Tree diversity in primary forest and different use systems in Central Sulawesi, Indonesia

MICHAEL KESSLER[1,*], PAUL J.A. KEßLER[2], S. ROBBERT GRADSTEIN[1], KERSTIN BACH[1], MICHAELA SCHMULL[1] and RAMADHANIL PITOPANG[3]

[1]*Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, Untere Karspüle 2, D-37073 Göttingen, Germany;* [2]*National Herbarium of the Netherlands, University of Leiden Branch, P.O. Box 9514, 2300 RA Leiden, The Netherlands;* [3]*Faculty of Agriculture, Universitas Tadulako, Kampus Bumi Tondo, Palu, Sulteng, Indonesia;* *Author for correspondence (e-mail: 106606.464@compuserve.com)*

Abstract. We studied the tree communities in primary forest and three different land use systems (forest gardens, ca. 5-year-old secondary forests, cacao plantations) at 900–1200 m elevation in the environs of Lore Lindu National Park, Central Sulawesi. The primary forests had ca. 150 tree species ≥ 10 cm diameter at breast height (dbh) per hectare, which is unusually high for forests at this elevation in southeast Asia. Basal area in the primary forest was 140 m^2 ha^{-1}, one of the highest values ever recorded in tropical forests worldwide. Tree species richness declined gradually from primary forest to forest gardens, secondary forests, and cacao plantations. This decline was paralleled by shifts in tree family composition, with Lauraceae, Meliaceae, and Euphorbiaceae being predominant in primary forests, Euphorbiaceae, Rubiaceae and Myristiaceae dominating in the forest gardens and Euphorbiaceae, Urticaceae, and Ulmaceae in the secondary forests. Cacao plantations were composed almost exclusively of cacao trees and two species of legume shade trees. Forest gardens further differed from primary forests by a much lower density of understorey trees, while secondary forests had fewer species of commercial interest. Comparative studies of birds and butterflies demonstrated parallel declines of species richness, showing the importance of trees in structuring tropical forest habitats and in providing resources.

Introduction

With about 40,000 vascular plant species the Malesian region ranges among the most diverse worldwide (Baas et al. 1990; Roos 1993). One of the most striking features of the region is the strong floristic differentiation of the islands, caused by their distinct geological and palaeoecological histories. Sulawesi, lying between Wallace's and Weber's biogeographic lines and taking a central position in the Malesia, has been isolated from the mainland of Southeast Asia since the end of the Miocene (Audley-Charles 1983). The long-term isolation of Sulawesi has allowed the development of a characteristic flora with a unique composition. Of an estimated 5000 recorded species of vascular plants (including over 2100 woody ones) almost 15% are endemic (Whitten et al. 1987; Keßler et al. 2002, unpublished). A striking biogeographical feature is the almost total absence of Dipterocarpaceae, which are the dominant trees in the rain forests of Borneo, Sumatra and Malaysia. Only six species of dipterocarps occur on Sulawesi, most of them in the southern

part of the island and always below 500 m in elevation (Keßler et al. 2002). The density of plant herbarium collections on Sulawesi (23 specimens per 100 km^2; Whitten et al. 1987) is the lowest of all major islands of Indonesia, however, and no single quantitative study on plant diversity has yet been carried out in the rain forests of the island.

Tropical rainforests are converted into pastures and cropland, and later develop into secondary forest, at an alarming pace. It is generally considered that human exploitation causes major changes in the biodiversity of these forests, even though research on this subject has been limited and results often controversial (Whitmore and Sayer 1992; Turner 1996). Some studies reveal conspicously reduced species richness in secondary (developed after clear-felling) or degraded (affected by logging) rainforests (Parthasarathy 1999; Keßler et al. 2002), even in over 100 years old regrowth stands (Turner et al. 1997), while in other studies it is increased (Kappelle et al. 1995; Fujisaka et al. 1998). The impact of human activities on plant diversity must therefore be interpreted with caution (e.g., Mooney et al. 1995).

In the framework of the interdisciplinary research project STORMA of the German Research Foundation, which was created to understand the ecological and social processes causing the regression and degradation of tropical rainforest margins and to develop strategies to stabilize these margins (Gerold et al. 2002), we have undertaken an analysis of the tree diversity in different habitat types in the region Lore Lindu National Park in Central Sulawesi, Indonesia. The main objectives of the present study were to determine (a) the taxonomic composition and structural diversity of the tree flora of the primary forests in the area, and (b) the impact of different land use practices on the tree diversity of these forests.

Material and methods

Study area

The study area is located in Central Sulawesi (Indonesia) ca. 75 km southeast of the town of Palu at the northeastern margin of Lore Lindu National Park. The park is mountainous, ranging from 800 m to 2700 m in elevation. Precipitation levels vary considerably with elevation and topography, and climatic stations are few, but mean annual precipitation can be estimated to be around 2000–3000 mm per year in the study area. Periodic droughts due to El Niño-Southern Oscillation (ENSO) events strongly influence the vegetation. Geologically, the mountains of the study area consist of cristalline and metamorphic granites, granodiorites, schists, and phyllitic rocks. The actual study plots were located in valley and foothill situations were the substrate consists of mixed colluvial material. Soils correspond to weathered, acidic inceptisols. Further information on the climate, geology and soil types in the area is given in Whitten et al. (1987). The margins of the park are characterized by a mosaic of near-primary forests, degraded forests, secondary forests, forest gardens, and plantations with cacao, coffee, maize, and paddy rice as the most important crops.

The study sites were located in the northern part of Napu Valley in the vicinity of the villages Kamarora and Wuasa, at elevations between 900 m and 1200 m asl. Three or four replicate sites were selected in each of the four studied habitat types: primary forest, forest gardens, ca. 5 years old secondary forest, and cacao plantations. The primary forests were affected by limited human disturbance, mainly including hunting and selected extraction of rattan (Schulze et al. 2004). Forest gardens consisted of patches of primary forest with gaps where understory trees had been removed by the farmers and replaced by cacao and coffee trees. These differed somewhat from forest gardens found in other parts of the park and described elsewhere in Southeast Asia (e.g., de Jong et al. 2001; Marjokorpi and Ruokolainen 2003), where most canopy trees are planted, that is, where forest gardens are largely artificial systems. The secondary forest sites were represented by small patches with a closed canopy. Cacao plantations corresponded to completely cleared areas where *Gliricidia sepium* and *Erythrina* sp. (Leguminosae) were planted as shade trees above the cacao. A detailed description of the study sites can be found in Schulze et al. (2004).

Field sampling

Plots were selected as much as possible at similar elevations and distances to the border of the primary forest, to exclude the influence of distance and habitat fragmentation. Size and number of plots per habitat type were adapted to the total diversity of the respective systems and the spatial homogeneity of the habitats. For this reason, plot size varied from 1 to 0.04 ha. Primary forest was studied at 1100–1200 m elevation near Kamarora in one plot of 100 m × 100 m and at Wuasa in two plots of 50 m × 50 m each. Forest gardens were studied at 900 m at Kamarora in four plots of 50 m × 50 m each. Cacao plantations and secondary forests were studied at 1100–1200 m at Wuasa in four plots each; plot sizes were 50 m × 50 m for cacao plantations and 20 m × 20 m for secondary forests. Each plot was subdivided into subplots of 10 m × 10 m, in each of which all trees with ≥10 cm diameter at breast height (dbh) were recorded. Additionally, a 5 m × 5 m subplot was nested in each 10 m × 10 m plot in which all tress ≥5 cm dbh were sampled. Full spatial coverage of these smaller trees would have been logistically impractical. For each tree of any size, botanical name, dbh (on buttressed trees measured above the buttresses), estimated height, and location within the plot were recorded.

All recognizable morphospecies of trees were collected with at least seven duplicates. Since many of the tree species found in the plots were lacking flowers or fruits at the time of the fieldwork, and were therefore difficult to identify, several hundred fertile plants with flowers or fruits were additionally collected randomly in the fieldwork area to serve as reference material for identification. Identification of the plant specimens was done in Indonesia and in Leiden (National Herbarium of The Netherlands); species difficult to determine were sent to specialists for identification. The collected specimens were deposited in Indonesian herbaria

(Herbarium Celebense, Palu; Herbarium Bogoriense, Bogor; Herbarium SEAMEO-BIOTROP, Bogor; and Herbarium Waraniset, Kalimantan) with duplicates in the herbaria of the universities of Leiden (L) and Göttingen (GOET).

Data analysis

The calculations were made separately for all trees ≥10 cm dbh on the 10 m × 10 m subplots and for all trees ≥5 cm dbh on the 5 m × 5 m plots.

To account for differences in sample area and forest structure, we compared species richness not on the basis of the total number of species recorded per plot but rather via species-accumulation curves and richness estimators, in three different ways: (1) as species accumulation curves based on area, (2) as species accumulation curves based on number of individuals, and (3) as estimated total species numbers. The distinction between area- and individual-based accumulation curves is important because secondary forests have a much higher density of small trees and can therefore have higher species richness within small sample areas than mature forests dominated by a few large tree individuals (Kappelle et al. 1996; Köhler 2002). Estimation of total richness was performed with the program *EstimateS* (Colwell 1997) using the MMMeans richness estimator, which was found by Herzog et al. (2002) to be the least biased and most consistent estimator among those provided in the package.

Additionally, we compared the taxonomic and structural composition between the habitat types. Taxonomic composition was quantified on a family basis by calculating the number of individuals per hectare (NI), the basal area per hectare (BA), the relative density (RD = % of NI of a family of the total NI), the relative diversity (RDi = % of number of species of a family relative to total species number), the relative dominance (RDo = % of BA of a family of the total BA), the family importance value (FIV = RD + RDi + RDo), and the relative frequency (RF = % of subplots in which family is present relative to sum of occurrences of all families in subplots) (Mori et al. 1983; Kappelle 1996). Structural composition was analyzed by comparing the distribution of tree height and diameter classes.

Results

In the primary forest we recorded a total of 148 tree species ≥10 cm dbh belonging to 82 genera in 42 families in 1 ha. The 0.25 ha plots of primary forests had about half the number of species (76 each), those of forest gardens (0.25 ha) 19–35 species and of secondary forests (0.04 ha) 6–17 species. Cacao plantations only had a total of five tree species in the four plots of 0.25 ha. For trees ≥5 cm dbh the patterns were roughly similar: 81 species in 0.25 ha and 29–32 species per 0.0625 ha in primary forest, 9–19 species per 0.0625 ha in the forest gardens, 14–17 species per 0.01 ha in secondary forests, and 2–3 species per 0.0625 ha in cacao plantations.
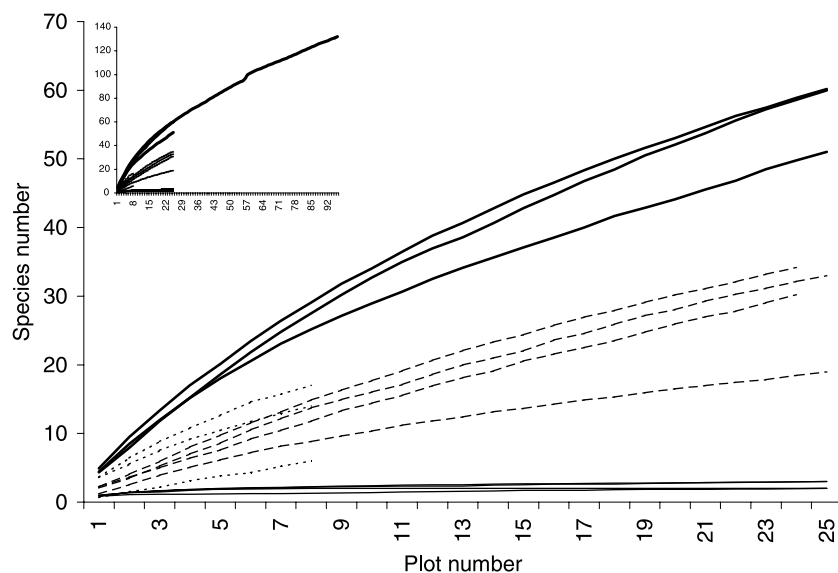
Figure 1. Plot-based species accumulation curves of trees ≥10 cm dbh in primary forest (thick continuous lines), forest gardens (dashed lines), secondary forests (stippled lines), and cacao plantations (thin continuous lines). The inset shows the entire accumulation curve for the 1 ha primary forest plot. Size of subplots is 10 m × 10 m.

Visual inspection of the species-accumulation curves (Figures 1–4) allowed a more detailed analysis of the differences in species richness within and among habitat types. For trees ≥10 cm, area-based accumulation curves showed that the three primary forest plots had much higher richness than the other forest types (Figure 1). Secondary forests and forest gardens had intermediate richness levels, while cacao plantations were extremely species poor. When trees ≥5 cm dbh were included, however, secondary forest had similar or higher species richness than primary forests, while forest gardens remained intermediate and cacao plantations very low (Figure 2). When the same data were analyzed with individual-based accumulation curves, the picture changed somewhat. For trees ≥10 cm dbh, the species richness of secondary forests and forest gardens were closer to that of the primary forests, and in the case of one forest garden even similar (Figure 3). For trees ≥5 cm dbh, three forest gardens approached the richness of the primary forests, while all secondary forests and one forest garden were noticeably poorer (Figure 4). As before, cacao plantations had very low richness.

The estimated total species numbers mirrored these results, with cacao plantations being the most species-poor habitats, followed by secondary forests, forest gardens, and primary forests (Figure 5). Closer examination of the estimated numbers showed several interesting results. First, the totals estimated for all trees ≥5 cm dbh were not higher than those for trees only ≥10 cm dbh, even though it might be expected that some understorey trees do not reach the 10 cm cutoff value
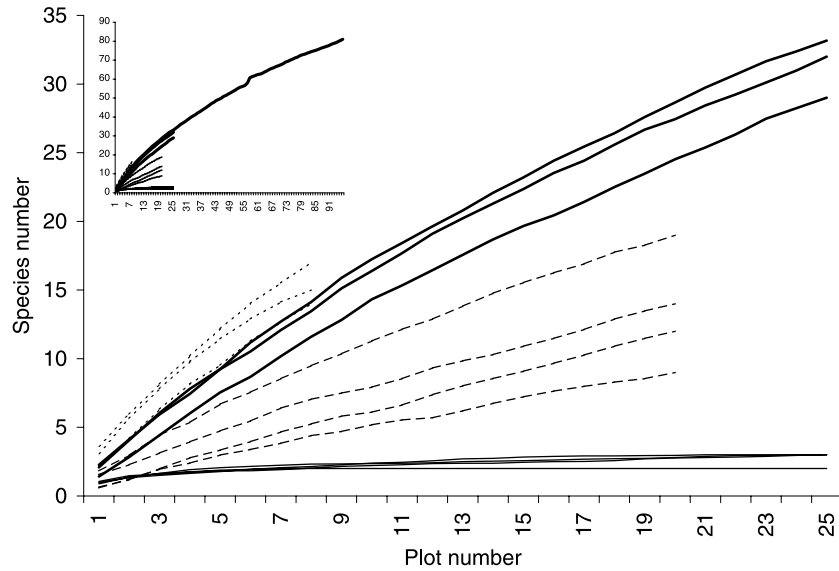
Figure 2. Plot-based species accumulation curves of trees ≥5 cm dbh in primary forest (thick continuous lines), forest gardens (dashed lines), secondary forests (stippled lines), and cacao plantations (thin continuous lines). The inset shows the entire accumulation curve for the 1 ha primary forest plot. Size of subplots is 5 m × 5 m.
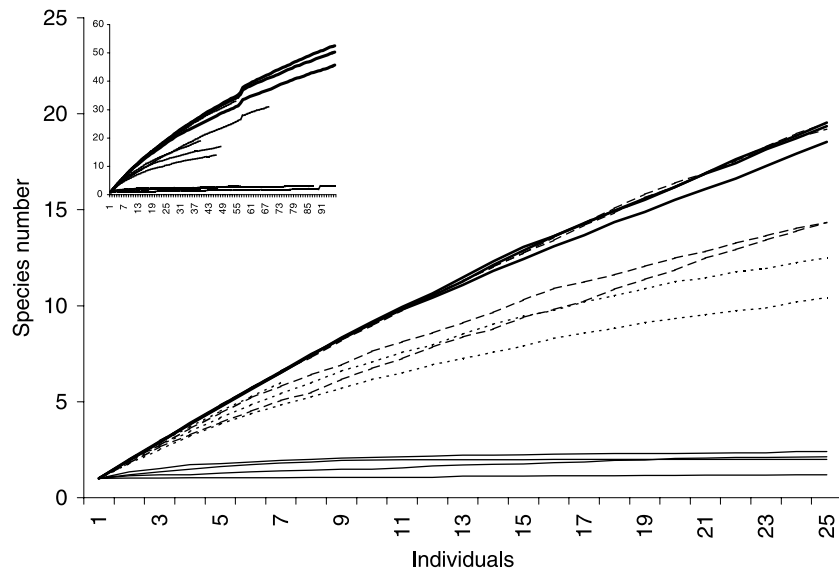

Figure 3. Individual-based species accumulation curves of trees ≥10 cm dbh in primary forest (thick continuous lines), forest gardens (dashed lines), secondary forests (stippled lines), and cacao plantations (thin continuous lines). The inset shows the curves up to 100 individuals.

Figure 4. Individual-based species accumulation curves of trees ≥5 cm dbh in primary forest (thick continuous lines), forest gardens (dashed lines), secondary forests (stippled lines), and cacao plantations (thin continuous lines). The inset shows the curves up to 100 individuals.
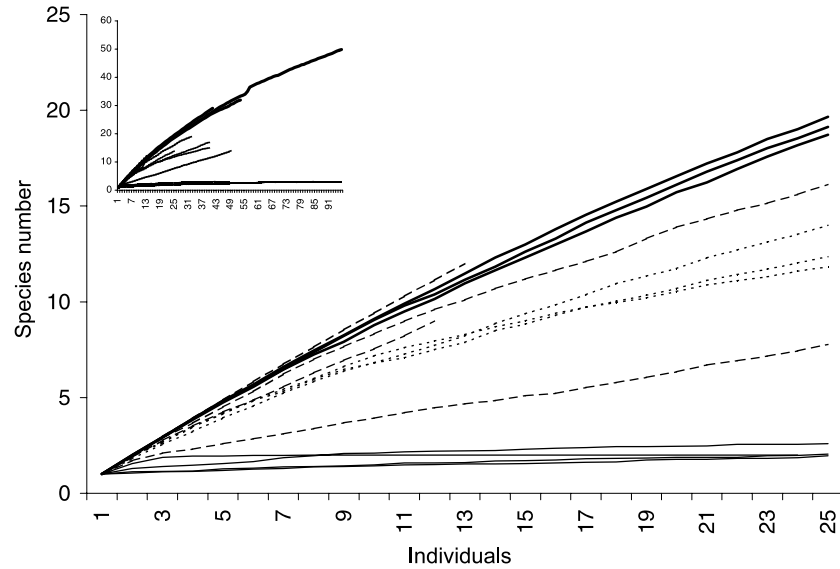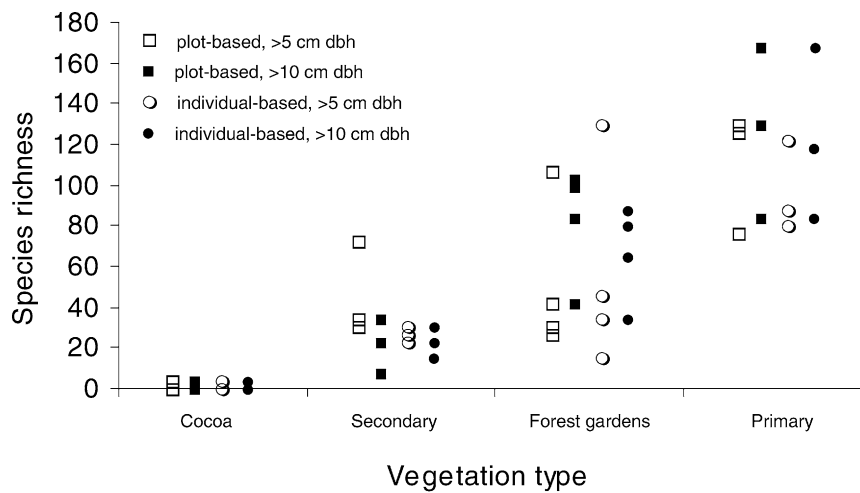

Figure 5. Total species numbers estimated with the MMMeans richness estimator for four different habitat types (three to four replicates per system).

and that the ≥5 cm dbh category should therefore include more species. This is not merely a result of the larger sample area for trees ≥10 cm because when these are analyzed on a total area comparable to that of the 5 m × 5 m plots, they remain at

Table 1. The 10 most important tree families ≥10 cm dbh in primary forest, forest gardens, secondary forests, and cacao plantations in the environs of Lore Lindu National Park, central Sulawesi. NI = number of individuals per hectare; BA = basal area (m^2 ha^{-1}); RD = rel. density; RDi = rel. diversity; RDo = rel. dominance; FIV = family importance value; RF = rel. frequency. Values are means for all plots of the respective habitat types.

Family	NI	BA	RD	RDi	RDo	FIV	RF
Primary forest							
Meliaceae	73	19.46	13.44	10.54	13.92	37.9	14.67
Euphorbiaceae	45	8.53	8.29	8.32	6.1	22.71	10.55
Lauraceae	78	6.43	14.36	11.35	4.6	30.31	10.5
Urticaceae	53	2.37	9.76	4.74	1.7	16.2	8.35
Sabiaceae	15	3.29	2.76	1.46	2.35	6.57	5
Moraceae	27	31.95	4.97	9.88	22.86	37.71	4.92
Elaeocarpaceae	11	3.77	2.03	2.67	2.7	7.4	4.17
Anacardiaceae	9	14.39	1.66	1.46	10.3	13.42	3.59
Ulmaceae	9	5.92	1.66	1.21	4.24	7.11	3.53
Rubiaceae	28	0.64	5.16	3.03	0.46	12.55	3.1
Remaining families	195	43	35.91	45.34	30.77	108.12	31.62
Sum	543	139.75	100	100	100	300	100
Forest gardens							
Euphorbiaceae	28	1.07	12.61	11.7	3.83	28.14	12.55
Rubiaceae	28	0.6	12.61	2.12	2.15	16.88	10.02
Myristicaceae	18	1.74	8.11	5.53	6.22	19.86	9.61
Sterculiaceae	19	3.46	8.56	9.33	12.37	30.26	9.24
Urticaceae	20	3.61	9.01	4.56	12.91	26.48	8.03
Magnoliaceae	13	2.59	5.86	3.59	9.26	18.71	6.99
Lauraceae	13	2.3	5.86	8.75	8.23	22.84	6.33
Sapotaceae	9	1.12	4.05	4.31	4.01	12.37	4.06
Sabiaceae	7	0.28	3.15	2.79	1	6.94	3.73
Remaining families	67	11.19	30.18	47.32	40.02	117.52	29.44
Sum	222	27.96	100	100	100	300	100
Secondary forests							
Euphorbiaceae	188	11.22	44.66	19.75	24.41	88.82	32.1
Urticaceae	25	1.01	5.94	20.59	2.2	28.73	16.37
Ulmaceae	33	1.74	7.84	6.72	3.79	18.35	5.68
Annonaceae	29	1.84	6.89	1.96	4	12.85	4.86
Compositae	4	0.07	0.95	5.56	0.15	6.66	4.76
Polygalaceae	4	0.21	0.95	5.56	0.46	6.97	4.76
Palmae	25	9.26	5.94	6.72	20.14	32.8	4.32
Leguminosae	21	5.5	4.99	2.38	11.96	19.33	3.62
Rubiaceae	17	11.61	4.04	1.96	25.26	31.26	2.78
Sonneratiaceae	17	0.99	4.04	1.96	2.15	8.15	2.78
Remaining families	58	2.52	13.76	26.84	5.48	46.08	17.97
Sum	421	45.97	100	100	100	300	100
Cacao plantations							
Leguminosae	256	14.59	91.1	41.67	88.32	221.09	88.64
Sterculiaceae	14	0.39	4.98	29.17	2.36	36.51	6.93

Table 1. (continued)

Family	NI	BA	RD	RDi	RDo	FIV	RF
Moringaceae	9	1.41	3.2	8.33	8.54	20.07	3.88
Myrtaceae	2	0.13	0.72	20.83	0.78	22.33	0.55
Sum	281	16.52	100	100	100	300	100

roughly similar levels (data not shown). Second, the plot-based estimates were in most cases higher than those of the individual-based estimates. This is a result of the shallower curves in the individual-based analysis.

At the family level, the taxonomic composition of the habitat types showed major differences (Table 1). Primary forests were dominated by Meliaceae, Lauraceae, and, in the understory, Euphorbiaceae, while Euphorbiaceae, Rubiaceae, and Myristicaceae were the most common forest tree families in the forest gardens. Euphorbiaceae was also the dominant family in the secondary forests (25% of basal area), followed by Urticaceae and Ulmaceae. In cacao plantations trees were essentially represented by the planted cacao trees (Sterculiaceae) and two species of legume shade trees (Leguminosae).

The analysis of forest structure revealed considerable differences in canopy height (Figure 6), reaching 30–35 m in primary forest, 45–55 m in forest garden, and 5–10 m in secondary forests. In cacao plantations the canopy rather uniformily reached to 10 m. The greater tree heights in forest gardens than in primary forest are probably the result of the lower elevation (900 m) of the forest garden study plots relative to the primary forest plots (1100–1200 m). In any case, they reflect that at least some original canopy trees still persisted in this land use system. When stem diameters and basal area (Table 1, Figure 6) are compared the picture changes, primary forests having many more larger size trees and a 4.5 times higher basal area than forest gardens. This clearly shows that many large trees were selectively extracted from the forest gardens as timber sources. Both secondary forests and cacao plantations contained mostly small-sized trees and had low basal area values.

Discussion

The primary forest data can be compared with the large number of similar forest plots inventoried in southeast Asia and elsewhere in the tropics. The recorded species number of 148 tree species of ≥ 10 cm dbh is within the range of 100–150 species typically recorded in southeast Asian lowland rain forests (Whitmore 1995). Considering the rather high, submontane elevation of the study region, however, the number of species recorded is surprisingly large. For example, a wet submontane forest at 1000 m elevation on Negros Island in the Philippines, located at roughly the same elevation as our plots, had only 92 tree species (Hamann et al. 1999). Thus, in contrast to animal groups such as mamals, birds, and butterflies (Whitten at al. 1987), the tree flora of Sulawesi appears not to be depauperate
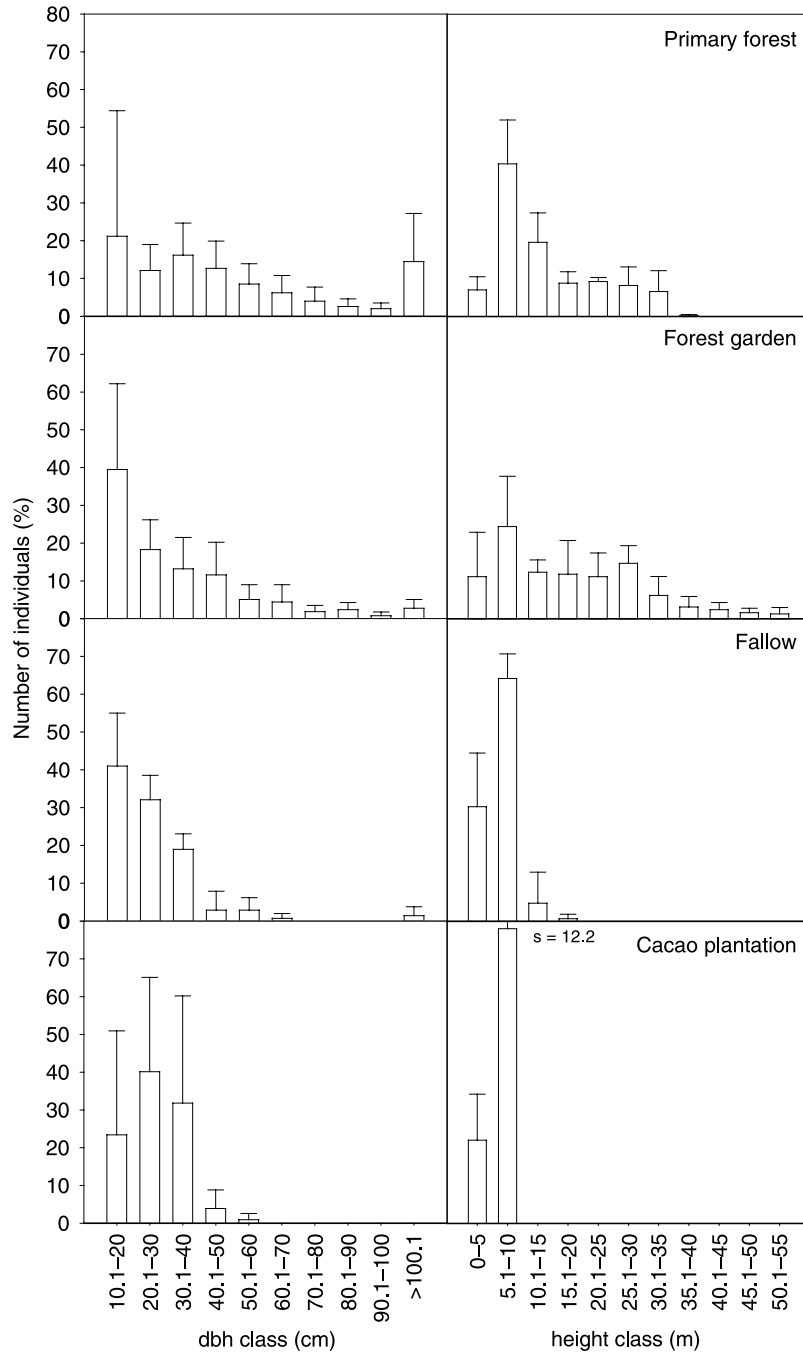
Figure 6. Relative distribution of diameter and height classes among trees ≥10 cm dbh in the four studied habitat types. Error bars indicate ±1 standard error.

relative to the rest of southeast Asia. Preliminary data on ferns likewise show comparable levels of species richness on Sulawesi, Java, and Borneo (M. Kessler, unpublished).

The basal area of $139.7 \, m^2 \, ha^{-1}$ recorded in the primary forest is among the highest values ever recorded in tropical forests, which on average have a basal area of $32 \, m^2 \, ha^{-1}$, with most values below $60 \, m^2 \, ha^{-1}$ (Dawkins 1959; Turner 2001). This is partly due to the presence of numerous large fig trees (*Ficus* spp.), one of which had a diameter of 6 m (equivalent to $28.3 \, m^2 \, ha^{-1}$), in the study plots. Since figs often have hollow trunks or consist of several separate stems, their diameter values may not be strictly comparable to those of other trees. However, even if all figs are excluded from the calculation, the basal area of the primary forest remains at ca. $108 \, m^2 \, ha^{-1}$. The reasons for such high basal area values on Sulawesi may partly involve the relatively high elevation of the study site relative to most other southeast Asian tree plots, but may also reflect the unique taxonomic composition of the flora in which large size trees may be overrepresented. Further studies are needed to document the extent of such high values of basal area on Sulawesi.

Comparison of the tree richness in the different habitat types shows that overall primary forests are the richest, followed by forest gardens, secondary forests, and cacao plantations. This pattern is consistent with the results of other recent studies in southeast Asia (Turner et al. 1997; Parthasarathy 1999). There is some overlap, however, and varying patterns emerge when trees of different sizes and different accumulation axes (area/individuals) are considered. These details will now be discussed separately for each land use type.

Forest gardens had a high tree richness because they were carved out of the primary forest and only some large trees and part of the understorey were been extracted to allow for planting of cacao and coffee. Similarly high tree species richness in forest gardens has also been documented in Borneo (de Jong et al. 2001; Marjokorpi and Ruokolainen 2003). The human activities lead to some important changes, however. The extraction of trees appears to have been selective and de-termined a shift in the tree community composition, with Meliaceae, Lauraceae, Moraceae, and Anacardiaceae decreasing in forest gardens relative to primary for-ests, and Rubiaceae and Myristicaceae increasing. Forest gardens were especially impoverished in comparison with primary forest by the removal of small and medium-sized trees emerging from natural regeneration and their replacement by planted trees. Primary forests and forest gardens accordingly differed considerably in number of trees 5–15 m in height. While in primary forest they contributed the great majority (70%) of all trees, in forest gardens they represented only ca. 35% of all trees. The high number of treelets in primary forest is reflected in the structure of the forest understorey, which was denser than in forest gardens.

Secondary forests developed on previously totally clear-felled, cultivated areas that were allowed to regrow. As a result, larger trees were almost completely missing. The high richness of trees ≥5 cm in secondary forests, however, shows that this forest type has the potential to recover a considerable richness, if allowed to mature. The higher richness of small trees in secondary forests relative to pri-mary forests in the plot-based accumulation curves is a result of the tighter spatial

species-packing among small trees. When accumulation curves are compared on an individual basis, secondary forests are clearly less species-rich than primary forests. The taxonomic composition shows that the abundance of Meliaceae, Lauraceae, and Moraceae is considerably reduced in secondary forests relative to primary forests, whereas in Urticaceae, Ulmaceae, and Asteraceae it is increased. The latter families are typical fast-growing pioneer taxa of early successional stages throughout the tropics (Turner 2001) that are of little economic interest. Field observations show that, in common with other tropical forests (Turner et al. 1997), even 50-year-old secondary forests in Lore Lindu Park, despite attaining a height comparable to primary forests, have a conspicuously different taxonomic composition (M. Kessler, unpublished). As regenerating forests, at least in southeast Asia, not only have fewer trees of commercial value but also have fewer species with large, animal-dispersed fruits than primary forests (Brown and Lugo 1990), the economic and ecological value of the old secondary forests must be considered limited as compared with the primary forest.

Not surprisingly, cacao plantations, representing an agroforestry system, had by far the lowest tree species richness. The contrast is especially conspicuous relative to the forest gardens, where cacao trees are planted under the natural forest canopy and where much higher levels of tree diversity are maintained. High levels of biodiversity in cacao plantations with low management intensity such as forest gardens have also been reported for other rain forest biota, including ants, lizards, birds, mammals, and epiphytes (Perfecto et al. 1996; Rice and Greenberg 2000; Klein et al. 2002a, b). It clearly shows that land use systems of the same crop species different in management intensity may hold different levels of biodiversity.

Parallel studies in the same habitat types in the study area show that the decline of tree species richness is roughly paralleled by similar declines among understorey plants, birds, butterflies, and dung beetles (Schulze et al. 2004). This is not surprising considering the crucial role of trees in structuring tropical forest habitats and in providing ressources for many other organisms. As a result, tree species richness explains 88% of the variation of fruit- and nectar-feeding birds and 83% of the variation among fruit-feeding butterflies (Schulze et al. 2004). Understorey herbs deviated somewhat from this general pattern by showing higher richness in old secondary forests, presumably as a result of the higher light availability at ground level, relative to the dark primary forests.

Overall, the study has revealed a surprisingly rich natural tree vegetation on Sulawesi and major differences in the structure and composition of the tree vegetation of the studied habitat types. Methodologically, we have confirmed the importance of distinguishing between area- and individual-based species accumulation curves for documenting and interpreting tropical tree species richness.

References

Audley-Charles M.G. 1983. Reconstruction of eastern Gondwanaland. Nature 306: 48–50.

Baas P., Kalkman K. and Geesink R. (eds) 1990. The Plant Diversity of Malesia. Kluwer, Dordrecht, The Netherlands.

Brown S. and Lugo A.E. 1990. Tropical secondary forests. Journal of Tropical Ecology 6: 1–32.

Colwell R.K. 1997. Estimates: Statistical Estimation of Species Richness and Shared Species from Samples. Version 5. User's Guide and Application. Published at: http://viceroy.eeb.uconn.edu/estimates.

Dawkins H.C. 1959. The volume increment of natural tropical high-forest and limitations to improvements. Empire Forestry Review 38: 175–180.

de Jong W., van Noordwijk M.S., Liswanti N. and Sujanto 2001. Farming secondary forests in Indonesia. Journal of Tropical Forest Science 13: 705–726.

Fujisaka S., Escobar G. and Veneklaas G.E. 1998. Plant community diversity relative to human land uses in an Amazon forest colony. Biodiversity and Conservation 7: 41–57.

Gerold G., Fremery M., Leuschner C. and Guhardja E. 2002. Land use, nature conservation, and the stability of rainforest margins in Southeast Asia. International Symposium, Sept. 30–Oct. 4, 2002, Bogor, Indonesia, 254 pp.

Hamann A., Barbon E.B., Curio E. and Madulid D.A. 1999. A botanical inventory of a submontane tropical rainforest on Negros Island, Philippines. Biodiversity and Conservation 8: 1017–1031.

Herzog S.K., Kessler M. and Cahill T.M. 2002. Evaluation of a new rapid assessment method for estimating avian diversity in tropical forests. The Auk 199: 749–769.

Kappelle M. 1996. Los bosques de roble (*Quercus*) de la Cordillera de Talamanca, Costa Rica: Biodiversidad, ecología, conservación y desarollo. InBio, Costa Rica.

Kappelle M., Kennis P.A.F. and De Vries R.A.J. 1995. Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest. Biodiversity and Conservation 4: 10–34.

Kappelle M., Geuze T., Leal M. and Cleef A.M. 1996. Successional age and forest structure in a Costa Rican upper montane *Quercus* forest. Journal of Tropical Ecology 12: 681–689.

Keßler P.J.A., Bos M., Sierra Daza S.E.C., Kop A., Willemse L.P.M., Pitopang R. and Gradstein S.R. 2002. Checklist of woody plants of Sulawesi, Indonesia. Blumea, Supplement 14: 1–160.

Klein A.-M., Steffan-Dewenter I., Buchori A. and Tscharntke T. 2002a. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nestig bees and wasps. Conservation Biology 16: 1003–1014.

560

Klein A.-M., Steffan-Dewenter I. and Tscharntke T. 2002b. Predator–prey ratios on cocoa along a land-use gradient in Indonesia. Biodiversity and Conservation 11: 683–693.

Köhler L. 2002. Die Bedeutung der Epiphyten im ökosystemaren Wasser- und Nährstoffumsatz verschiedener Altersstadien eines Bergregenwaldes in Costa Rica. Berichte des Forschungszentrums Waldökosysteme A, 181: 1–134.

Marjokorpi A. and Ruokolainen K. 2003. The role of traditional forest gardens in the conservation of tree species in West Kalimantan, Indonesia. Biodiversity and Conservation 12: 799–822.

Mori S., Boom B.M., de Carvalho A.M. and dos Santos T.S. 1983. Southern Bahian Moist Forests. The Botanical Review 49: 155–232.

Mooney H.A., Lubchenco J., Dirzo R. and Sala O.E. 1995. Biodiversity and ecosystem functioning: basic principles. In: Heywood V.H. and Watson R.T. (eds) Global Biodiversity Assessment. Cambridge University Press, Cambridge, UK, pp. 275–325.

Parthasarathy N. 1999. Tree diversity and distribution in undisturbed and human-impacted sites of tropical wet evergreen forest in the southern Wastern Ghats, India. Biodiversity and Conservation 8: 1365–1381.

Perfecto I., Rice R.A., Greenberg R. and Van der Voort M.E. 1996. Shade coffee: a disappearing refuge for biodiversity. Bioscience 46: 598–608.

Rice R.A. and Greenberg R. 2000. Cacao cultivation and the conservation of biological diversity. Ambio 29: 167–174.

Roos M.C. 1993. State of affairs regarding Flora Malesiana: progress in revision and publication schedule. Flora Malesiana Bulletin 11: 133–142.

Schulze C.H., Waltert M., Keßler P.J.A., Pitopang R., Shahabuddin, Veddeler D., Mühlenberg M., Gradstein S.R., Leuschner C., Steffan-Dewenter I. and Tscharntke T. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. Ecological Applications 14: 1321–1333.

Turner I.M. 1996. Species loss in fragments of tropical rain forests: a review of the evidence. Journal of Applied Ecology 33: 200–209.

Turner I.M., Wong Y.K., Chew P.T. and bin Ibrahim A. 1997. Tree species richness in primary and old secondary tropical forest in Singapore. Biodiversity and Conservation 6: 237–543.

Turner I.M. 2001. The Ecology the Tropical Rainforest. Cambridge University Press, Cambridge, UK.

Whitmore T.C. and Sayer J.A. (eds) 1992. Tropical Deforestation and Species Extinction. Chapman & Hall, London.

Whitmore T.C. 1995. Comparing Southeast Asian and other tropical rainforests. In: Primack R.B. and Lovejoy E. (eds) Ecology, Conservation and Management of Southeast Asian Rainforests. Yale University Press, New Haven, Connecticut, pp. 5–15.

Whitten A.J., Muslim M. and Henderson G.S. 1987. The Ecology of Sulawesi. Gadjah Mada University Press, Yogyakarta, Indonesia.