

The Vegetation of Lore Lindu National Park

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Brief Summary

The Lore Lindu National Park contains a unique range and mixture of forest types of exceptional conservation value. Recently, Sulawesi was chosen as one of the 25 most important global hotspots to be protected and conserved {Myers, 2000 #2987}. Lying at the western frontier of the Australasian biogeographic zone, it is THE gateway for movement of plants and animals between the two ancient, vanished continents, Gondwana and Laurasia {Whitmore, 1982 #2983}. Positioned at the center of the tectonic mélange forming Sulawesi, it is also the crossroads for the minor biogeographic regions represented by each of the island's arms. The species composition of the forests generally reflect those found throughout the archipelago at the family level but complete enumeration would reveal abundant new species, including many endemics and species with narrow distributions. At this time, what we do not know about these forests greatly outweighs what we do know. Preliminary results from a series of vegetation surveys have produced a number of important biological findings, several with significant management implications.

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Major findings

New species and endemism

Conclusions about the potential for new species discovery and degree of endemism on the island are based solely on studies of the mammal and bird communities. No comprehensive systematic study of any large plant group has been completed on the island, therefore our knowledge about the plants is limited. Given this lack of general information, my expertise with the stone oaks (*Lithocarpus*) in the oak family (Fagaceae) can be used as a persuasive case study for the plants.

There are several reasons while this group should be a useful model group: 1) most of the park is above 1000 m elevation, roughly half is above 1400 m, and numerous peaks scattered throughout the park exceed 1800 m - an elevational range commonly dominated by tropical Fagaceae {Julia, 2000 #2798; Aiba, 1999 #2327}; 2) because of their close relationship with temperate oaks and easily recognizable fruit, the tropical oaks are one of the better known and collected groups of trees in Southeast Asia; and 3) taxonomic distinctions within the group are primarily based on

mature fruit characteristics and because these fruits are woody, adequate material for identification can commonly be found under the tree for over a year after fruiting (obtaining adequate reproductive material in these forests is a major stumbling block to most ecological studies!).

Previously only four species of stone oaks have been reported from the island {Soepadmo, 1972 #2191; Whitten, 1987 #2966} but at least twice that many species were encountered during the recent surveys. Two of these species are new to science. While formal descriptions of these species are impossible at this time, the unusual combinations of leaf and fruit characters, including some novel characteristics, were convincingly different from other species known from neighboring Borneo. One provisional new species is common in the Lower Montane forests and regenerates well in the disturbed margins surrounding villages. The other new species was infrequently found in the transition zone between Montane and Upper Montane forest, near Mt. Tamuela east of Lake Lindu. Overall, the highest diversity and concentration of stone oaks was found in this area. Additionally, two species previously unknown from the island, *L. enclesiacarpus* and *L. luteus*, were found near the summit of Mt. Tamuela.

Among the species previously reported from the island, variation in fruit morphology and tree form for two species would be sufficient for classification as sub-species. *Lithocarpus grandifolius* (= *elegans*), a species found in southern China and throughout the archipelago west of Wallace's Line, was observed only one time, in Moist Lower Montane forest (an unusual habitat for this species). The mature fruit were slightly different than those found elsewhere in the range of the species: the nuts were not congested along the fruiting branch and fruit clusters seldom held more than three fruit. The other species, *L. havilandii*, is very frequent on Mt. Kinabalu, Borneo across a wide elevational range and tends to inhabit forest margins and exposed ridges and peaks, being of small stature and producing small fruit. On the island of Sulawesi, trees of this species are more frequently found in mature phase forest and reach a much greater diameter and produce more robust, thicker-walled fruit. These differences between Bornean and Sulawesi populations suggest limited gene flow over a significant period of time.

Because these two landmasses have never been connected and the Asian origin of the stone oaks, the species found on both sides of Wallace's Line must have migrated from west to east. In other words, Sulawesi was invaded at some time in the past by all of the plants now found there. Comparative genetic studies could determine whether this invasion occurred at the same time for all species and whether the endemic species of Sulawesi truly evolved independently on the island.

Vegetation map

In an attempt to properly classify the vegetation throughout the park, surveys have been performed through much of the park to collect over 200 ground-truthing points with the Global Positioning System. These points were then used as guides for the classification of the rest of the park, in combination with several recent Landsat-7 satellite images and remote sensing technology {Clark Labs, 1999 #2998}. A total of ten natural and eleven anthropogenic vegetation types have been described (see the following section "Forest types of TNLL" for detailed descriptions and Appendix A for a brief field guide to their identification). The vegetation map resulting from the initial classification is remarkably complex and several generalizations must be

performed to simplify the image (see Figure 1). This complexity is largely due to the steep topography and complicated drainage patterns found within the park.

The total area included within the park boundary, as determined from the satellite image, is 221,415 hectares with an additional 18,178 hectares found in the Lindu and Besoa enclaves. Clouds and their shadows obscured more than 5% of the image (see Table 1), while water bodies and bare soils were negligible (although Lake Lindu covers over 18% of the enclaves). The most abundant natural forest type within the park is Montane, covering almost a quarter of the park. Lower Montane and “Swamp” forest were also significant, although the amount of swamp is probably greatly overestimated (see discussion of problems with the analysis below). Lowland forest, the least known and poorly sampled in the park, forms almost ten percent of total forest area. This important and vulnerable forest type should be explored further. Cloud and heath forests, two very distinctive types, are confined to only 2% of the park, which is scattered in tiny islands across numerous peaks.

Table 1. Area contribution of vegetation types within Lore Lindu National Park. Total area of each forest type in the two enclaves and within the park is shown in the first three columns. The next three columns contain relative percentages of each forest type: 1) within the national park only; 2) within the two enclaves only; and 3) within both the park and the enclaves. Largest types are in bold-face.

Vegetation Types	Lindu Enclave	Besoa Enclave	National Park	% National Park	% Enclaves	% Total
Natural forest types						
Monsoon	201	3	5229	2.4	1.1	2.2
Marsh	526	215	193	0.1	4.1	0.1
Swamp	1658	224	30934	14.0	10.4	12.9
Moist Lower Montane	860	9	8709	3.9	4.8	3.6
Lowland	644	218	18596	8.4	4.7	7.8
Lower Montane	958	213	27221	12.3	6.4	11.4
Montane	185	34	53318	24.1	1.2	22.3
Upper Montane	58	4	18578	8.4	0.3	7.8
Cloud	0	0	986	0.4	0.0	0.4
Heath	27	19	3526	1.6	0.3	1.5
Disturbed forest types						
Secondary Swamp	98	0	84	0.0	0.5	0.0
Secondary Lowland	495	12	10333	4.7	2.8	4.3
Sec. Lower Montane	272	42	19492	8.8	1.7	8.1
Anthropogenic types						
Garden & Settlement	1102	686	5247	2.4	9.8	2.2
Settlement	1	12	1864	0.8	0.1	0.8
Mixed Garden	1828	802	2376	1.1	14.5	1.0
Cocconut	0	0	153	0.1	0.0	0.1
Rice Paddy	516	170	422	0.2	3.8	0.2
Shrimp Pond	67	0	17	0.0	0.4	0.0
Savannah	60	130	567	0.3	1.0	0.2
Grass	114	2225	1164	0.5	12.9	0.5
Burnt	0	11	108	0.0	0.1	0.0
Physical features						
Water Body	3403	0	6	0.0	18.7	0.0
Bare Soil	5	50	27	0.0	0.3	0.0
Cloud & Shadow	13	7	12268	5.5	0.1	5.1

Within the enclaves, the existence of Lowland, Moist Lower Montane and Lower Montane forests is considerable, along with the enigmatic ‘Swamp’. Surprisingly, larger proportions of disturbed forest types are found within the much larger area of the park than within the enclaves, suggesting that much of the accessible land area surrounding the villages has already been converted into other land uses. Mixed Gardens and Grass are the two largest anthropogenic types within the two enclaves, while the Settlements themselves comprise less than ten percent of the area. The relatively small amount of area used for Rice Paddy (less than 4%) is surprising.

There are several problems with the final classification of the vegetation types within the park, particularly the issue of “Swamp” forest mentioned above. According to the current classification scheme, this forest type is scattered throughout the lower elevations of the park and is particularly prevalent along the southwestern border, where steep terrain and narrow valley systems make the presence of poorly drained areas unlikely. True swamp forests often have poorly structured canopies due to a high frequency of natural treefalls and large blowdowns and can superficially resemble young regenerating forests. Currently, our analysis is unable to distinguish between these true swamp forests and other well drained but probably heavily disturbed Lowland and Lower Montane forests. The fact that the best satellite images are obtained during the dry seasons, when cloud cover is least, also confounds this analysis because the standing water and general water content in the swamp forests would be low.

Another obvious problem is the influence of the park’s complex topography and its aspect in relation to the sun when the image was taken. Several examples where the boundary between forest types follows a ridgeline can be found, particularly in the dramatic Gumbasa Valley in the northern extension of the park. In order to compensate for this effect, a much more complicated and computer intensive analysis would have to be performed. Reed Beaman, an expert in GIS techniques, has attempted such an analysis of vegetation types on Mount Kinabalu, Borneo with rather limited success (pers. com.). Given the overall robust nature of the current analysis and its general similarity to previous results despite the addition of a considerable number of ground-truthing points, the classification of vegetation types through remote sensing techniques has apparently reached its limits.

The most practical way to improve current inconsistencies and problems with the map is to survey them on the ground. Most of the doubtful areas are near the border and would be relatively easy to access. Again, the most urgent example is the southwestern edge of the park, below the village of Toro, where the most abundant patches of Lowland forest are found, mixed in with a great deal of “Swamp” forest. If this ‘Swamp’ forest represents highly disturbed areas, it would be important to know the source of this disturbance and whether the remaining pristine areas of Lowland forest are threatened.

Indicator species for forest types

Although considerable overlap in species composition exists among the recognized forest types, indicator species for the sampled types were identified. The figure below represents the significant positive (left side, Figure 2) and negative (Right side, Figure 2) associations between forest type and species distribution (see the following section “Species associations with forest type” and Appendix B for more details).

Figure 2. Species associations with forest types

Unfortunately, most of these species can only be recognized tentatively to the genus level and must remain as unidentified morphotypes, until the collected samples can be compared with adequate herbarium collections. This work could not be completed because of the global political situation in late 2001 and permission to export the necessary leaf samples was not granted.

Only one species was positively associated with more than one forest type – *Buchanania* sp. (#154, Anacardiaceae) with both Moist and well-drained Lower Montane forest – while several negative associations were found for most species. The strongest positive associations were found in the cloud forest. Several individuals of *Syzygium* C (#303, Myrtaceae) and an unidentified morphotype (#144) were only observed in this forest type. As can be seen from Figure 2, the strength of the positive associations vary a great deal among the species and forest types. *Dillenia* cf. *serrata* (#192, Dilleniaceae, local name “dongi”) is quite characteristic of Moist Lower Montane forest and in moist areas which have a history of disturbance, almost pure stands of these small trees with enormous leaves grow. In Lower Montane forest on well-drained soils, a dense stand of small Flacourtiaceae trees (#223, *Hydnocarpus*?) was observed to the west of Besoa and nowhere else. This pattern must be considered carefully because the ‘association’ may simply be a problem of a clumped growth pattern around a successful mother tree and not a preference for one habitat over another. In the Montane forests, *Castanopsis acuminatissima* (#212, Fagac., local name “kaha” or “haleka”) clearly dominates. Although occasional individuals of this tree were observed from 1200 to 1900 m asl, it only formed dominant stands between 1500 and 1800 m asl.

The distribution of the other indicator species was generally not as restricted and presence and/or absence alone cannot be used to classify the forest type in a particular location. Many of these indicator species were observed outside their ‘preferred’ forest type and the classification of forest type must rely on a combination of the presence of indicator species and several other characteristics (see Appendix A). It is also highly probable that transition zones between forest types will be ‘unclassifiable’ based on these indicator species because of their overlapping distributions. The biological significance and existence of these transition zones should not be denied or ignored.

‘Indicator species’ analysis has a great deal of promise in detecting patterns in species composition and distribution among different forest types. A detailed description of the method is provided in a later section of this report. The results would be useful in developing a dependable field guide for the identification of the different forest types by park staff and non-botanists. This work would require complete identification of the indicator species and adequate illustrations or examples of their distinctive characteristics.

Moderate Diversity

Island biogeographic theory would predict that only moderate levels of biodiversity should be expected on Sulawesi: a medium sized island which has never been connected to a major continent but its proximity to the Sunda Shelf islands would prevent it from being depauperate. This is indeed the case for the tree communities at all elevations of the park. On Mt. Kinabalu, Borneo, evenness and diversity indices of 0.90(4.6), 0.87(4.2), and 0.71(2.2) were reported for forests at 700, 1700, and 2700 m asl respectively {Aiba, 1999 #2327}. The values found in

were all substantially lower (see Table 2). For trees above 15 cm DBH, forests on granite soils between 500 and 1000 m asl in the Gunung Palung National Park were considerably more even and diverse, 0.74(3.9), than the same size class of trees in all forest types of TNLL: Moist Lower Montane (MLM) - 0.66(2.7); Lower Montane (LM) - 0.72(2.7); Montane (M) - 0.47(2.2); Upper Montane (UM) - 0.65(2.0); and Cloud (C) - 0.63(1.2).

Table 2. Evenness measures (E) and Shannon-Weiner diversity indices (H) for five forest types (left side) and four elevation ranges (right side) in Lore Lindu National Park.

Type	MLM	LM	M	UM	C	m (asl)	900- 1200	1200- 1500	1500- 1800	1800- 2100
E	.64	.66	.47	.59	.48	E	.64	.63	.43	.60
(H)	(3.0)	(3.1)	(2.5)	(2.3)	(1.3)	(H)	(3.2)	(2.7)	(2.2)	(2.0)

The significantly lower evenness of the montane forest type, generally found between 1400 to 1800 m elevation, is due to dominance of a single tree species, *Castanopsis acuminatissima* or 'kaha'. Among trees 40 cm diameter at breast height (DBH) and above, kaha contributed over 53% of the stand and 56% of the basal area. The size class distribution of kaha reflected a stable population, with relatively equal numbers of individuals across small to medium size classes, the level of dominance is slightly lower when the entire stand above 5 cm DBH is taken into consideration (21% of the stems and 48% of the basal area). This type of monodominance is typical of island ecosystems {Denslow, 2001 #2988}, although the significant decline in diversity at midelevations is not consistent and emphasizes the powerful influence kaha and its associates are having on the Montane forests.

These trees have a unique growth form, where several stems arise from a single broad base. Often a large number of smaller stems, below 10 cm DBH, are present, while two or three larger stems form the majority of the tree crown. In older individuals, the main central stem may have already died and be completely missing, leaving an internal cavity in the base of the tree. Because of their obligate symbiotic relationship with ectomycorrhizal fungi, this growth form may be associated with the efficient capture and recycling of nutrients and water (T.W. Henkel, pers. comm.). The fruits are also edible and gathered for local consumption by villagers.

Invasive species

Going hand in hand with the moderate overall diversity of island ecosystems is their vulnerability to invasive exotic organisms. The historical isolation and small size characteristic of these ecosystems creates sheltered communities of plants and animals which have not been exposed to the full range of possible competition and predation and often possess ecosystem processes idiosyncratic to the 'random' subset of species which managed to colonize the island previously. Given a limited and random assortment of species, many ecological niches filled on the mainland remain unoccupied on the island, resulting in a few big winners (thus the high level of dominance and moderate diversity discussed above). An introduced species, while not aggressive or invasive on the mainland, may suddenly overrun these sheltered communities because its mainland predators or competitors are entirely absent on the island.

Although monitoring the presence of invasive plants was not an objective of the surveys, casual observation revealed no obvious aggressive or pervasive colonist plants. Regeneration in the human-disturbed forest margins remains diverse and apparently native. As should be expected, a few cosmopolitan pioneer species, such as *Duabanga moluccana*, *Octomeles sumatrana*, and *Macaranga* spp., are common but the secondary communities also contain numerous apparently endemic species, such as the new species of *Lithocarpus* discussed above. These communities are relatively well-structured and do not appear to suffer from significant ecological erosion. Careful attention should be paid to the presence of invasive plants and animals because of the park's island status.

The presence of the two enclaves within the park creates an interesting opportunity for the study of plant regeneration along human disturbed margins. The outer or "external" boundary of the park, passing through the Kulawi and Napu valleys, is exposed to a much higher level of human activity and movement than the inner or "internal" boundaries of the park, encircling the Besoa and Lindu enclaves. The composition and structure of these two boundaries is quite different and should be expected to follow different trajectories. The internal margins are often sharp and apparently stable, involving a narrow transition zone between open grasslands and secondary lower montane forests. These grasslands are burned every four or five years to maintain their vigorous growth for livestock grazing but few effects on the forest margins are apparent. Pioneer species on the internal margins are uncommon elsewhere and quite different than those on the external margin. Several important ecological questions about the dynamics of secondary regeneration and the role of dispersal limitation and forest margins could be directly examined through comparative studies of these two different boundaries.

Important and endangered forest types

The Lowland and Monsoon forest types have relatively small representation within the park, with much more extensive areas outside. The Lowland forest of Sulawesi contains several endemic species of the Dipterocarpaceae (Y. Kusumadewi, pers. com.) and is threatened by illegal logging and agricultural conversion. The majority of the lowland forest is found in the Kulawi and Sopa valleys and has already experienced historical and sustained levels of human disturbance. Patches of old-growth, undisturbed patches of lowland forest have been reported by other survey teams, particularly between Toro and Moa, near the park boundary. No vegetation surveys of these areas have been made and should be a high priority in the future.

The most unusual vegetation community is the Monsoon or seasonally dry forest above the Gumbasa River. This forest type is one of the few examples existing in the entire Malayan Archipelago and is historically and geographically isolated from the same forest type in the lesser Sunda Islands. Unfortunately, the extent of old-growth Monsoon forest within the park has been reduced to a small fringe in the extreme north and tiny patches scattered throughout the Gumbasa extension of the park. Most of its former area has been converted into forest gardens or left fallow and is now overgrown with massive clumps of bamboo.

The Monsoon forest has also experienced the greatest degree of invasion by exotic species, including numerous leguminous shrubs and trees (including *Tamarindus*) and the infamous prickly pear (*Opuntia* sp.). The hills and valleys in this region are also exceptionally steep and narrow and soil erosion appears to be a problem where clearing has occurred. The species composition and stand structure in old growth

patches is remarkably different than anywhere else in the park, including two species of ebony (*Diospyros*, Ebenaceae) and beautiful *Ilex* groves.

Implications and recommendations for management

- *Moderate biodiversity on historical, geographical islands may be more sustainable than megabiodiversity in newly created habitat islands.*

While a great deal of emphasis in the conservation biology of tropical forests has been placed on the maximization of species diversity within protected areas, arguments can be made that targeting areas of moderate diversity which have been historically isolated may be more effective. The highest levels of biodiversity are found in the expansive lowlands of Borneo and South America but human activity has already reduced old-growth forest to small, isolated habitat 'islands'. Most of the processes that historically maintained such high levels of biodiversity cannot function in these highly fragmented landscapes and the population sizes of most species in such diverse communities will necessarily be quite small and possibly unsustainable. On the other hand, the ecosystems in places like TNLL, with moderate biodiversity and a long history of isolation, may have already resolved many of the problems facing 'island' populations, such as inbreeding, population viability, and balance among ecosystem constituents. Comparative research between such historical and newly created islands should be initiated and the premium on megalevels of biodiversity should be reduced.

- *Proper zonation of the park should be sufficiently complex and not only consider current conditions but probable future changes in human activity around the border.*

Due to the steep topography and greatly dissected drainage systems of TNLL, the distribution of forest type is complicated and few large areas of a single forest type exist. Instead of attempting to oversimplify the description of these forest types, attempts should be made to incorporate this complexity into the zonation of the park. Choosing untouched areas with a diversity of forest types that will not require active protection is preferable to choosing marginal areas with heavy pressure from encroachment or utilization. Given its remoteness, recent immigration of villagers, and diversity of forest types, the area east of Lake Lindu is an obvious candidate for the 'core' zone of the park. On the other hand, the corridor between Katu and the Besoa enclave is heavily degraded, dominated by grasslands, and will suffer an increasing level of disturbance, as road access to the Besoa enclave improves, which it will. Attempts should even be made to exchange this area with more valuable, undisturbed forests now outside the park, e.g. for the cloud forests on Mt. Rorekatimbu or the large heath forests to the southeast, both highly valuable and underrepresented forest types in the park.

- *Aggressive protection and rehabilitation of the northern extension of the park above the Gumbasa river.*

This area represents one of the few examples of seasonally dry equatorial forest in Southeast Asia. Currently, few old growth patches exist within the park and very

little is known about their composition. Attempts should be made to protect it from continued human encroachment and disturbance.

- *Establish monitoring programs and comparative studies between the external and internal margins of the park on the processes of regeneration and the presence of invasive plants.*

As noted above, the process of regeneration along the internal and external margins of the park appear to be different. Understanding how these processes differ and how human activity affects them against the background of dispersal limitation and community composition will be important in the management of the forest margins. Numerous islands throughout the Pacific, particularly Hawaii, have experienced numerous rounds of invasion by aggressive plant colonizers. As better roads are developed and human traffic increases, the apparent difference in the regeneration process occurring along the two margins may change because of the dispersal of more cosmopolitan and invasive species into the interior margins. These comparative studies would also address fundamental questions about the ecology of regeneration and recovery along forest margins.

- *Further exploration of the ecological characteristics and geographical limits of the monodominant Castanopsis forest between 1500-1800 m asl.*

This forest type is clearly the dominant one in the park and involves an interesting symbiosis between “kaha” and ectomycorrhizal symbionts. Such a high level of dominance by one species of tree is unusual in equatorial Southeast Asia. These trees and their associates obviously have a profound influence on the Montane forest communities, as diversity and evenness unexpectedly drop at midelevations in TNLL. Distinguishing among the several hypotheses that might explain this phenomenon would enlighten the process of managing these forests.

Background

The rich and endemic flora of Sulawesi remains one of the least explored of the major Indonesian islands, both in terms of its taxonomic composition and ecological characteristics. No comprehensive source of information exists, other than brief accounts in the *Ecology of Sulawesi* {Whitten, 1987 #2966} and individual species descriptions from the Flora Malesiana series. These descriptions are scattered throughout the Malesia-wide monographs and must be found in reference to the most recent checklist {Whitmore, 1989 #2997}. In the introduction to the Flora, C.G.G.J. van Steenis placed Sulawesi in its own minor phytogeographic region and noted the importance of Wallace’s Line, which separates Sulawesi from the major Sunda Shelf islands {van Steenis, 1950 #2967}. The large number of endemic genera on Sulawesi (7 for Sulawesi, 10 for Java and 17 for Sumatra) in relation to its small area and historical isolation from continental Asia suggests an ancient and sustained flora. The potential for significant discovery and contribution provides a major opportunity for tropical botanists interested in floristic exploration and biogeographic studies.

Lore Lindu National Park, given its central location on the island, large land area, accessibility of its old-growth core regions, and critical conservation status, has potential to become an important center for research. Historically, few major

collecting programs have been performed {van Steenis, 1950 #2968}. Wirawan (1981) completed the most comprehensive vegetation survey more than twenty years ago. Using aerial photography, he created a preliminary vegetation map of the park and recognized four major vegetation zones {Wirawan, 1981 #2969}:

- Lowland - <1000 m asl.
- Submontane – 1000-1500 m asl. (well-drained and wet),
- Montane – 1500-2000 m, asl.
- Subalpine - >2000 m. asl.

Basic descriptions of the taxonomic composition of these types were provided and secondary regeneration after shifting agriculture was analyzed. The report also contains an appendix of local and scientific plant names, useful to both park rangers and villagers. This list should be incorporated into a larger database and expanded through ethno-botanical research.

The plant communities of the Sopa valley were compared along an elevational gradient during a collecting expedition led by van Balgooy and Tantra (1986). Vegetation plots were sampled in five different forest types: riparian, mixed forest on wet alluvial soils, mixed forest on elevated soils, montane forest at 1700 m asl, and montane forest at 2000 m asl. Unfortunately, selective logging had already occurred in much of the forest below 1700 meters and the results should be considered representative of regenerating secondary forest and not old growth. The riparian and wet alluvial forests were the most similar in taxonomic composition, sharing more than a third of the genera observed in each location. The mixed forest on elevated soils appeared to be rather heavily damaged by logging activities, as the three dominant tree genera, *Dendrocnide* (Urtic.), *Macaranga* (Eupho.), and *Vernonia* (Aster.) are early successional specialists. Additionally, the number of trees per hectare was substantially lower than any other forest type, which certainly goes against expectations.

The montane forest at 1700 m asl contained the greatest number of species and stems of all the forest types sampled, despite being heavily dominated by *Castanopsis acuminatissima* (Fagac.) and *Eugenia* (= *Syzygium*) spp. (Myrta.). The pristine condition of this location must be responsible for this result because current surveys suggest that Montane forest is among the least diverse in the park (see above). The montane forest at 2000 m asl was the lowest in diversity and was still dominated by the genus *Eugenia* (= *Syzygium*). The presence of *Agathis* (Arauc.) and *Weinmannia* (Cunon.) attest to its upper montane condition. The montane forests were quite distinct in taxonomic composition from the three former forests and from one another.

What is striking about these two earlier studies {Wirawan, 1981 #2969; van Balgooy, 1986 #2996}, both conducted at about the same time, is the small degree of overlap in the “dominant” species observed. Wirawan described the well-drained submontane areas as *Santiria-Vernonia-Acer* forests, while only *Vernonia* was even mentioned by van Balgooy. Also, the most common tree, according to van Balgooy and Tantra, was *Dendrocnide* (Urtic.), a name not even listed in Wirawan’s appendices. Wirawan described the poorly-drained submontane areas as *Symplocos-Dysoxylum-Siphonodon* forests, while van Balgooy and Tantra observed only *Dysoxylum* in these areas. Whether these differences are merely due to differences in taxonomic opinion, the disturbed condition of the sites sampled by van Balgooy and Tantra, or actual differences in forest composition is unclear but may point to a highly complex distribution of plant species in the park.

In the initial stages of the vegetation survey by the Nature Conservancy, Webb and Yani (1999) established several permanent vegetation plots. Family composition of montane tree communities between Sulawesi and Kalimantan were found to be similar, although the Sulawesi plots contained lower species diversity. Several plots were dominated by few species and the lowest diversity was found at the elevational and climatic extremes of the sample. The plots did contain a unique mixture of Gondwanan and Laurasian floristic elements.

In the next step of the survey, a detailed map of the vegetation types within the park was created by supervised classification based on a recent Landsat 7 image and a training set of GPS reference points collected in the field {Jarvie, 2000 #2971}. Further ground-truthing and ecological descriptions of the types will refine this map and provide baseline ecological descriptions {Cannon, 2001 #2973}. The establishment of a local herbarium and an ambitious collecting programme based at Tadulako University in Palu in conjunction with STORMA is expected to be a great resource to further floristic work within the park.

Forest types of TNLL

The geographic distribution of vegetation type depends on many environmental factors, such as elevation, temperature, rainfall, drainage, and soil conditions. The delimitation of types can be difficult as transitions are often subtle and the interaction among environmental factors can create large variation in their distributional limits. Many different classification systems have been proposed and their usefulness depends on the purposes of classification and the amount and quality of data available. Given the current lack of reliable information about species composition and the environmental factors affecting the distribution of vegetation types within the Lore Lindu National Park, a simple but adequate classification system should be adopted until a more refined and detailed system can be established based upon solid information. The original nomenclatural system for altitudinal zones proposed by van Steenis (1950b) provides a good starting point and was directly adopted by Wirawan (1981).

The following nine major types of vegetation are currently recognized within the park, many containing further subdivisions:

- Marsh – open areas, dominated by grasses and sedges, on poorly drained soils at several elevations.
- Swamp – forested areas on poorly drained soils, generally at low elevations on old lake deposits.
- Monsoon – seasonally dry forest in the northwest corner of the park at low elevations (300-700 m asl).
- Lowland – well-drained forest around the margins of the park below 900 m asl.
- Lower montane – forest between 900-1500 m asl, on well-drained to moist soils.
- Montane – forest between 1400-1800 m asl.
- Upper montane – forest above 1700 m asl.
- Heath – stunted forest on poor soils with significant humic accumulation, at several elevations but often above 1800 m asl.
- Cloud – wet stunted forest above 1900 m asl.

- Anthropogenic – a wide variety of types, from old secondary forests, normally below 1500 m asl., to open grasslands.

General comments

The topography of the park differs dramatically between the western “external” Kulawi watershed and the two “internal” watersheds, eastern Napu and northern Palolo. These differences should be expected to strongly affect the distribution and structure of vegetation types and the transitions among them. The western edge of the park consists primarily of short drainages and steep slopes, creating straight and ordered valley systems, while the two internal drainages consist of long rivers across relatively gentle slopes, creating complex and highly dissected systems. The external western edge is also the most altered by human activity. The transitions among types along the external watershed could be expected to be more regular and predictable than in the internal watersheds. In the same sense, the juxtaposition of types should be more diverse and complicated in the internal watersheds.

This topographic complexity may, in part, cause the local species dominance apparent in the park {Webb, 1999 #2970} by dissecting habitat into “islands” and limiting the establishment of rare species. Moving between habitat islands, this local dominance is offset by rapid turnover in dominant tree species composition, without any obvious difference in environmental conditions. Further research to examine the extent and cause of these patterns, site-specific local dominance, rapid species turnover, and overall high species diversity, should be pursued. Possible causes are dispersal limitation, low natural disturbance rates, and the relatively rich and young soils within the park. The biogeographic effects of small island size and the absence of a continental land bridge throughout the geological history of Sulawesi should not be forgotten.

Table 3. Structural differences among five forest types. Differences in the mean distance to the nearest tree for each of the four size classes (5-10, 10-20, 20-40, ≥40 cm DBH) are shown in pair-wise comparisons of forest types: MLM – moist lower montane, LM – lower montane, M – montane, UM – upper montane, C – cloud. A “0” indicates no significant difference, + a greater mean distance in the forest type in the row heading, -- a greater mean distance in the forest type in the column heading.

	MLM	LM	M	UM	C
MLM	0, 0, 0, 0	0, 0, +, 0	+, 0, +, +	+, +, 0, 0	+, +, +, 0
LM	0, 0, --, 0	0, 0, 0, 0	0, 0, 0, 0	0, +, 0, 0	+, +, +, 0
M	--, 0, --, --	0, 0, 0, 0	0, 0, 0, 0	0, +, 0, 0	+, +, +, 0
UM	--, --, 0, 0	0, --, 0, 0	0, --, 0, 0	0, 0, 0, 0	0, +, +, 0
C	--, --, --, 0	--, --, --, 0	--, --, --, 0	0, --, --, 0	0, 0, 0, 0

The steep topography also causes numerous landslides that create large natural clearings. This additional and significant type of disturbance in montane forests allows ephemeral species in mature phase forests, e.g. *Macaranga* (Eupho.) and *Rubus* (Rosac.), to establish and maintain their populations in mature phase forest. These slopes are found at various elevations but are concentrated above 1700 m asl. The ultimate stability of these communities depends largely on immediate topography and soil conditions but it should be expected that many steep slopes undergo a relatively frequent and sustained cycle of disturbance, generating unique communities of specialized plants.

Marsh

These areas are often small pockets (>5 ha) of standing or slow moving water, either at the headwaters of small rivers or in the large drainage basins of rivers, e.g. east of Danau Lindu. Tall pandan trees (>20 m tall), much branched with many stilt roots, often dominate the edges of these areas (Fig. 2), with a mixture of *Dacrydium* sp. trees. The open parts of the marsh are dominated by grasses and sedges (Fig. 3), and are punctuated by clusters of the semi-parasitic, purple flowered *Burmanna disticha* (Burma.; see Fig. 4), a large terrestrial orchid (*Phaius tankervilleae*), climbing and terrestrial pitcher plants (*Nepenthes* spp.), and a white-flowered species of *Rhododendron* (Erica.). The amount and seasonality of standing water will strongly affect the plant communities.

Numerous upland marshes (>1700 m asl) are present in the southwestern and northeastern portions of the park. Along the road through the Napu valley pass, several trails lead to the lakes near the Rorekatimbu summit. Being isolated by and radically different than the surrounding montane forests, these upland marshes are an important and highly vulnerable component of the rich biodiversity of the park. A comparative study between the more extensive marsh regions in and around the two enclaves and the upland marshes could yield interesting differences.

Monsoon

Only found in the extreme northern extension of the park, these forests are probably one of the few equatorial examples of such forest in the archipelago (van Balgooy and Tantra, 1986). Large areas can be found in the Palu valley outside the park, meaning that only a small fraction of this unique forest type enjoys protected status. Recent surveys suggest that even the small amount of this forest type found within the park has experienced a high degree of human disturbance, although some remote valleys appear to be relatively pristine. Although these forests are not deciduous, they are remarkably distinct in their species composition. The legume family largely dominates the tree flora, along with *Ziziphus jujube* (Rhamn.) and *Ilex* spp. (Aquif.). Striking individuals of *Dracaena* sp. (Lilia.), pandan-like in habit, are probably the easiest indicator of this forest type, being quite visible from a great distance. A woody liliaceous tree, the bark is very smooth and clearly marked with leaf scars and the bole is highly branched. A small statured *Diospyros* sp. (Ebena.) or ebony tree is also quite common. Numerous small valley systems, mostly running north-south, are dry for the majority of the year, only containing water during periods of heavy rainfall. Well-structured groves of *Ilex* sp. and *Garuga floribunda* (Burse.) are found in these valleys. The understory in these areas is quite open and clear of undergrowth, while the slopes and ridges are densely tangled with thorny plants. *Pterospermum* cf. *diversifolium* (Sterc.), a pioneer species, dominated one plot sampled in the area {Webb, 1999 #2970}.

Lowland

Almost 90% of the park is above 900 m asl, therefore lowland forest will contribute little to the vegetation types found in the park. Because all of the lower elevations are found along the boundaries of the park, this forest type will only be found in narrow strips near the rivers forming the boundaries. These strips of lowland forest are often found on steep slopes and are strongly affected by human activity in these marginal areas {Webb, 1999 #2970} and little pristine lowland forest can be expected to exist within the park boundaries. Few floristic surveys have been performed and little information exists about its original taxonomic composition.

Many of the species, e.g. *Artocarpus vriesianus* (Morac.) and *Elmerillia ovalis* (Magno.), mentioned by Wirawan (1981) as characteristic lowland species, have also been observed in moist lower montane and old secondary forests between 1000-1300 m asl. The presence of these species in lowland areas may be influenced by the moist conditions found near rivers. Species of the Dipterocarpaceae should dominate any well-drained areas on moderate to gentle slopes but botanists have observed very few individuals of this family within the park boundaries. Anecdotal reports from Awam Green members who have visited areas near the western border of the park suggest that pristine forests do exist but are currently slated for timber harvest. Further study of this endangered type should be aggressively pursued and attempts should be made to identify and protect undisturbed lowland forests currently outside of the park.

Lower montane

Because of the rapid steep slopes along the Kulawi valley, the majority of the lower montane forest is found in the two internal watersheds and the difference in drainage conditions strongly affects the structure and composition of this forest type. The transition between lowland and lower montane forests on the well-drained slopes of the exterior appears to be fairly sharp, but it is difficult to untangle human and environmental factors. The families Sapotaceae and Fagaceae dominate well-drained lower montane forest, while numerous individual species are characteristic (but not confined to) this forest subtype, such as *Acer niveum* (Acer.), *Bruinsmia styracea* (Styra.), and *Santiria* sp. (Burse.). The Annonaceae, Moraceae, and Lauraceae are also frequent and diverse families. Terrestrial palms (*Calamus* sp.) and climbing woody plants are common. Trees larger than 60 cm DBH are common and the canopy is well-structured, closed, and multi-layered.

Forest structure and composition under poorly-drained conditions, predominantly in the internal watersheds, suggests a much higher rate of natural disturbance and appears to undergo seasonal flooding. The canopy in these areas is often quite ragged, with large isolated individual trees and the lowest strata of the canopy densely closed with small trees. Distinguishing human disturbance from natural disturbance in this forest type is difficult. The moist lower montane forests on the north slopes of Mt. Nokilalaki have been strongly influenced by human activity but they are rather indistinguishable from the same conditions, due east of the Besoa enclave, near the park boundary, which have experienced little or no human disturbance. Large individuals of strangling figs (*Ficus*, Morac.) and several species of uru (*Elmerillia* and *Manglietia* (Magno.) are particularly prominent. *Eucalyptus deglupta* (Myrta.) grows in almost pure stands along rivers and streams. *Pigafetta filaris* (Arace.) are also more frequent near rivers and streams. Latter-stage pioneer species are frequent and can reach significant sizes, e.g. *Octomeles sumatrana* (Datis.), *Duabanga moluccana* (Sonne.), and *Cinnamomum* sp. (Laur.). Another common and distinctive tree is *Bischofia javanica* sp. (Eupho.), with its dark brown, curling flaky bark, trifoliate leaves, and red sap in the inner bark. The undergrowth is usually quite lush, with numerous species of *Elatostema* (Urtic.), *Piper* (Piper.), and *Impatiens* (Balsa.) creating a nearly continuous herbaceous layer. Woody climbers are very frequent.

In the flat alluvial areas in the center of the Napu watershed, north of Besoa, extensive areas of almost swampy lower montane forests exist, as suggested by Wirawan (1981). Here the families Magnoliaceae and Annonaceae dominate among the emergent trees and *Dysoxylum* spp. and *Aglaiia* spp. (Melia.) are common mid-canopy trees. The large fragrant white flowers and thick leathery leaves of the hemi-

epiphytic *Fagraea* (Logan.) can frequently be seen on the forest floor and growing along the riverbanks. At least three species of *Saurauria* (Saura.) are also common on the riverbanks, flowering profusely. A high density of lianas and rattans is also present. Dense stands of *Elatostema* (Urtic.) with scattered individuals of *Impatiens* (Balsi.) are found in the undergrowth.

This vegetation type should be subdivided into well-drained and moist lower montane forests because of the significant differences in composition and structure. This classification corresponds closely to Wirawan's two submontane forest types. The transition between lower montane and montane forest is often quite sharp. Although many "lower montane" species can be found in montane forests, they are not common and the composition of dominant species is often changes dramatically around 1500 m asl.

Montane

Beyond the high elevations of the main mountain range snaking its way through the centre of the park, this forest type is confined to narrow ridge tops and isolated hills, particularly in the highly dissected interior watersheds. As noted above, the transition into this forest type can usually be noted by a dramatic change in species composition of trees and generally, species diversity is lower than in the lower montane forests. A clear indicator of this forest type is the appearance of *Castanopsis accuminatissima* (Fagac.). Locally known as "kaha" or "haleka", these trees can form almost 60-70% of the stand and are easily recognized by the numerous trunks and slender stems arising from the base of a single individual and the rather golden hue of the underside of their leaves. Several other species are commonly associated with kaha, particularly "lihu" or "tawako" - *Tristania whiteana* (Myrta.) and "betau" - *Calophyllum* sp. (Clusi.). The myrtle species is found slightly higher than kaha and appears to be limited to drier sites. Their slick, peeling bark is similar to *Eucalyptus* but is white to tan in hue. Locally, lihu can form almost solid stands, particularly on exposed ridges with thin soils. The closely packed crowns of these stands can be seen on the slopes of the mountains facing the Besoa enclave, as they follow the contours of the ridges. The leaves of *Calophyllum* are quite distinctive, being rigid and smooth with the secondary veins tightly parallel. Their outer bark is ringed by sulphur-yellow bands and they also have abundant white to bright yellow sap in their inner bark.

The elevational limits of this forest type vary widely across the park and the causal environmental factors are unclear. Patches of high species diversity and low dominance of kaha and lihu are frequently encountered and occasionally, different species, like *Podocarpus neriifolius* (Podoc.) and *Dacrydium imbricatus* (Podoc.), can obtain comparable levels of dominance, in the absence of kaha. The majority of the soils are well-drained, although patches of poorly-drained areas can be found in saddles and raised benches in the major mountain ranges. The undergrowth is often rather sparse, particularly in drier areas, and changes most notably in the transition into upper montane forest. In particular, *Drymis piperta* (Winte.), a small, unbranched shrub producing clusters of white flowers, and several species of *Alpinia* (Zinge.) become common with increasing moisture and elevation. On Mt. Nokilelaki, species composition of both trees and undergrowth are strikingly different, perhaps because of the very wet conditions on the mountain. 'Kaha' may not even be present and only a limited population of 'lihu' has been observed. Species diversity appears to be quite rich as well.

The dominance of kaha throughout the park at mid-elevations deserves further comment. The unusual growth form mentioned above has been noted in other

monodominant tropical forests, e.g. *Dicymbe* forests in Guyana. Kaha also has an obligate association with ectomycorrhizal (ECM) symbionts, e.g. *Amanita* spp., *Russula* spp., and *Boletus* spp., another feature of monodominant forests elsewhere. Such high levels of dominance may be possible because of the efficient capture of nutrients through this symbiosis. On the other hand, monodominant forests normally occur on ancient poor soils, not the relatively young soils of Lore Lindu NP. The elevational range of this species is also quite wide (1300-1900 m asl) but it dominates most heavily between 1400-1600 m asl on ridge tops. The amount of rainfall may influence its level of dominance as water stress may promote dominance, e.g. on Mt. Tuwo, where a uniform 'kaha' forest was found all the way to the peak at 1900 m asl., perhaps because the area may receive less rainfall than other southern mountains.

Another abundant and diverse group of species in this forest type is the genus *Eugenia* (Myrta.). Although no single species dominates, the genus as a whole contributes a large proportion to the stand. Throughout the Southeast Asian region, these trees are very diverse and thrive in most well-drained habitats. They are also quite difficult taxonomically and provide a major challenge to any field botanist in the region. The myrtle family, including *Eucalyptus* and *Tristania*, predominantly has symbiotic relationships with fungi through their roots, either ECM or VAM (Vascular arbuscular mycorrhizae). Further exploration of these prevalent symbioses between trees and fungi should be a major focus in future ecological vegetation studies. Throughout the tropics, the fundamental and critical role that fungi play has been largely ignored and discounted. Fungal floras are often almost completely unknown and the amount of expert knowledge on the subject is a major limiting factor. Basic surveys, either through fruiting body, spore prints, or molecular sequence collections, should be pursued. Digital photography can also be a useful form of documentation, because many key features, such as color and general shape are often lost upon drying.

Upper montane

Generally found above 1800 m asl, this forest type is rather limited in area (also <10%) but represents a surprisingly diverse community (Fig. 16). The easiest indicators for this forest are the large erect *Dawsonia* (spiky and Christmas tree-like, these mosses are often 10 cm tall, see Fig. 15). Small herbs, such as *Begonia* spp. (Begon.), *Elatostema* spp. (Urtic.) and *Cyrtandra* spp. (Scrop.) are quite diverse and frequent in the undergrowth under wet conditions. Scattered individuals of *Agathis* cf. *celebica* (Aurac.), *Ternstroemia* spp. (Theac.), *Lithocarpus* spp. (Fagac.), and *Phyllocladus hypophyllus* (Podoc., see Fig. 17) replace the kaha and lihu found at lower elevations. The families, Lauraceae and Myrtaceae, are also quite frequent and diverse here. Tree ferns, *Cyathea* spp. (Cyath.), several species of pandan, *Pandanus* spp. (Panda.), and pinang palms (*Arenga* spp.) are common in the understory. Unfortunately, the transition between montane and upper montane forest can be quite difficult, particularly as scattered individuals of kaha are present above 1800 m asl and 'characteristic' understory and undergrowth plants are often found in both forest types.

Heath

A very distinctive forest type primarily found within the park above 1700 m asl in isolated and rather small patches (1-15 ha) on ridge tops and in saddles. The soil is covered by a significant accumulation of humic matter and the forest structure consists almost entirely of slender trees, mostly red and white-flowered

Rhododendron sp. (Erica.) and a tiny-leaved *Eugenia* (Myrta.). Occasional stunted individuals, reaching large diameters, can be found, especially *Phyllocladus hypophyllus* (Podoc.). A white-flowered, semi-parasitic herb, *Burmanna* sp. (Burma.), and a climbing pitcher plant, *Nepenthes* sp. (Nepen.), are abundant (Fig. 18). The transition between this forest type and surrounding types is sudden and unmistakable.

Cloud

On mountain peaks above 2000 m asl, this forest is distinguished by the thick growth of mosses and lichens covering the boles, branches, and even leaves of the trees (Fig. 19). The heavy moisture and insulation from constant direct sunlight provided by the constant cloud cover in these areas maintains these lush bryophyte communities. The majority of the trees are stunted and leaning. Although not comparable to forests at lower elevations, initial surveys of this forest type suggest a surprisingly rich community, including numerous *Eugenia* spp. (Myrta.), *Weinmannia* cf. *descombesiana* (Cunon.), and several Theaceae genera. A large fraction of the trees observed in this forest type are poorly known and relatively few could be identified confidently to family in the field.

Anthropogenic

Human activity, both historical and current, has had a profound impact on the park vegetation, ranging from minor activities like damar tapping of *Agathis* trees and collection of rattans (*Calamus* spp.) to major impacts like clearing and burning of forests for hill rice cultivation, coffee and chocolate plantations, and the creation of grasslands for livestock grazing. As with most types of disturbances, these activities have both negative and positive effects on the overall condition of vegetation in the park. While clearing of forest for pasture causes reduced coverage and increased margins and fragmentation, the pastures in the Besoa enclave appear to be stabilized. If managed properly, such activities can introduce a previously unrepresented vegetation type into the park's ecosystem. The identification of these anthropogenic forests and their future status is critical to maximize the positive effects while minimizing the negative.

Grasslands or 'padang' are primarily found within the two enclaves but also extend into the park, particularly west of the trail between Katu and the Besoa enclave (Fig. 20). The species composition is fairly low in these areas, primarily composed of six or seven species of grass and *Melastoma* sp. (Melas.). Villagers and local park rangers report that these areas are burned once every four or five years to replenish the vigorous growth of the grasses. The forest margins are amazingly sharp and do not show clear signs of erosion. Few classical pioneer genera are present, such as *Macaranga* (Eupho.) *Trema* or *Celtis* (Ulmac.), and within a few hundred meters of the margin, the forest is indistinguishable from ordinary secondary regeneration. These grasslands have been present for many decades and possibly hundreds of years. Comparative studies of margin stability and regeneration between the enclaves and the margins along the external park boundary should be pursued.

Secondary regeneration after clearing for hill rice cultivation is present along all of the park's boundaries but with the increasing focus of village efforts on wet rice cultivation, the frequency of this type of disturbance within the park appears to be declining. Very old secondary regeneration is present in the flat areas near the rivers of the Katu watershed, which is the original location of Toro (Fig. 21). It is largely indistinguishable from the moist lower montane forests that would be present in these

areas. In comparison to some areas where forests have never been cleared, e.g. the eastern slopes of Mt. Tuwo, species diversity of forests below 1400 m asl may have actually been increased by human activity, particularly in drier areas. *Castanopsis acuminatissima* can apparently dominate lower montane forests to 1300 m asl and the clearing of these communities may actually allow more diverse forests to establish themselves. But the forests must be given sufficient time to recover and the disturbance frequency must be kept to a minimum. Examples of highly degraded forests are found between Katu and the Besoa enclave, where a series of possible disclimax communities are mixed with grasslands, including open stands of trees comprising of small poles dominated by a few tree species. These areas do not appear to be recovering a closed, tall structure because little regeneration of latter-stage succession trees was observed.

General composition and structure of five forest types

The following tables summarize the taxonomic composition and structural differences among the sampled forest types (815 trees measured at 51 quadrats and 163 ground-truthing points). These results include the plot data collected previously {Webb, 1999 #2970}, although they should be considered temporary at this time.

Table 4. Most common families observed in six forest types. Number of individuals observed in each forest type are shown, along with total basal area for all forest types combined. LL – lowland, MLM – moist lower montane, LM – lower montane, M – montane, UM – upper montane, C – cloud.

	LL	MLM	LM	M	UM	C	BA
Myrtaceae	1	2	8	93	27	26	3.3
Fagaceae	0	2	19	93	11	1	8.8
Lauraceae	0	12	39	18	2	3	1.4
Podocarpaceae	0	0	8	3	0	37	2.2
Meliaceae	0	13	17	8	0	0	0.4
Anacardiaceae	2	4	17	4	0	0	0.7
Moraceae	0	6	16	3	0	0	4.3
Theaceae	0	0	2	21	2	0	0.5
Rubiaceae	0	5	13	2	3	0	0.4
Euphorbiaceae	0	6	12	4	0	0	0.6
Sapindaceae	2	11	6	3	0	0	0.3

Generally, three families dominate the forests of TNLL: Myrtaceae, Fagaceae, and Lauraceae (thus the name ‘oak-laurel’ forest). The Fagaceae hold an overwhelming dominance when basal area is taken into consideration, although this figure might be inflated because of the difficulty in properly measuring the many stems of heavily coppiced individuals. This difficulty also applies to the large figure for BA in the Moraceae, as most of the big individuals are strangling figs and the stems are complicated latticeworks, instead of solid cylinders. The Myrtaceae have a broad range, being present in all forest types, although both the Myrtaceae and Fagaceae appear to be concentrated in the montane forest. The Meliaceae and Sapindaceae, both usually lowland groups are more frequent at the lower elevations.

Table 5. Frequency of ten most abundant genera across six forest types. Number of individuals observed in each forest type are shown. Total basal area across all types is also shown. LL – lowland, MLM – moist lower montane, LM – lower montane, M – montane, UM – upper montane, C – cloud.

	LL	MLM	LM	M	UM	C	BA
Castanopsis (Fagac)	0	0	5	79	6	0	7.1

Ficus (Morac)	0	5	7	3	0	0	3.9
Syzygium (Myrta)	1	1	8	93	20	26	2.6
Lithocarpus (Fagac)	0	2	14	14	5	1	1.7
Podocarpus (Podoc)	0	0	6	3	0	10	1.0
Phyllocladus (Podoc)	0	0	0	0	0	27	0.9
Calophyllum (Clusi)	0	0	6	7	0	0	0.5
Vitex (Verbe)	0	5	6	1	0	0	0.2
Aglaia (Melia)	0	3	3	6	0	0	0.1
Ilex (Aquif)	0	3	9	3	0	2	0.1

Here, the obvious dominance of two genera in the Fagaceae and one in the Myrtaceae is clear. Most of the family contribution seen above is comprised of these three genera. The speciose Syzygium has a broad ecological range, being present in all forest types.

Table 6. Forest structure in five forest types. Mean distance to the nearest tree (and standard deviation) is shown for each of the four size classes. MLM – moist lower montane, LM – lower montane, M – montane, UM – upper montane, C – cloud.

	MLM	LM	M	UM	C
5-10	5.3 (1.2)	5.1 (1.2)	4.4 (1.2)	4.1 (1)	3.2 (1.3)
10-20	6.6 (2.9)	6.5 (2.2)	5.9 (2.6)	4.1 (2.4)	2.5 (3.2)
20-40	9.6 (4.3)	7.6 (5.2)	7.8 (5.2)	7.5 (5.4)	5 (6.8)
>40	12.3 (31.4)	9.9 (27.5)	9.9 (21.4)	9.6 (13)	14.3 (4.9)

The differences in structure can best be examined by comparing the two tables above. The top table presents the actual mean distance to the nearest tree and its standard deviation for each size class in each forest type. The following table presents the statistical results from pairwise comparison among all forest types for each of the size classes. Each cell in this table lists the four size classes in order and positive and negative differences in the mean distance are shown.

Trees of almost all size classes in the cloud forest are obviously much closer together than trees in all of the other forest types. These significant results obtained with a very small sample size too! The moist lower montane forest also contains a higher density of trees, in general, than the other forest types.

Species associations with forest types

The detection of associations between the distribution of species and forest or habitat types found in a natural community can be surprisingly difficult. A number of factors influence these associations, including natural disturbance history, variation in the degree of habitat specialization among species, patchiness of species due to dispersal or regeneration limitations, and mere stochastic effects. Some researchers even suggest that most associations detected by traditional methods are merely random and historical and that habitat specialization among rain forest trees is extremely limited {Hubbell, 1997 #2794; Harms, 2001 #2992}. Of course, the strength of these associations are strongly affected by the range of forest types present, with peat and swamp forests possessing distinctly different tree communities than well-drained areas at the same elevation and in close proximity {Cannon, in review #2993}. Most authors looking at the distribution of species along an elevational gradient have found unique communities in the different forest types {Aiba, 1999

#2327; Kitayama, 1996 #2194}. To investigate species associations in TNLL, a plotless sampling technique was adopted.

While a vegetation plot, commonly 0.1 to 1 ha in size, provides a detailed spatial description of a single location, considerable effort is required to establish the boundaries and substantial error can be introduced into the analysis by inaccurate or inconsistent boundaries. Pointless sampling techniques, on the other hand, can be quickly and accurately applied with minimal training and supervision. While these techniques do not lend themselves to longterm monitoring programs, they can provide a rapid snapshot of any community. Plotless techniques more accurately sample the range of variation in species distribution as they focus less effort in a small effort but instead can be tailored according to the variation observed in the community itself. In these vegetation surveys, 5 sample points were measured along a 200 meter transect (one point each 50 meters) within a single forest type. Four quadrants were established using the points of the compass. Within each quadrant, the distance to the nearest tree in each of four size classes (5.0-9.9 cm, 10-19.9 cm, 20-39.9 cm, 40 and above cm DBH) were measured and the tree was identified, if possible, and collections and descriptions were made, if not. A total of 51 points (816 trees) were sampled, 5 in MLM (moist lower montane); 10 in LM (lower montane); 24 in M (montane); 10 in UM (upper montane); and 2 in C (cloud) forests.

The associations were tested using a modification of a new randomization test {Webb, 2000 #2990}. In this test, the “expected” distribution of species and forest types is generated by randomizing the individual distribution of all species 1000 times, while keeping forest type constant. Observed distributions are considered significant if they are above the 95% confidence level of the expected distribution. deviation from the mean expectation. Given the circumstances of the current test, “patchiness”, or dispersal limitation, should not affect the results as forest types and not points were used as categories in the randomization test. Therefore, the number of trees at any one point would not carry enough weight to influence the outcome.

Because identification and matching of leaf vouchers was not completed, two approaches, “lumping” and “splitting”, were used in determining the number of unique morphotypes. “Lumping” means that unless some evidence suggested that two individuals were different, then they were considered to be the same species. “Splitting” means that unless evidence suggested two individuals were distinct, they were considered to be different species. Obviously, “lumping” should be much more conservative than “splitting”. The descriptions of leaf arrangement and bark characteristics were very helpful in distinguishing among otherwise unknown taxa, especially for the “splitting” approach. Unfortunately, the taxa from plots sampled previously {Webb, 1999 #2970} could not be integrated into this analysis because of too many uncertainties between the two datasets.

Two different approaches can be taken during the randomization test, concerning the smallest unit of independence. The more conservative approach accepts each point as independent and the individuals dependent upon the point at which they were sampled, i.e. this test relies upon “frequency” of observation for each species. The less conservative approach accepts each individual as independent. This approach is strongly influenced by the number of observations for each species. The results presented in the “Major findings” section represent the most liberal test: species determined by “splitting” and independence determined by the individual. The following figure contains the results obtained from the most conservative test: species determined by “lumping” and independence determined by the sampling point.

The overlap in species between the two tests is large (see Appendix A). The more conservative approach, as would be expected, found fewer significant associations between species and forest type distribution. Also, in the more conservative test, several species are positively associated with more than one forest type, for example *Syzygium* (#256, Myrta) with montane, upper montane, and cloud forest. In creating a list of 'indicator' species, the more conservative method is the most reliable at this time and the results from the more liberal method can only be provisionally accepted until all samples are properly identified.

Appendix A. Brief field guide to the forest types in TNLL. This guide is loosely structured as a key to the natural forest types in the park. The most obvious distinctive characteristics of each forest type are described and illustrations are provided to assist the reader in identifying forest types. The minor types, such as Heath and Swamp forest, are sharply differentiated from surrounding forest and easily recognizable in the field, while most of the major types, such as Montane and Upper Montane forest, tend to blend slowly into one another through transition zones. These transition zones occur at varying elevations and of varying significance and are an ecological reality, not simply an artifact of the analysis. Therefore, it is more appropriate to note that the forest resembles two major types and is thus a transition zone between them, instead of improperly classifying the area as one or the other type.

Wet or seasonally flooded soils on level terrain

- A. Marsh – open, dominated by grasses and sedges, often fringed by tall pandans, with abundant pitcher plants, terrestrial orchids, and a purple *Burmannia*
- B. Swamp – poorly structured forest, canopy usually not over 20 meters tall, lots of climbing rattans, many trees have stilt roots and/or pneumatophores, occasional open areas dominated by large parapa grass, abundant *Nauclea* trees.
- C. Moist Lower Montane – well structured forest on generally level terrain below 1200 m, soils often only seasonally flooded, alluvial in origin and generally dark from abundant organic matter. Characteristic trees include dongi (*Dillenia serrata*), Tahiti (*Dysoxylum* spp.), and kume (Sapotaceae, probably *Palaquium* spp.).

Well drained soils

Stunted growth

- D. Savannah/grassland – open area, generally not native in origin, dominated by tall grasses and sedges.
- E. Monsoon – generally a fairly low canopy, although occasionally well developed (up to 25 m tall). Abundant thorny plants from several families, including Leguminosae, Rhamnaceae, and Flacourtiaceae. Occasional lily trees (*Dracaena*) in more open areas. Streams are often seasonal, even fairly large drainages are often dry.
- F. Heath – often at high elevations, on exposed ridges and very thin soils, with a thick humic accumulation. Climbing pitcher plants and *Rhododendrons* common. Stems are often very dense and the canopy low (5-10 m).
- G. Cloud – usually found above 2000 m elevation on mountain summits. Low canopy (10 m) formed by mostly poorly formed trees, leaning at odd angles. Tree trunks densely covered by mosses and hepatics. A tiny-leaved *Syzygium* is very frequent (although not strictly confined to cloud forest), along with *Phyllocladus*.

Tall growth

H. Lowland

- I. Lower Montane
- J. Montane
- K. Upper Montane

Appendix B. Detailed notes on indicator species found in five forest types. **S#** and **L#** refer to the morphotype number assigned “splitting” and “lumping”, respectively. Significant associations between species distribution and forest type are shown in columns **SI**, **SP**, **LI**, and **LP**, using four different combinations of “splitting vs. lumping” morphotyping and “individual vs. point” based independence testing (see section ‘Species associations with forest types’ for detailed explanation). Field notes on leaf, bark, and additional notes are included for each species.

Family	Genus/ species	S#	L#	SI	SP	LI	LP	Leaf type	Outer bark	Inner bark
?	?	76	65	UM	0	UM	0	spiral simple	gray cracked	tan dense
?	?	144	87	C	0	C	0	spiral simple	white with large lenticels	yellow clt vessels, b quickly
Anaca	<i>Buchanania</i>	154	99	MLM, LM	MLM, LM	0	MLM, LM	spiral-pseudowhorled simple	brown-gray, boat-fissures, solitary large lenticels	fibrous re
Annon	?	159	105	LM	LM	LM	LM	alternate-spiral simple	brown-black, knobby, shallow fissures-cracks	rufous-ye fibrous sti
Aurac	<i>Agathis</i>	175	122	UM	0	UM	0	spiral simple	brown, scalloped flakes large lenticels	—
Anaca	<i>Semecarpus</i>	176	123	LM	0	LM	0	spiral (5+1) opposite leaflets	white large lenticels	red dense
Cyath	?	190	138	M	0	M	M	—	—	—
Dille	<i>Dillenia cf. serrata</i>	192	140	MLM	MLM	MLM	MLM	spiral simple	red-maroon scaly-smooth papery	rufous rec thick
Fagac	<i>Castanopsis acuminatissima</i>	212	162	M	M	M	M	spiral simple	tan-gray fissures	brown-tar
Fagac	<i>Lithocarpus sp nov</i>	213	163	LM	LM	LM	LM	spiral simple large	light gray, big lenticels in lines, flaky-smooth	red-yellow
Fagac	<i>Lithocarpus sp nov</i>	214	164	UM	UM	UM	UM	spiral simple	—	—

Appendix B (cont.)

Family	Genus/ species	S#	L#	SI	SP	LI	LP	Leaf type	Outer bark	Inner bark
Flaco	<i>Hydnocarpus</i>	223	173	LM	LM	LM	LM	spiral kneed simple	smooth, small lenticels in lines	red-tan st
Morac	<i>Ficus</i>	_	226	0	0	MLM, LM	0	spiral simple	smooth gray	_
Laura	?	235	182	MLM	MLM	MLM	MLM	opposite simple	dark brown cracked	light brow fibrous w white ring
Laura	?	252	198	LM	0	LM	0	spiral simple	white some lenticels	fibrous
Magno	<i>Magnolia?</i>	259	205	MLM	0	MLM	0	spiral simple	_	_
Malva	?	265	211	LM	0	LM	0	spiral simple	gray smooth tiny crack	red granu
Myris	<i>Horsfieldia</i>	298	244	MLM	MLM	MLM	MLM	alternate-spiral simple	brown cracked tiny cracks	yellow fit
Myrta	<i>Syzygium A</i>	303	249	C	UM, C	C	UM, C	opposite simple	dark rufous, flaky-scaly	light brow
Myrta	<i>Syzygium B</i>	305	251	UM	0	UM	UM	opposite simple	rufous scaly-smooth	dark red f
Myrta	<i>Syzygium C</i>	310	256	0	M, C	0	M, C	opposite simple	brown cracked with big vertical hanging flakes	dark red-t
Myrta	<i>Tristania whiteana</i>	345	291	0	UM	0	UM	spiral simple	whitish-orange smooth peeling	_
Palma	<i>Pinang</i> _	347	293	0	MLM, C	0	MLM, C	_	_	_

Appendix B (cont.).

Family	Genus/ species	S#	L#	SI	SP	LI	LP	Leaf type	Outer bark	Inner ba
Sapin	?	371	317	0	MLM	0	MLM	spiral (4+0) subopposite leaflets	—	—
Sapot	?	380	326	0	MLM	0	MLM	spiral simple	brown cracked	brown fib