal component (PC) axes. Gray points indicate species position in ordination space. (b) Clustergram from UPMGA scaling of Jaccard dissimilarity between communities. Colors show the region.
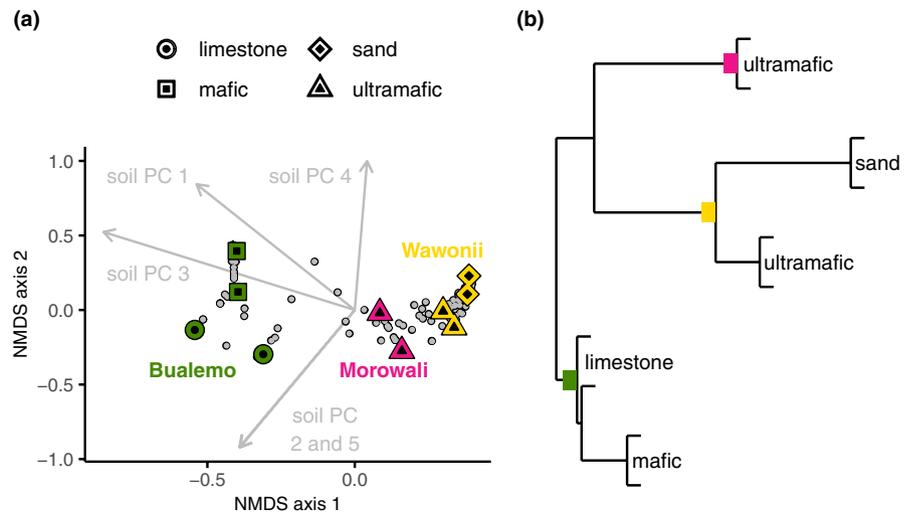
those underlying the soil types studied here), but it also has an on-togeny with the potential to influence biogeography irrespective of geological similarity or dissimilarity. In addition, Sulawesi is mountainous with large areas of mafic and ultramafic soils. This combination has been linked to particularly 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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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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