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Diversity, endemism, and composition of tropical mountain forest communities in Sulawesi, Indonesia, in relation to elevation and soil properties



Fabian Brambach^{a,*}, Christoph Leuschner^a, Aiyen Tjoa^b, Heike Culmsee^{a,c}

^a Plant Ecology and Ecosystems Research, Albrecht-von-Haller-Institute for Plant Sciences, University of Goettingen, Untere Karspüle 2, 37073 Goettingen, Germany

^b Agriculture Faculty, Tadulako University, Palu, Central Sulawesi, Indonesia

^c DBU Natural Heritage, German Federal Foundation for the Environment, An der Bornau 2, 49090 Osnabrück, Germany

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ABSTRACT

Explaining the diversity and distribution of tree taxa in the isolated tropical mountain forests (TMF) of the Malesian archipelago remains one of the great challenges of tropical biogeographical research. We investigated tree diversity, endemism and community composition in 13 plots of 0.24 ha between 700 and 2400 m in the TMF of Central Sulawesi's (Indonesia) highlands and related the patterns to gradients in elevation, climate and soil properties. Special attention was paid to understorey trees with stem diameters as low as 2 cm, not exceeding 2/3 of stand canopy height. Based on extensive taxonomic work on the plots, we found that Sulawesi's TMF flora is with 27–78 species per 0.24 ha not species-poorer than that of other Malesian islands, and vascular plant endemism is higher (22% of the species endemic to Sulawesi) than previously thought. Alpha diversity was mainly dependent on elevation and not soil factors (7 parameters tested). The alpha diversity of tree species, genera and families declined linearly with elevation, as did the number of species and genera per family, revealing higher phylogenetic clustering at lower elevations. Indicator Species Analysis and cluster analysis identified three main forest belts (sub-montane at c. 700–1400 m, lower montane at c. 1400–2000 m, upper montane at > c. 2000 m), deviating from earlier zonation concepts by separating sub-montane (rich in taxa related to the lowlands) and lower montane communities (rich in Fagaceae and Myrtaceae). With 27–51% of all tree species in a plot never found in the upper canopy, our data suggest that the guild of true understorey tree species is species-rich (estimated at c. 130 species in our region), contradicting the hypothesis that Southeast Asian tropical forests with mass-flowering trees (here: Fagaceae) are particularly poor in understorey tree species. We conclude that the mountains of Sulawesi harbour remarkably species-rich, but still understudied, TMF with a unique tree flora rich in understorey trees, which are of high conservation priority.

1. Introduction

Tree species richness is not uniformly distributed across the tropics. In addition to differences at the continental scale (Barthlott et al., 2007; Slik et al., 2015), driven in part by the available species pool as a result of geological history (Parmentier et al., 2007), environmental factors like climate and soil properties (Koponen et al., 2004; ter Steege et al., 2003) and biological interactions (Noguchi et al., 2007) are important determinants of tree diversity patterns. Both climate and soil conditions change markedly along mountain slopes, making them preferred objects of research on the drivers of tree species diversity (Aiba and Kitayama, 1999; Culmsee et al., 2011; Culmsee and Leuschner, 2013; Culmsee and Pitopang, 2009; Homeier et al., 2010; Merckx et al., 2015;

Ohsawa et al., 1985). Due to the close proximity of different habitats and communities and resulting high beta diversity along the slope, tropical mountain forests (TMF) constitute one of the biologically richest landscapes on earth (Aldrich et al., 1997) and often contain a large number of endemic species (Merckx et al., 2015). Along tropical mountain slopes, two principal patterns of plant alpha diversity change with elevation have been observed; a hump-shaped pattern, often found in herbs and ferns (Bhattarai et al., 2004; Bhattarai and Vetaas, 2003; Dossa et al., 2013; Kessler, 2000; Willinghöfer et al., 2011), and a monotonic decline with elevation, apparently prevalent in trees (Aiba et al., 2002; Culmsee and Leuschner, 2013; Dossa et al., 2013; Homeier et al., 2010; Ohsawa et al., 1985). It has been argued that the latter pattern might be an artefact caused by incomplete sampling along the

Abbreviations: LLNP, Lore Lindu National Park; TMF, tropical mountain forest

* Corresponding author.

E-mail addresses: fbramba@gwdg.de (F. Brambach), cleusch@gwdg.de (C. Leuschner), aiyenb@yahoo.com (A. Tjoa), h.culmsee@dbu.de (H. Culmsee).

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elevation gradient (Rahbek, 2005, 1995), but studies on the complete vascular plant flora on the slope of Mount Kinabalu (Borneo) have confirmed the existence of both elevation patterns for the groups of ferns/herbs and trees (Grytnes and Beaman, 2006). In Malesian TMF, where patterns of tree alpha diversity have been studied at the genus level (Culmsee and Leuschner, 2013; van Steenis, 1962, 1935), a monotonic decline in taxonomic diversity was found as well. Here, the number of genera per family also decreased with elevation, reflecting phylogenetic clustering at lower elevations and overdispersion further upslope. It has been suggested that the diversity pattern of genera closely reflects that of species in Amazonian lowland forests and that therefore genus-level analyses are sufficient in many cases (Higgins and Ruokolainen, 2004). However, the relationship between elevational patterns of species, genera, and family diversity of trees is so far unknown for Southeast Asian forests. We also lack information as to whether elevational patterns of species diversity differ between different phylogeographic regions in Southeast Asia. The geologically relatively young region of Wallacea, which includes Sulawesi, is generally assumed to harbour lower levels of biodiversity than the better-explored continental shelf area known as Sundaland to the west (e.g. Barthlott et al., 2007; Kier et al., 2009), but this may merely be an artefact caused by differences in land area (Roos et al., 2004). Elevational gradients represent experiments of nature with respect to the response of plant communities to gradual environmental change (Körner, 2007). In humid tropical mountains, the most influential abiotic factor that changes more or less monotonically with elevation is temperature. Temperature not only influences the physiology of the trees but also key ecosystem functions such as decomposition and mineralisation rates and the accumulation of soil organic matter (Letts et al., 2010). However, small-scale variation in topography on mountain slopes and related gradients in bedrock and soil properties are often overlaying the effects of the temperature decrease with elevation and they considerably increase habitat diversity in tropical mountains. For example, the extraordinarily high tree species richness in the TMF of the eastern slopes of the Ecuadorian Andes is in part the consequence of a high diversity of habitats on upper, mid, and lower slope positions and variable slope aspects (Homeier et al., 2010). On Mount Kinabalu, Borneo, bedrock and thus soil chemical properties show a marked change along an elevation transect spanning about 2400 m (Kitayama and Aiba, 2002). Although elevation was the most influential environmental correlate for the diversity and composition of tree communities in that elevational transect study, a significant proportion of the variation in tree diversity on Borneo was explained by soil properties (Slik et al., 2009). It appears that large differences in edaphic conditions, such as the contrast between soils on silicate, calcareous, or ultramafic rocks, may in certain cases lead to larger differences in tree diversity and community structure than the elevation gradient itself (Aiba et al., 2015). Since the first studies of Alfred Russel Wallace (1869), the strong endemic element in Sulawesi's fauna has been well recognised (e.g. Michaux, 2010; Musser, 1987; Stelbrink et al., 2012), while endemism in Sulawesi's flora has been thought to be less pronounced with estimates ranging from 12.3 to 14.2% (Roos et al., 2004; van Balgooy, 1987; van Welzen et al., 2011). If valid, this proportion would be much lower than for the neighbouring islands of Borneo, the Philippines, and New Guinea (Culmsee et al., 2011; van Welzen et al., 2011; van Welzen and Slik, 2009). However, reliable estimates of plant endemism are difficult to obtain for Sulawesi, mainly due to insufficient knowledge of the island's flora (Cannon, 2001; Culmsee et al., 2011; Keßler et al., 2002). The presence of mountain ranges is an important factor which increases the number of endemic organisms. Unique biotas are also the main cause for the high conservation values of tropical mountains (Aldrich et al., 1997; Brehm et al., 2005; Brummitt and Lughadha, 2003; Richter, 2008). In the Malesian region, patterns of plant endemism in TMF have rarely been investigated (Merckx et al., 2015; Raes et al., 2009). On Sulawesi, which has 7% of its total land surface area at montane elevations (> 1500 m; Culmsee and Leuschner,

2013), tree inventories at mid- and upper montane elevations (Culmsee et al., 2011) found higher values (20%) for endemic trees than those previously reported (see above) suggesting that endemism patterns in vascular plants at higher elevations of this island should be re-evaluated. Many diversity analyses in tropical forests are incomplete because part of the understorey species is neglected due to the conventional stem diameter threshold of 10 or 7 cm. However, this neglected guild of shade-tolerant, low-stature trees may significantly contribute to overall tree diversity and play an important role in canopy light interception, as it reduces transmission to very low levels. According to LaFrankie et al. (2006), the guild of understorey trees is less species-rich in Asian lowland rainforests than in Neotropical forests; this assumption needs verification by carefully collected field data. We investigated tree diversity, endemism and community composition of natural forests along an elevational gradient from 700 to 2400 m in the highlands of Central Sulawesi and related the patterns to gradients in climate and soil properties. Special attention was placed on the inclusion of the understorey trees with stem diameters as low as 2 cm. We expanded the dataset of earlier work (Culmsee et al., 2011; Culmsee and Leuschner, 2013; Culmsee and Pitopang, 2009) to 13 intensive tree inventory plots, focused rigorously on correct species-level identification, and analysed endemism patterns in the woody flora in detail. The poor knowledge of the forest vegetation in this region required elaborating a basic forest community classification as a foundation for the analysis of diversity patterns. Specifically, we addressed the following questions:

1. How does tree alpha diversity at different taxonomic levels (species, genera, families) vary along environmental gradients (climate, soil)?
2. How does alpha diversity change along the elevation gradient in comparison with other mountain ridges in Malesia?
3. Does the diversity of endemic tree species change along the gradients?
4. How do beta diversity and community composition change along these environmental gradients?
5. Do true canopy and understorey species disperse differently along the climate and soil gradients?

2. Material and methods

The study was carried out in Lore Lindu National Park (LLNP; Fig. 1) in the central mountain range of Sulawesi, Indonesia, an area dominated by acid plutonic and metamorphic rocks and displaying a variety of soil types. The climate of the area is perhumid with most rainfall occurring during April–May and November–December and a slightly drier period from July to October. Drought stress can occur periodically in the intermontane valleys below 1500 m and at irregular intervals due to ENSO events (Wündsche et al., 2014). Seasonal temperature variation is minimal; mean annual temperature decreases by c. 5.2 K per 1000 m elevation from 23.0 °C at 700 m to 14.1 °C at 2400 m (Hijmans et al., 2005; WorldClim, 2014). LLNP was created in 1999 and predominantly comprises rainforest from colline (c. 500 m a.s.l.) to upper montane (2525 m a.s.l.) elevations (Cannon et al., 2007; Culmsee et al., 2010) with a variety of forest types of high conservation value (Le Saout et al., 2013). With a size of c. 2215 km² and 84% of its area at > 1000 m, it is the largest protected area of montane forest on Sulawesi. The park's forests have been little affected by human activities until the end of the 19th century, but since then, impact has steadily increased (Biagioni et al., 2015; Weber, 2006), in particular in the valleys. We selected thirteen study sites of primary forest in LLNP at elevations between 700 and 2400 m a.s.l. (Appendix A; Table A.1) and carried out tree inventories from February 2011 to April 2012. At each site, we censused all trees with diameter at breast height (dbh) ≥ 10 cm ('large trees') in a rectangular plot of 0.24 ha size (60 m x 40 m) and additionally all small trees (dbh 2–9.9 cm) in subplots totalling 0.06 ha. All censused trees were permanently marked with a number, measured (dbh and height), and pre-identified in the field; we collected extensive herbarium

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