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ORIGINAL ARTICLE

Forest aboveground biomass along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain forests

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ABSTRACT

Aim This study investigates how estimated tree aboveground biomass (AGB) of tropical montane rain forests varies with elevation, and how this variation is related to elevational change in floristic composition, phylogenetic community structure and the biogeography of the dominant tree taxa.

Location Lore Lindu National Park, Sulawesi, Indonesia.

Methods Floristic inventories and stand structural analyses were conducted on 13 plots (each 0.24 ha) in four old-growth forest stands at 1050, 1400, 1800 and 2400 m a.s.l. (submontane to upper montane elevations). Tree AGB estimates were based on d.b.h., height and wood specific gravity. Phylogenetic diversity and biogeographical patterns were analysed based on tree family composition weighted by AGB. Elevational trends in AGB were compared with other Southeast Asian and Neotropical transect studies ($n = 7$).

Results AGB was invariant from sub- to mid-montane elevation (309–301 Mg ha^{-1}) and increased slightly to 323 Mg ha^{-1} at upper montane elevation. While tree and canopy height decreased, wood specific gravity increased. Magnoliids accounted for most of the AGB at submontane elevations, while eurosids I (including Fagaceae) contributed substantially to AGB at all elevations. Phylogenetic diversity was highest at upper montane elevations, with co-dominance of tree ferns, Podocarpaceae, Trimeniaceae and asterids/euasterids II, and was lowest at lower/mid-montane elevations, where Fagaceae contributed > 50% of AGB. Biogeographical patterns showed a progression from dominant tropical families at submontane to tropical Fagaceae (*Castanopsis*, *Lithocarpus*) at lower/mid-montane, and to conifers and Australasian endemics at upper montane elevations. Cross-continental comparisons revealed an elevational AGB decrease in transects with low/no presence of Fagaceae, but relatively high AGB in montane forests with moderate to high abundance of this family.

Main conclusions AGB is determined by both changes in forest structure and shifts in species composition. In our study, these two factors traded off so that there was no net change in AGB, even though there were large changes in forest structure and composition along the elevational gradient. Southeast Asian montane rain forests dominated by Fagaceae constitute important carbon stocks. The importance of biogeography and species traits for biomass estimation should be considered by initiatives to reduce emissions from deforestation and forest degradation (REDD) and in taxon choice in reforestation for carbon offsetting.

Keywords
Aboveground biomass, biogeography, Celebes, elevation, Fagaceae, phylogenetic diversity, REDD, Sulawesi, tropical montane forest.

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INTRODUCTION

Tropical forest biomass plays an important role in the global carbon cycle, but the magnitude of this pool and its regional variation are not well understood (Dixon *et al.*, 1994; Clark *et al.*, 2001; Clark, 2004; Malhi & Phillips, 2004; Chave *et al.*, 2005). Recently published syntheses on aboveground biomass (AGB) in Amazonian forests (Baker *et al.*, 2004; Malhi *et al.*, 2006; Saatchi *et al.*, 2007) have greatly increased our understanding of old-growth forest AGB variation across environmental gradients in the lowlands. However, much less is known about the biomass of tropical montane rain forests and changes in tree biomass carbon pools along elevational gradients. Increasing elevation may affect tree growth rates and stand structure because of reduced air and soil temperatures, often increased rainfall, and alterations in nutrient availability and soil chemistry (Coomes & Allen, 2007; Körner, 2007). Previous studies along tropical mountain slopes have detected a decrease in tree height (Lieberman *et al.*, 1996; Aiba & Kitayama, 1999; Moser *et al.*, 2008) and an increase in stem density with increasing elevation (Aiba & Kitayama, 1999; Moser *et al.*, 2008). However, the existing information indicates that the pattern in AGB varies significantly between different tropical mountain ranges (Weaver & Murphy, 1990; Lieberman *et al.*, 1996; Raich *et al.*, 1997; Kitayama & Aiba, 2002; Wang *et al.*, 2003; Moser *et al.*, 2008).

A better understanding of elevational changes in tropical forest AGB and the underlying causes is important in the context of reducing emissions from deforestation and forest degradation (REDD) initiatives (UNFCCC, 2007). Such knowledge is helpful for the selection of taxa in reforestation, particularly for the purposes of carbon offsetting, and it could improve our ability to predict the future changes in tropical forest AGB that may result from increasing temperatures in the tropics under global change (Clark, 2004; Lewis *et al.*, 2004; Malhi & Phillips, 2004).

Both phylogeny and biogeography may have a profound influence on the structure, composition and functioning of tropical forests. It has been suggested that over evolutionary timescales, lowland forests served as speciation centres and maintained tree diversity in tropical montane floras (Slik *et al.*, 2009), whilst tropical montane regions have acted as refugia for many taxa during times of palaeo-climatic change (Malhi & Phillips, 2004; Mayle *et al.*, 2004; VanDerWal *et al.*, 2009). We therefore expect steep elevational gradients in floristic and phylogenetic tree community composition. The AGB in Amazonian lowland rain forests has been found to be determined largely by wood specific gravity (Baker *et al.*, 2004; Malhi *et al.*, 2006), a trait that is itself highly dependent on phylogeny (Baker *et al.*, 2004; Slik, 2006). Therefore, if more general patterns are to be recognized, analyses of changes in AGB with elevation must consider profound changes in forest community composition and their related traits, in addition to changes in forest structure.

This paper reports on an elevational transect study in Central Sulawesi, Indonesia, covering an elevational range of about 1400 m from the submontane to the upper montane belt. Sulawesi is part of the biogeographical region Wallacea, one of the major biodiversity hotspots in the Palaeotropics (Myers *et al.*, 2000; Sodhi *et al.*, 2004), but also one of the most poorly known ecoregions of Southeast Asia (Cannon *et al.*, 2007). Because tropical taxa of the Fagaceae are abundant in many Southeast Asian tropical montane rain forests (Ashton, 1988, 2003; Ohsawa, 1993; Corlett, 2007), we expect that this is also the case in Sulawesi.

The study is based on a thorough floristic tree inventory of four mountain forest sites. The aim was to understand how the AGB of these forests varied with elevation, and how this variation was related to changes in tree community composition. We hypothesized that (1) there would be a directional change in AGB with increasing elevation because of forest structural changes (tree height, basal area and stem density), and (2) changes in tree family composition, reflecting the phylogenetic and biogeographical community structure, would have a secondary effect on forest AGB. We conclude by comparing elevational patterns in AGB found in this study with those found in other Southeast Asian and Neotropical mountain forest transects.

MATERIALS AND METHODS

Study region

The study was conducted in submontane to upper montane tropical rain forests of Lore Lindu National Park, Central Sulawesi, Indonesia, 120°03′ E to 120°18′ E latitude, and 01°14′ S to 01°39′ S longitude (Fig. 1). With an area of about 2180 km^2, Lore Lindu National Park is one of the last remaining large, contiguous blocks of intact forest in Sulawesi.

Four study sites, at 1050, 1400, 1800 and 2400 m a.s.l., were selected in forests on level or gently sloping terrain that showed no sign of recent human impact (Table 1). According to the regional classification system of Cannon *et al.* (2007), the condition of the forests is characterized as 'good' or 'old-growth'. Mean annual precipitation ranges between 1891 and 2131 mm (Hijmans *et al.*, 2005; WorldClim, 2006), mean annual temperature decreases by about 5.3 K per 1000 m elevation from 21.3°C at 1050 m to 14.1°C at 2400 m. The climate is perhumid, with at most 2 months a year receiving < 100 mm rainfall on average. The soils are Ferralsols or Nitisols at submontane to lower montane elevations and Histic Cambisols at mid- and upper montane elevations (FAO classification; FAO, 2006). The bedrock consists of granite or various types of metamorphic rock.

Situated east of Wallace's Line in the Wallacea biogeographical region, the forests of the study region represent species-rich tropical montane forests composed of predominantly tropical taxa with > 100 species ha^{-1} at submontane elevations (Culmsee & Pitopang, 2009). Tree species richness and importance of lowland tropical tree families decrease above 1000 m a.s.l. In total, we surveyed 13 plots of 60×40 m over four study sites, covering in total a forest area of 3.12 ha

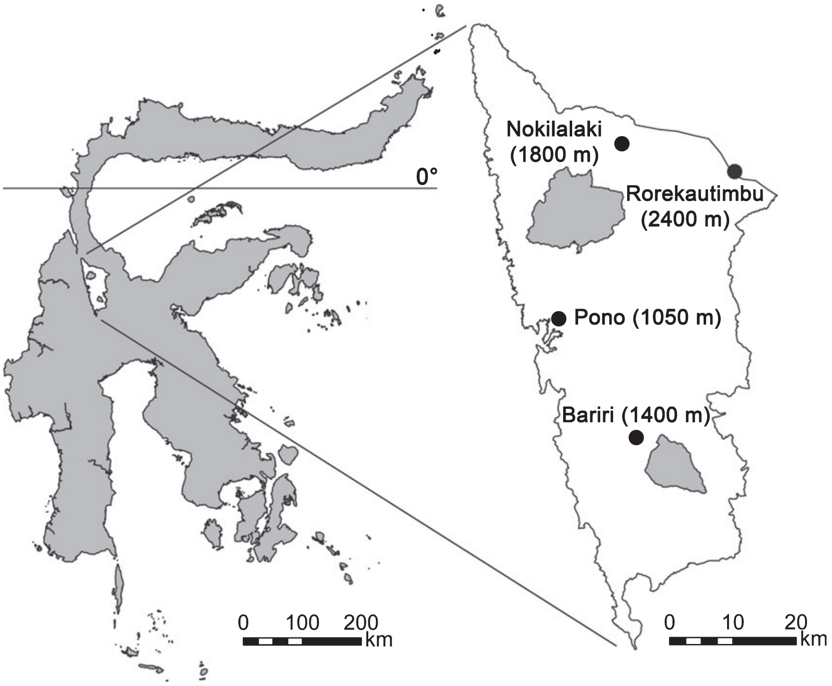

Figure 1 Location of the four study sites in Lore Lindu National Park, Central Sulawesi, Indonesia (Universal Transverse Mercator projection 51 south).

Table 1 Location and characteristics of the four study sites in Lore Lindu National Park, Sulawesi, Indonesia.

Forest type	Elevation (m a.s.l.)	Location	Coordinates GC-WGS 84	Slope, position	Soils and bedrock	Rainfall (mm yr^{-1})	Temperature (°C)	No. plots	Total area (ha)
Submontane forest	1050	Pono Valley	01°29.6′ S 120°03.4′ E	Level terrain on mid-slope terrace	Ferralsol on metamorphic rocks	1894	21.3	6	1.44
Lower montane forest	1400	Bariri Forest	01°39.5′ S 120°10.4′ E	Level terrain on fluvio-lacustrine terrace	Nitisol on metamorphic rocks	1975	19.1	3	0.72
Mid-montane forest	1800	Mt Nokilalaki	01°14.6′ S 120°09.2′ E	Level terrain on a mid-slope terrace	Histic Cambisol on granite	1891	17.9	2	0.48
Upper montane forest	2400	Mt Rorekautimbu	01°16.8′ S 120°18.5′ E	Gently sloping ridge	Histic Cambisol on granite	2131	14.1	2	0.48

and containing more than 3400 tree individuals of 236 species in 62 families.

Stand structural inventories

Stand structural inventories were carried out in the periods from July to September 2006 and August to September 2007. At each of the four study sites, two to six 0.24-ha plots were selected in stand areas that met the following criteria: (1) mature forests, (2) level or gently sloping terrain, (3) well drained soils lacking depressions with seasonal waterlogging, and (4) a mean canopy height that was representative of the forest types. The stands contained small tree-fall gaps, as is typical for natural forests, but no large gaps. A 10 × 10-m grid was placed on the 40 × 60-m plots and all trees (including palms, tree ferns and tree-like stranglers) ≥ 10 cm d.b.h. (at 1.3 m) were tagged, their plot coordinates were determined, d.b.h. was measured with a measuring tape (Richter Measuring Tools, Speichersdorf, Germany), and tree height was recorded using a Vertex III height meter equipped with a T3/60° transponder (Haglöf, Långsele, Sweden). Where stilt roots were present, d.b.h. was measured above them following the recommendations of Clark *et al.* (2001) and Phillips *et al.* (2002). To survey understorey trees of 2–9.9 cm d.b.h., one 5 × 5-m subplot was installed in each of the 24 10 × 10-m plots and was surveyed as described for the larger trees.

Tree species identification

Tree species identification was based on about 3000 specimens collected from tagged trees and supplementary trees inspected in flower or fruit. Specimens have been deposited at the herbaria at Leiden (L), Göttingen (GOET), Palu (CEB) and London (K). Tree species were identified by H.C. and by specialists for Elaeocarpaceae (M.J.E. Coode, K), Moraceae (C.C. Berg, L) and Myristicaceae (W.J. de Wilde, L). Taxa that were difficult to identify to species level, especially in the Myrtaceae, were distinguished as separate species based on morphology of vegetative characters (leaves, twigs and bark). Of 3408 tree individuals in total, 3197 trees were identified to the species level (including 12 morpho-species of the Myrtaceae), 165 trees to genus and 20 trees to family level. Only 26 individuals (< 1%) remained unidentified. So far, one new species has been described (Culmsee, 2008). Species were assigned to families according to IPNI (2008), with the exception of the species of *Quintinia* A.DC. and *Sphenostemon* Baill., which were included in the Southeast Asian endemic family of the Paracryphiaceae following Stevens (2001 onwards). The complete species list for the sites at 1050 and 1400 m elevation is given in Culmsee & Pitopang (2009).

Sample-based rarefaction analysis

Rarefaction analysis (Gotelli & Colwell, 2001) was used to confirm that the sampled area at each site was sufficiently large to represent the species pool, which may affect the variation in wood specific gravity. Sample-based rarefaction curves (MaoTau = expected species accumulation curves) based on all species discovered in 0.01-ha subplots per site, including all tree individuals of d.b.h. ≥ 2 cm, were computed using EstimateS ver. 8.0.0 (Colwell, 2006) with the 'randomize by samples without replacement' protocol option and 999 Monte Carlo permutations. The species–area curves (Fig. 2) showed that species richness decreased with increasing elevation. The plateau segments of the species–area curves were reached earlier at higher elevations than at lower ones, thus demonstrating that smaller sampling areas are sufficient at higher elevations.

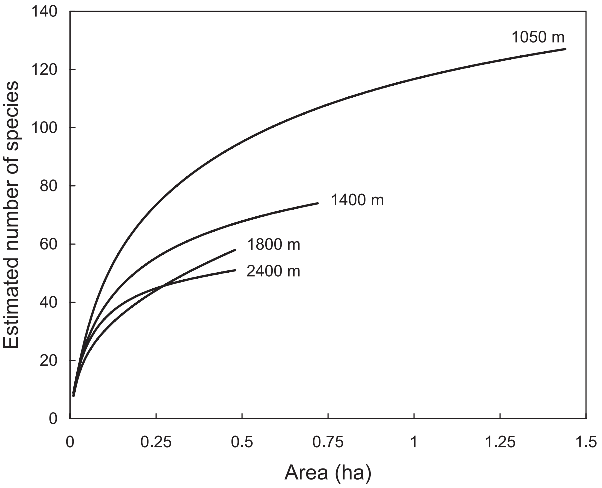

Figure 2 Sample-based rarefaction curves for submontane (1050 m), lower montane (1400 m), mid-montane (1800 m) and upper montane (2400 m) elevations summarizing the tree species accumulation curves for all plots of a site in Lore Lindu National Park, Sulawesi.

Estimation of aboveground biomass

The choice of the allometric regression model for converting tree structural data into AGB estimates is one of the most important sources of uncertainty in estimates of carbon stocks in tropical forests (Araújo *et al.*, 1999; Chave *et al.*, 2005). Another important component is wood-specific gravity, ρ (Baker *et al.*, 2004; Slik, 2006). In the pan-tropical analysis of Chave *et al.* (2005), which included a large data set of 2410 harvested trees from 27 study sites, wood specific gravity, trunk diameter and forest type were identified as being the variables with the highest predictive power. The consideration of tree height further increased the accuracy of the models.

Considering the bioclimatic conditions in the study area, we decided to adopt the equation used by Chave *et al.* (2005) for wet forest stands:

$$\mathrm{AGB}_{\mathrm{est}} = \exp[-2.557 + 0.940 \times \ln(\rho \times D^2 \times H)] \tag{1}$$

where $\mathrm{AGB}_{\mathrm{est}}$ is estimated aboveground biomass (in kg per tree), D is trunk diameter (d.b.h., in cm), H is total tree height (in m), and ρ is oven-dry wood specific gravity (in g cm^{-3}). Wood specific gravity is rarely reported for tropical trees; instead, a density value based on the mass of a sample at 12 or at 15% moisture is frequently given (Chave *et al.*, 2006). The wood specific gravity values used in this study were obtained from various sources (Oey, 1990; Soerianegara & Lemmens, 1993; Lemmens *et al.*, 1995; Sosef *et al.*, 1998). Where a range of values was reported, we used the median value. Where wood density data were unavailable for a species, the average across all species in that genus in the corresponding habitat was applied, as wood density is a taxonomically conserved trait (Baker *et al.*, 2004; Slik, 2006). Where only the family was identified (n = 20), we used the average among the known species. In the few cases where a tree individual could not be identified at least to family level (n = 26) or where no literature was available (n = 143), we used the plot average among all known species. To convert wood density at 12% moisture (r_{12}) into oven-dry wood specific gravity ρ, Chave *et al.* (2006) found the following stable relationship across a large data set obtained from many tropical forests (n = 1893):

$$\rho = 0.872 \times r_{12} \tag{2}$$

We converted the data available from the literature by using the factor 0.872 at 12% moisture content, or (by assuming a linear ρ/r relationship) the factor 0.84 at 15% moisture content.

Some taxa required a specific calculation procedure for estimating AGB as a result of their distinct growth pattern and allometry.

1. *Castanopsis acuminatissima* Blume (Fagaceae) is a common tree species of the sub- and lower montane forests that builds clusters of root suckers sprouting from a common compact base of up to 2 m tall (Soepadmo, 1972). Each stem of ≥ 2 cm d.b.h. was measured above the common base and AGB_{est} was calculated separately for each stem.

2. Stranglers of the genus *Ficus* L. (Moraceae, $n = 5$ at the site at 1050 m a.s.l.) that have developed into a free-standing, tree-like structure are characterized by a large central cavity that was originally filled by the trunk of the host tree. For an approximation of the hollow space, d.b.h. of the original tree was recalculated (D_{est}) using the logarithmic equation derived from the tree height – d.b.h. regression model of all trees occurring at the study site at 1050 m a.s.l. (excluding *C. acuminatissima* and *Ficus* species) that has the form:

$$y = 13.759 \times \ln(x) - 19.622 \qquad (3)$$

where y is the tree height and x is the estimated trunk diameter D_{est} ($R^2 = 0.68$, $P \leq 0.001$). Based on the growth pattern of stranglers of *Ficus* species as outlined by Hallé *et al.* (1978), we assumed the total height of the host tree to be equivalent to the mean of the total height H and trunk height T of the strangler tree. AGB_{est} was calculated for both the strangler and the hollow space based on equation 1, and subsequently the latter was subtracted from the former:

$$\begin{aligned} AGB_{est} = {} & \exp[-2.557 + 0.940 \times \ln(\rho_{Ficus\_sp} \times D^2 \times H)] \\ & - \exp\{-2.557 + 0.940 \times \ln[\rho_{Ficus\_sp} \times D_{est(eqn3)}{}^2 \\ & \times \text{mean}(H;T)]\} \end{aligned} \qquad (4)$$

Statistical analyses

Stand structural patterns were analysed for (1) large trees (≥ 10 cm d.b.h.), and (2) all trees (≥ 2 cm d.b.h.). In analyses referring to stem density, only the biggest stem of a cluster was counted in species with a sprouting growth habit, such as *C. acuminatissima* (Fagaceae), *Elaeocarpus steupii* Coode (Elaeocarpaceae), *Rapanea minutifolia* J.Knoester, M.Wijn & Sleumer (Myrsinaceae), *Trimenia papuana* Ridl. (Trimeniaceae), and several morpho-species of the Myrtaceae.

Significant differences in individual-based traits (tree height, d.b.h., wood specific gravity) between the four sites were tested with the nonparametric Behrens–Fisher test for multiple comparisons (Munzel & Hothorn, 2001) using the R package (R ver. 2.8.1, with the LAWSTAT and NPMC add-on packages).

Community structural similarity in terms of family composition along the elevational gradient was analysed by indirect gradient analysis (detrended correspondence analysis, DCA) using the CANOCO 4.5 package (ter Braak & Šmilauer, 2002).

Phylogenetic and non-phylogenetic diversity analyses

Phylogenetic community structure was analysed based on community tree family composition weighted by absolute AGB estimates instead of abundance data. A basic Newick phylogeny file was produced using PHYLOMATIC (Webb *et al.*, 2008a) with the mega-tree version R20080417 based on the angiosperm consensus tree (Davies *et al.*, 2004). Phylogenetic diversity (Rao's quadratic entropy index, PD_Q; Rao, 1982), non-phylogenetic diversity (Simpson's index, $1-D$; Magurran, 2004) and inter-sample phylogenetic distance (COMDISTNN, nearest taxon method; Webb *et al.*, 2008b) were calculated with PHYLOCOM (Webb *et al.*, 2008a). Non-metric multidimensional scaling (NMDS) based on the inter-sample phylogenetic distance was performed with WINKYST 1.0 (Šmilauer, 2002–2003).

Biogeographical pattern analysis

Each tree family was assigned to a biogeographical or functional group. Angiosperm families were classified based on biogeographical criteria that followed the families' main geographical distribution patterns and richness centres, as described by Heywood *et al.* (2007), where (1) 'tropical' families are restricted to tropical regions; (2) 'centred in tropics' means the family has experienced its greatest radiation in tropical regions but may also occur in subtropical and temperate regions, albeit with a considerably smaller number of species; (3) 'endemic to Malesia' are families that are restricted mostly to Southeast Asia while a few species may reach East Asia or Australasia; (4) 'tropical montane' families are restricted to, or are found primarily in, the montane elevational belt of tropical regions; (5) 'centred temperate' includes families that occur in the tropics but have a clear species density centre in the southern and/or northern temperate regions; (6) the 'Fagaceae' show a unique distribution pattern, being a dominant family in the temperate broad-leaved forests of Eurasia and North America, but also being important in the evergreen tropical montane rain forests of Southeast Asia, where the genera *Lithocarpus* Blume and *Castanopsis* have their evolutionary and richness centres. Other vascular plant families are included in the groups: (7) 'conifers' referring to Southern Hemisphere or tropical conifers; and (8) 'tree ferns' referring to pteridophytes with a d.b.h. ≥ 2 cm. 'Others' (9) include all vascular plant families that are cosmopolitan or cannot be classified under (1)–(8). Based on this classification, patterns across the four sites were analysed according to (i) the total AGB (Mg ha^{-1}) including all trees ≥ 2 cm d.b.h., and (ii) the number of trees ≥ 10 cm d.b.h. (n ha^{-1}). In species with a sprouting growth habit, the stems of each cluster were combined to give one count for the individual.

RESULTS

Elevational changes in stand structure and biomass

Both individual trees and height of the forest canopy grew steadily shorter with increasing elevation (Table 2). There was no elevational trend in mean stem diameter in large trees (≥ 10 cm d.b.h.); however, the submontane forest plots contained several very high and large diameter trees (≥ 100 cm d.b.h.) that were absent at higher elevations. These trees were primarily hollow-stemmed *Ficus* stranglers, which greatly reduced the impact of the large d.b.h. classes on aboveground

Table 2 Aboveground stand structural characteristics of the four study sites in Lore Lindu National Park, Sulawesi, giving means ± SE.

	Upper canopy height (m)	Mean tree height, trees ≥ 10 cm d.b.h. (m)	Max. tree height (m)	Mean d.b.h., trees ≥ 10 cm d.b.h. (cm)	Max. d.b.h (cm)	Basal area, trees ≥ 10 cm d.b.h. (m^2 ha^{-1})	Basal area, trees ≥ 2 cm d.b.h. (m^2 ha^{-1})	Wood specific gravity, ρ, at MC 0%, trees ≥ 10 cm d.b.h. (g cm^{-3})	Stems ≥ 10 cm d.b.h. (n ha^{-1})	AGB_{est}, trees ≥ 10 cm d.b.h. (Mg ha^{-1})	AGB_{est}, trees ≥ 2 cm d.b.h. (Mg ha^{-1})
Submontane forest (1050 m)	29.2 ± 0.5	20.9 ± 0.4^{a}	47.9 ± 1.1	23.5 ± 0.7^{a}	149.0 ± 14.9	35.4 ± 2.5	38.8 ± 2.6	0.521 ± 0.004^{a}	476 ± 21	299.1 ± 18.7	308.7 ± 18.8
Lower montane forest (1400 m)	24.6 ± 0.8	18.2 ± 0.3^{b}	37.4 ± 1.4	22.7 ± 0.9^{a}	94.9 ± 2.7	37.1 ± 0.9	40.9 ± 0.7	0.535 ± 0.005^{ac}	508 ± 22	293.4 ± 13.0	304.6 ± 12.6
Mid-montane forest (1800 m)	22.3 ± 0.1	17.6 ± 0.3^{b}	39.7 ± 6.9	21.9 ± 0.7^{a}	91.9 ± 4.9	36.0 ± 2.6	40.5 ± 2.5	0.606 ± 0.005^{b}	697 ± 110	286.5 ± 10.2	301.4 ± 9.5
Upper montane forest (2400 m)	19.8 ± 2.4	15.8 ± 0.3^{c}	37.4 ± 2.3	22.2 ± 0.6^{a}	98.9 ± 0.8	46.5 ± 4.3	51.4 ± 3.9	0.559 ± 0.004^{c}	879 ± 146	306.9 ± 9.5	322.6 ± 6.5

Different superscripted letters indicate significant differences in individual-based traits between the sites ($P \leq 0.05$, non-parametric Behrens–Fisher test for multiple comparisons). Site-based characteristics take into account the variation between 0.24-ha plots at each site. MC, wood moisture content. AGB_{est}, estimated aboveground biomass.

biomass (AGB = 38.5 Mg ha^{-1}, i.e. 46.7–8.2 Mg ha^{-1} cavity). Mean wood specific gravity, ρ, was lowest at submontane and highest at mid-montane elevation. This is mainly as a result of the dominance of *Lithocarpus* (Fagaceae) species, which, with an average genus ρ = 0.672 g cm^{-3}, yielded the highest mean wood specific gravity of all genera present. Stand basal area was more than 10 m^2 ha^{-1} higher in the upper montane forest than in lower elevations.

Stem density rose continuously with increasing elevation. In all forests, the smallest diameter class (< 5 cm d.b.h.) was the most numerous, and the number of stems decreased in an inverse J-shaped curve towards bigger tree diameter classes (Fig. 3). In contrast, estimated tree AGB decreased marginally from submontane to mid-montane elevations before increasing again at upper montane elevations, where the highest AGB values for both large trees and all trees were found. In all forests, trees ≥ 30 cm d.b.h. contributed 3–5% of all stems (i.e. of the stems ≥ 2 cm d.b.h.) and 18–20% of large tree stems (i.e. of the stems ≥ 10 cm d.b.h.), but constituted the major part of estimated AGB fractions: 65–77% of the AGB of all trees and 68–80% of the AGB of large trees.

Tree family distribution and dominance patterns along the elevational gradient

The montane forests were highly species-rich, with 236 tree species in 62 families (Table 3). The submontane forest contained the largest number of families (42), with family number decreasing progressively with increasing elevation to a minimum of 26 in the upper montane forest. Tree family composition and dominance patterns changed steadily along the elevational gradient, with only the Fagaceae and Myrtaceae contributing an important AGB fraction over the whole range. The tree family assemblage of the submontane forest was most even (Simpson's index) with the Fagaceae and Sapotaceae co-dominant and, together with 13 additional families, contributing 90% of the estimated stand AGB. Simpson's diversity was lowest at lower and mid-montane elevations, where the Fagaceae contributed more than half of the stand AGB, but increased again in the upper montane forest. There, the Podocarpaceae became the most important family, contributing about a third of the stand AGB followed by the co-dominating Myrtaceae and Fagaceae.

Phylogenetic community structure and elevational forest transition

Phylogenetic community structure changed directionally along the elevational gradient (Fig. 4); however, all elevations were greatly influenced by the Fagaceae and numerous other families in the eurosids I. Families included in the eurosids II and the euasterids I dominated the submontane and lower montane forests in terms of AGB. Magnoliids contributed substantially to AGB of submontane and lower montane forests, but were gradually replaced by asterids as the most prominent family at higher elevations. Rao's entropy index

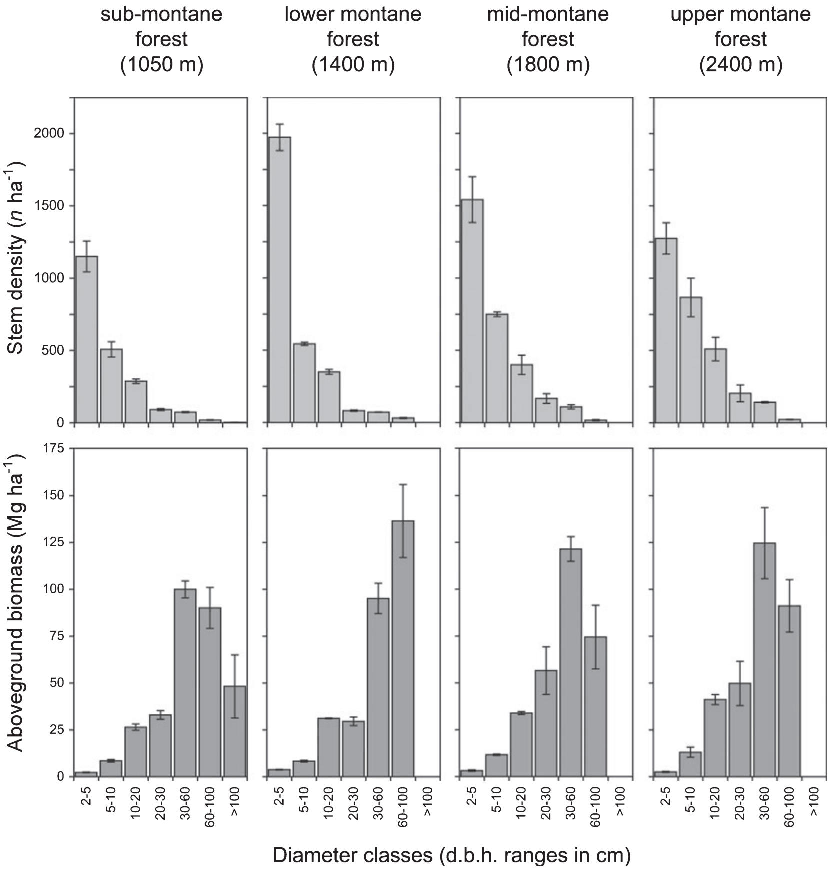

Figure 3 Stem density (n ha^{-1}) and aboveground biomass (Mg ha^{-1}) for the four study sites in Lore Lindu National Park, Sulawesi, given separately for seven different tree diameter classes (thresholds at 5, 10, 20, 30, 60 and 100 cm d.b.h.).

indicated that the upper montane tree community held the highest overall phylogenetic diversity (Table 3). However, when considering only angiosperm families, phylogenetic diversity was highest at submontane elevations. At upper montane elevations, phylogenetic diversity was strongly determined by gymnosperms and tree ferns. Together with the basal angiosperm family of the Trimeniaceae (Austrobaileyales), they were highly contrasting to the prominent young groups of the asterids (Ericaceae, Theaceae) and euasterids II (Paracryphiaceae).

Elevational changes in biogeographical patterns

Biogeographical patterns altered significantly with elevation (Fig. 5). Strictly tropical families provided about a third of both the number of stems and AGB in the submontane forest, but became less important at higher elevations. The Sapotaceae, in particular, contributed a substantial fraction of the AGB in the submontane forest (Table 3). Tree families with a distribution centre in the tropics showed the most constant elevational distribution pattern, comprising 20–45% of AGB and stems at all elevations. Of these families, the Myrtaceae were the most important in terms of AGB at all elevations, but particularly in the mid-montane and upper montane forests. In contrast to the other families, the Fagaceae with their tropical genera *Castanopsis* and *Lithocarpus* exhibited major differences between AGB and stem numbers. They were abundant at all elevations, accounting for more than half of the AGB in lower and mid-montane forests and nearly a quarter of the AGB in the submontane and upper montane forests. At mid-montane elevations, however, they reached the highest density, comprising up to a third of the stems. With the increase in Hamamelidaceae and Magnoliaceae at mid-montane elevations, tree families with a species density centre in temperate regions then gained significance. The upper montane forest was inhabited by a distinct assemblage of biogeographical elements. The Trimeniaceae and Paracryphiaceae, endemic to Australasia (Eastern Wallacean distribution), made up 7% of the AGB and 19% of the stems. The Podocarpaceae abruptly increased in significance here and made up about a third of both AGB and stems.

DISCUSSION

Forest AGB in relation to elevational trends in stand structure

Forest AGB is a function of attributes that vary between tree species and with community composition, and that may change depending on elevation. Baker *et al.* (2004) pointed out that for regionally comparable estimates of AGB, an equation is required that incorporates those aspects of forest structure that vary significantly at regional scales. Our study shows that: (1) stem and canopy height decrease progressively with

Table 3 Aboveground biomass (AGB) per tree family at the four study sites in Lore Lindu National Park, Sulawesi, as estimated from stem numbers and basal area (all stems ≥ 2 cm d.b.h.), tree height and wood specific gravity with the allometric wet forest equation given by Chave *et al.* (2005) (in Mg ha^{-1}).

Family	Biogeography	Submontane forest (1050 m)	Lower montane forest (1400 m)	Mid-montane forest (1800 m)	Upper montane forest (2400 m)	DCA scores
Annonaceae	TROP	**4.7**				−1.028
Arecaceae	cTROP	0.4				−1.028
Chrysobalanaceae	TROP	< 0.1				−1.028
Dracaenaceae	TROP	1.4				−1.028
Gesneriaceae	cTROP	< 0.1				−1.028
Leguminosae	others	1.2				−1.028
Pandanaceae	TROP	0.5				−1.028
Rhizophoraceae	TROP	0.1				−1.028
Verbenaceae	cTROP	< 0.1				−1.028
Meliaceae	cTROP	**11.0**	0.3			−0.998
Asteraceae	others	**3.9**	0.2			−0.957
Moraceae	cTROP	**39.2**	2.9	< 0.1		−0.946
Sterculiaceae	TROP	0.2	< 0.1			−0.930
Sapindaceae	cTROP	2.1	0.3			−0.897
Staphyleaceae	others	0.5		< 0.1		−0.881
Sapotaceae	TROP	**62.5**	**18.5**	0.5		−0.745
Cyatheaceae	FERN	0.8		0.1		−0.714
Myristicaceae	TROP	**4.9**	1.8			−0.712
Monimiaceae	cTROP	0.6	0.3			−0.647
Aceraceae	cTEMP	1.8	1.1			−0.581
Euphorbiaceae	cTROP	**10.5**	2.0	1.6	0.1	−0.560
Icacinaceae	TROP	**7.0**	4.8	< 0.1		−0.543
Rutaceae	others	2.2	0.5	< 0.1	0.3	−0.316
Meliosmaceae	cTROP	0.4		0.2		−0.316
Burseraceae	TROP	**7.3**	**29.3**			−0.081
Himantandraceae	ENDM	0.3	1.3			−0.068
Clusiaceae	cTROP	**6.2**	**9.9**	4.1		0.005
Lauraceae	cTROP	**25.8**	**9.7**	0.7	5.2	0.008
Araliaceae	cTROP	< 0.1	0.6			0.100
Melastomataceae	TROP	1.9	< 0.1	2.0		0.104
Ebenaceae	others		3.1			0.157
Oleaceae	others	0.4	**9.8**	0.5		0.163
Juglandaceae	cTEMP	2.3	1.4	4.6		0.428
Rubiaceae	cTROP	3.0	1.3	0.8	1.0	0.470
Apocynaceae	others	0.4		0.8		0.541
Caprifoliaceae	cTEMP		0.1	0.1		0.692
Elaeocarpaceae	cTROP	**7.1**	**10.3**		5.0	0.874
Fagaceae	FAG	**72.7**	**164.5**	**166.1**	**54.5**	1.008
Magnoliaceae	cTEMP	2.0	3.1	**20.5**		1.022
Hamamelidaceae	cTEMP		1.2	**5.2**		1.177
Styracaceae	others			**8.4**		1.456
Thymelaeaceae	others			< 0.1		1.456
Proteaceae	cTROP		1.9	0.8	0.6	1.525
Rosaceae	cTEMP	**3.5**	0.3	1.6	2.4	1.545
Escalloniaceae	cTROP	1.3	0.6	2.9	1.6	1.963
Myrtaceae	cTROP	**13.1**	**22.3**	**61.9**	**65.6**	2.530
Theaceae	others	0.1	0.6	**12.0**	**9.2**	2.654
Symplocaceae	tMONT			2.0	1.8	2.742
Aquifoliaceae	cTROP		< 0.1		0.1	2.820
Daphniphyllaceae	ENDM		0.3		1.9	3.147
Myrsinaceae	others	< 0.1	0.1	0.1	2.7	3.274
Winteraceae	tMONT			0.1	0.8	3.294

Table 3 Continued

Family	Biogeography	Submontane forest (1050 m)	Lower montane forest (1400 m)	Mid-montane forest (1800 m)	Upper montane forest (2400 m)	DCA scores
Paracryphiaceae	ENDM			0.3	**13.3**	3.348
Clethraceae	others			< 0.1	3.0	3.371
Podocarpaceae	CONIF		< 0.1	< 0.1	**118.1**	3.377
Chloranthaceae	tMONT				0.3	3.378
Cunoniaceae	others				1.1	3.378
Dicksoniaceae	FERN				**5.5**	3.378
Ericaceae	others				**9.7**	3.378
Loganiaceae	others				0.3	3.378
Myricaceae	cTEMP				**11.6**	3.378
Trimeniaceae	ENDM				**6.5**	3.378
Not identified		5.3	0.2	3.5	0.4	–
Stand total AGB_{est} (Mg ha^{-1})		**308.7**	**304.6**	**301.4**	**322.6**	
Total number of families (n)		42	36	32	26	
Simpson's index ($1-D$)		0.88	0.70	0.67	0.80	
Rao's quadratic entropy (PD_Q)		4.75	3.76	3.69	5.05	
Rao's quadratic entropy angiosperms only (PD_Q)		4.73	3.73	3.64	4.53	

Families are sorted by scores of the first detrended correspondence analysis (DCA) axis (eigenvalue 0.581). Bold numbers indicate the most important families that cumulatively gave 90% of total estimated AGB (AGB_{est}) of a site. Biogeographical and functional groups are: TROP, tropical; cTROP, centred in tropics; ENDM, endemic to Malesia; tMONT, tropical montane; cTEMP, centred temperate; FAG, Fagaceae; CONIF, conifers; FERN, tree ferns; others.

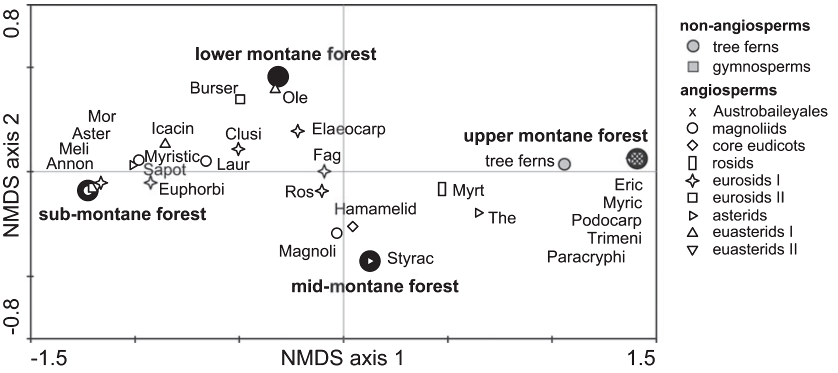

Figure 4 Ordination (non-metric dimensional scaling, NMDS) of the four montane forest tree communities in Lore Lindu National Park, Sulawesi, based on mean phylogenetic distance between samples (nearest taxon method) and position of the 26 most dominant families (based on aboveground biomass estimates, cf. Table 3). Symbols summarize the larger phylogenetic clades.

elevation, while stem density increases; (2) wood specific gravity differs significantly between sites; and (3) basal area is higher at upper montane elevation than elsewhere. It is thus necessary to consider not only stem diameter, but also tree height and wood specific gravity in the regression equation to estimate tree AGB, as proposed by Chave *et al.* (2005).

The consistent increase in mean stand-level wood specific gravity from submontane to mid-montane elevations is caused mainly by the increasing abundance of Fagaceae (*Lithocarpus* species) with particularly dense wood. This is consistent with the findings of Malhi *et al.* (2006), who identified wood specific gravity as one of the most influential structural attributes controlling AGB in Amazonian lowland rain forest. There, wood specific gravity is typically higher in slow-growing forests at sites affected by drought or low temperatures. In contrast, in the mountain forests of Ecuador, wood specific gravity was found to be invariant between 1000 and 3000 m (Moser *et al.*, 2008).

Stand basal area remains constant from submontane to mid-montane elevations, and increases by 25% in the upper montane forest, mostly as a result of the relatively high density of large trees (≥ 10 cm d.b.h.). In the upper montane forest, conifers (Podocarpaceae) contribute 14 m^2 ha^{-1} to stand basal area, while broad-leaved trees make up about 37 m^2 ha^{-1}, slightly less than is the case further downslope, where conifers are rare. This 'additive basal area phenomenon', i.e. greater basal area of mixed conifer–broad-leaved forests than of purely broad-leaved forests, may be explained by a more effective use of light and other resources in forest stands with a mixture of contrasting tree life forms (Enright & Ogden, 1995; Lusk,

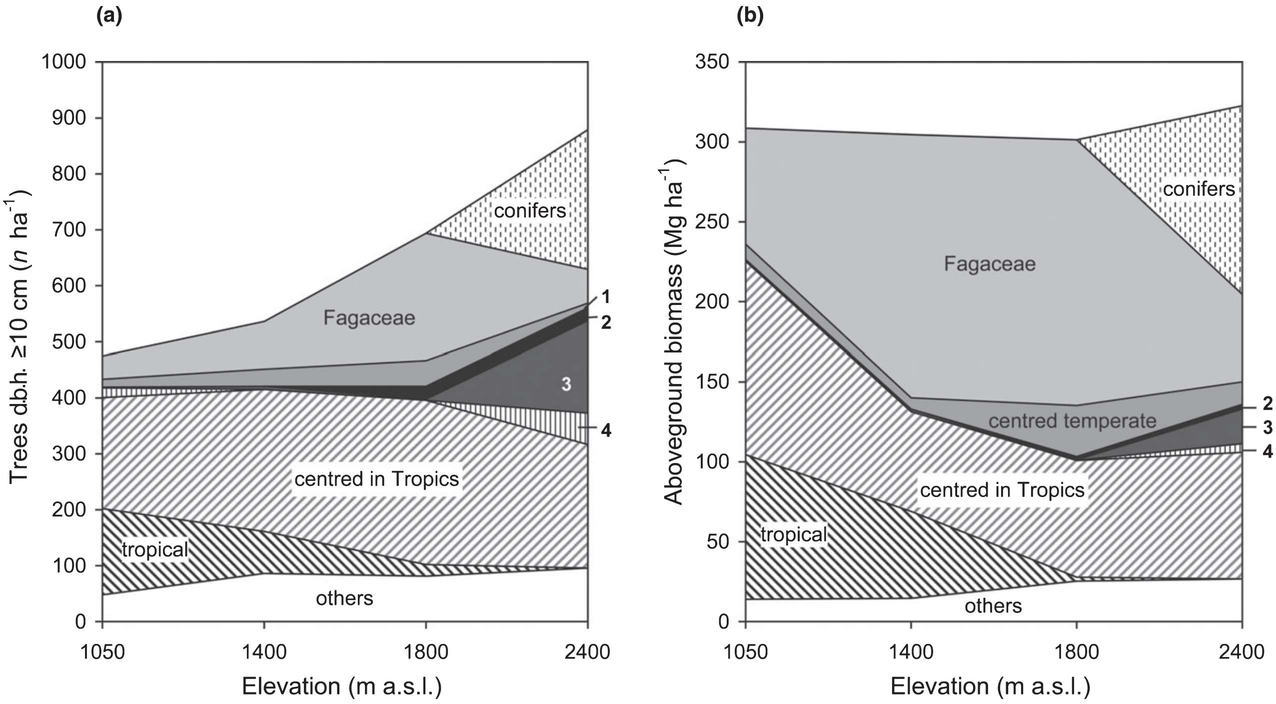

Figure 5 (a) Number of trees with d.b.h. ≥ 10 cm (n ha^{-1}) and (b) estimated aboveground biomass of all trees with d.b.h. ≥ 2 cm (Mg ha^{-1}) in relation to the biogeography of vascular plant families along the elevational transect in Sulawesi. 1, Centred temperate; 2, tropical montane; 3, endemic to Malesia; 4, tree ferns.

2002). Our study supports this, finding that large conifer trees were, on average, 4.2 m taller than broad-leaved trees. In contrast, Aiba *et al.* (2007) did not find additive basal area in the conifer-rich, single-storey montane forests of Mt Kinabalu, Malaysia, and suggested that the additive basal area phenomenon might be linked to the occupation of different canopy layers.

Elevational transects may include significant alterations in tree form, which typically changes from a tall, slender growth habit at lower elevation to a stunted, often multi-stemmed form higher up. As in our study, a progressive increase in stem density with elevation has been observed along several tropical mountain transects in Malaysia and Ecuador (Aiba & Kitayama, 1999; Moser *et al.*, 2008), but not in Costa Rica (Lieberman *et al.*, 1996). High proportions of sprouting stems (up to 10.5%) were also reported from high elevations on Mt Kinabalu (Aiba & Kitayama, 1999). In our study, the most prominent sprouter is *C. acuminatissima*. Multi-stemmed trees are a common component of tropical montane rain forests, and may be more frequent on soils with low nutrient supply (Bellingham & Sparrow, 2009).

We found that tree height decreased continuously with increasing elevation (in total by about 25%). Data from Ecuadorian mountain forests suggested that this effect is related to a progressive shift in carbon allocation from aboveground to belowground tree organs (Leuschner *et al.*, 2007). However, our results suggest that this is not an important factor in Central Sulawesi, as wood density remained constant with elevation. Here, it appears that the increase in wood specific gravity at higher elevations compensates the decrease in stem height, resulting in more or less invariant AGB.

Elevational changes in phylogenetic and biogeographical tree community structure

In tropical mountain forests, species composition and the biogeographical affinity of the flora are often variable with elevation (Kessler, 2002; Ashton, 2003). Our study supports this finding, showing marked elevational changes in the composition of the tree floras in terms of phylogeny and biogeography from submontane to upper montane elevations in Sulawesi.

In the submontane forest, tropical elements are still the most abundant group, but they decline rapidly towards higher elevations. In contrast to western Malesia, where members of the Dipterocarpaceae often dominate the lowland and submontane forests and reach elevations of up to 1600 m (Hamann *et al.*, 1999; Ashton, 2003), the family thins out in Sulawesi, where only seven of the 386 Malesian dipterocarp tree species are present (Ashton, 1982), none reaching elevations higher than 500 m (Kessler *et al.*, 2002). It seems that the niches filled by the Dipterocarpaceae in western Malesia are, in Sulawesi, mostly occupied by other Gondwanan elements with a strictly tropical distribution, among them many magnoliids. The submontane forest of Sulawesi resembles a submontane forest (900 m) in Papua New Guinea, where the Lauraceae play a pronounced role (Wright *et al.*, 1997). Phylogenetic diversity analysis supports these findings by showing that it is highest at submontane elevation when considering angiosperms only (Table 3). In contrast, Slik *et al.* (2009) showed that, in Borneo, angiosperm phylogenetic diversity is highest at high elevations, indicating that basal angiosperm lineages become more common, whereas at lower elevations phylogenetically more homogeneous groups dominate, namely members of the Dipterocarpaceae (rosids II).

The largely tropical genera *Castanopsis* and *Lithocarpus* (Fagaceae) are community-dominant in the Sulawesi plots, occurring along the entire transect with greatest presence at mid-elevations. Both genera emerged at least 40 Ma in the Southeast Asian wet tropics, where today they have their species density centres and where tropical rain forests have since been continuously present (Manos & Stanford, 2001; Cannon & Manos, 2003; Manos *et al.*, 2008). In western Malesia, the Dipterocarpaceae became dominant and experienced their major radiation in Asian everwet forests about 25 Ma. Subsequently in the Miocene, the Fagaceae evolved to become the most species-rich family in the tropical uplands (Morley, 2000). Tropical beech family members often produce remarkably high AGB at mid- to upper montane elevations, even though they are not always dominant, as for example on Tertiary sedimentary rocks at Mt Kinabalu, Malaysia (Aiba & Kitayama, 1999). In New Guinea, *C. acuminatissima* and other Fagaceae are important in lower and mid-montane forests, locally forming pure stands (Soepadmo, 1972; Johns *et al.*, 2007). Thus Ashton's assumption (Ashton, 1988; Corlett, 2007) that both the Dipterocarpaceae and the Fagaceae thin out east of Wallace's Line holds true for the Dipterocarpaceae. However, the situation is different for the Fagaceae, which occur with relatively few species in Wallacea (Soepadmo, 1972), but are nonetheless very important in terms of AGB in Eastern Malesian montane forests.

A major shift in species composition and floristic affinity occurs between mid- and upper montane elevations along the Sulawesi transect, where phylogenetic diversity (considering angiosperms, tree ferns and conifers) is highest because 'old' tree families intermingle with 'young' tree families. Higher up, tropical southern hemispheric conifers, together with tree ferns and families endemic to Australasia (Trimeniaceae, Paracryphiaceae), gain dominance. The community dominance of conifers in the upper montane forest of Sulawesi reflects the situation in other high mountains of tropical Southeast Asia (Grubb & Stevens, 1985; Aiba & Kitayama, 1999; Johns *et al.*, 2007). But with respect to elevational change in phylogenetic diversity, Sulawesi seems to differ from other tropical mountains, for example in Borneo (Slik *et al.*, 2009) and East Africa (Tallents *et al.*, 2005), where a linear increase in phylogenetic diversity was reported. In Sulawesi, phylogenetic diversity is lowest at mid-elevations, largely determined by the high abundance of Fagaceae, and highest at upper montane elevations.

Regional variability and elevational trends in the AGB of tropical moist forests

Plotting the AGB of seven tropical old-growth mountain forest transects against elevation up to 3000 m reveals a pronounced elevational AGB decrease in the majority of cases (Fig. 6). At low elevations, AGB reported from moist forests at the base of Mt Kinabalu, Malaysia, exceeds the corresponding values both of montane forests in this region (Kitayama & Aiba, 2002) and of lowland rain forests in the Neotropics (Weaver & Murphy, 1990; Lieberman *et al.*, 1996; Raich *et al.*, 1997; Wang *et al.*, 2003; Malhi *et al.*, 2006). This discrepancy may be explained by the fact that Southeast Asian lowland forests dominated by ectomycorrhizal Dipterocarpaceae are generally taller than rain forests elsewhere (de Gouvenain & Silander, 2003), and that the type of mycorrhiza (ectomycorrhiza versus arbuscular mycorrhiza) might be important for biomass accumulation. The transects in Puerto Rico and Hawai'i are unique in the sense that they refer to island forests with an oceanic climate and a comparatively small 'Massenerhebung' effect (Grubb, 1971), which lowers the alpine timberline. Raich *et al.* (1997) also relate low AGB values at Hawai'ian old-growth forest sites to high rainfall together with a slow rate of soil development.

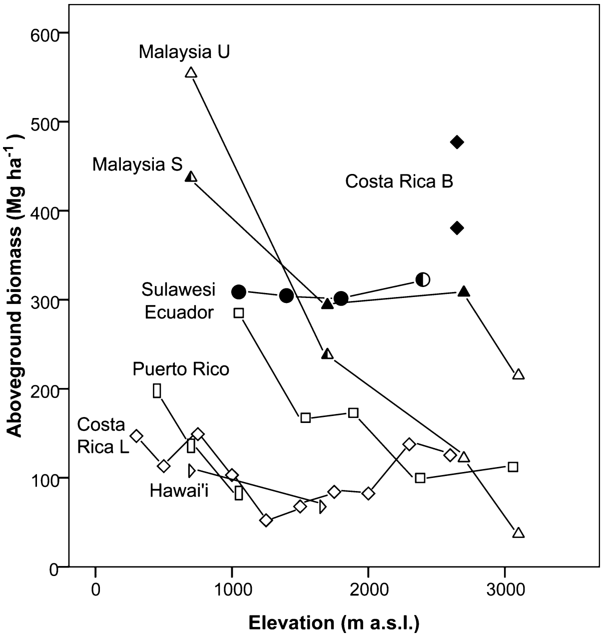

Figure 6 Comparison of estimated aboveground tree biomass (Mg ha^{-1}) in relation to elevation (m a.s.l.) in Southeast Asian and Neotropical forests. Data points from transect studies are connected by lines. Filled symbols indicate major (> 15 m^2 ha^{-1}), half-filled symbols minor (5–7 m^2 ha^{-1}), and empty symbols no contribution of the Fagaceae to the stand basal area. Sulawesi (circles): this study. Ecuador (squares): Moser *et al.* (2008). Malaysia (up-triangles): S (sediments) and U (ultra-basics), Aiba & Kitayama (1999) and Kitayama & Aiba (2002). Puerto Rico (boxes): Weaver & Murphy (1990) and Wang *et al.* (2003). Hawai'i (right-triangles): old flows > 3400 years, Raich *et al.* (1997). Costa Rica (diamonds): L, Lieberman *et al.* (1996), calculated from stand volume data and mean wood specific gravity of species composition; B, Blaser (1987), calculated from species volume data and wood specific gravity, the forests close to the timber line are dominated at a level of 95% and 98%, respectively, by *Quercus* species (Fagaceae).

Thus multiple factors, including tree species functional traits, the biogeography of species, and climatic and edaphic differences, might be responsible for the observed considerable AGB variability both between regions and along elevational gradients.

However, there are notable exceptions from the elevational trend of decreasing AGB. All high-elevation forests that show high AGB have in common a preponderance of Fagaceae. The montane forests of our Sulawesi transect study and of that on sedimentary rocks at Mt Kinabalu (Malaysia S, sediments, 1700–2700 m a.s.l.), both dominated by Fagaceae, apparently show no elevational AGB decrease. Also, upper montane oak cloud forests in Costa Rica possess extremely high AGB (381 and 477 Mg ha^{-1} at 2650 m; Blaser, 1987). This contrasts with the Costa Rican Volcan Barva transect study (Lieberman *et al.*, 1996), where oaks are mostly absent and estimated AGB at 2600 m a.s.l. is > 250 Mg ha^{-1} lower. Moreover, at Volcan Barva neither AGB nor basal area or stem density shows a directional elevational trend. AGB is lowest at mid-elevation sites, which may be attributable to marked changes in soil type and topography along the transect (Clark & Clark, 2000).

The role of Fagaceae in tropical montane rain forests

The phenomenon of invariant AGB along elevational gradients in montane forests of Sulawesi may be explained by the specific role played by the Fagaceae in terms of AGB production. Present-day genus-level diversity within Fagaceae is concentrated in the montane forests of Southeast Asia (Manos & Stanford, 2001; Manos *et al.*, 2008). Unlike for other tree families of strictly tropical distribution, the relatively low temperatures characteristic of montane forests do not seem to be disadvantageous for tropical Fagaceae. By referring to this putative adaptation, the presence of *Lithocarpus* in pollen records is used to infer cooler temperatures in lowland sites (Dam *et al.*, 2001). Accordingly, the transition to cooler, more seasonal climates is thought to have promoted the spread of the genus *Quercus* L. in northern latitude temperate forests (Manos & Stanford, 2001). However, in contrast, the current geographical distribution patterns of *Lithocarpus* and *Castanopsis* indicate an intolerance of seasonal climates (Soepadmo, 1972; Cannon & Manos, 2003). Outside Southeast Asia, only in certain upper montane Neotropical *Quercus* forests in Central America do the Fagaceae play a similar ecological role in terms of AGB. However, the current elevational range of the Neotropical oaks is large (1000–3500 m a.s.l., Kappelle & Brown, 2001) and the forests may be younger at least at their southern range limit in Colombia, where they began to form less than 1 Ma (van't Veer & Hooghiemstra, 2000). Thus specific ecological traits that favour adaptation to cool montane habitats, the long evolutionary history and probably the presence of the dipterocarps in the lowlands may have led to the unique importance in terms of AGB of this family in Southeast Asian compared with Neotropical montane forests.

CONCLUSIONS

Reducing emissions resulting from deforestation in developing countries (REDD) is of central importance in efforts to combat climate change. The carbon stored in the AGB of trees is that which is the most directly affected by deforestation and degradation, and the most relevant in reforestation efforts (Gibbs *et al.*, 2007). A major gap in our current knowledge of the global carbon cycle is the size and variability of the carbon pools in tropical forests (Kauffman *et al.*, 2009). The results from ground-based forest inventories in the montane forests of Central Sulawesi show no trend in AGB with elevation (301–323 Mg ha^{-1} from 1050 to 2400 m a.s.l.). Our results demonstrate that AGB of tropical forests may, to a large degree, be determined by species traits and shifts in species composition with elevation. As wood specific gravity is phylogenetically conserved, relying on published averages for trees in certain forest types can give incorrect results in the face of changes in taxonomic composition across environmental gradients. The high variability in primary montane forest AGB between different regions is evidenced by the large differences between Southeast Asian and Neotropical forest. The importance of Southeast Asian montane rain forests dominated by Fagaceae as carbon stores deserves greater attention.

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BIOSKETCH

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