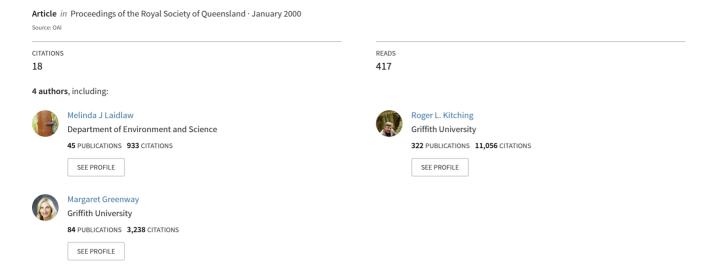
# Tree floristic and structural characteristics of one hectare of subtropical rainforest in Lamington National Park



# TREE FLORISTIC AND STRUCTURAL CHARACTERISTICS OF ONE HECTARE OF SUBTROPICAL RAINFOREST IN LAMINGTON NATIONAL PARK, QUEENSLAND

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Laidlaw, M., Olsen, M., Kitching, R.L. & Greenway, M. 2000 08 18: Tree floristic and structural characteristics of one hectare of subtropical rainforest in Lamington National Park, Queensland. *Proceedings of the Royal Society of Queensland* **109**: 91-105. Brisbane ISSN 0080-469X

A survey of trees has been conducted in one hectare of subtropical rainforest in Lamington National Park. All stems greater than 5cm diameter at 1.3m (dbh) were identified, their diameters measured and their positions plotted within the hectare. This is used to examine both the structure and the floristic composition of the vegetation. This reference plot exhibits high species richness and diversity, largely because of its location at a point of overlap between southern and northern floristic elements. The most important families on the plot are Sterculiaceae, Euphorbiaceae, Cunoniaceae, Rutaceae, and Lauraceae. The plot is dominated in terms of basal area by the family Sterculiaceae and within it, the genus Argyrodendron, which is represented by two species. Much floristic and structural information is lost if only those stems greater than 10cm dbh are analysed. The survey results are presented as baseline information for Australian sub-tropical complex notophyll vine forest at mid-elevation on basalt. These data are a contribution to the understanding of stand dynamics with respect to future disturbance and change. The need for a series of similar permanent vegetation plots across the range of diverse structural and floristic rainforest associations evident within the Australian flora is emphasised. 

Subtropical rainforest, floristics, stand structure, vegetation typology.

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Lamington National Park and contiguous reserves retain the most extensive areas of subtropical rainforest remaining on the globe and one of the last large remnants of subtropical wet and moist rainforests in Australia (Bryden, 1977). The National Park was one of the first areas set aside for conservation in Australia, largely due to the efforts of timber getter Romeo Watkins Lahey (Jarrott, 1977). The stated focus for the park has shifted over time from product utilisation and as a 'sanitarium', to conservation. Today Lamington National Park is one of the major ecotourism destinations in the world for naturalists and scientific researchers alike.

In February 1995, in conjunction with a detailed investigation of arthropod diversity, a one hectare rainforest plot was established in which the tree flora was surveyed. The protocol described below is not unique and has been used in many surveys conducted globally in order to assess forest structure, floristic composition and forest dynamics. Similar permanent vegetation plots have been established in Borneo, Sri Lanka (Ashton, 1998), India (Condit *et al.*, 1998), Panama (Foster & Hubbell, 1990; Condit *et al.*,

1998; Hubbell, 1998), Peru (Stern, 1998), Bolivia, Guyana (Hayek & Buzas, 1998), Uganda (Sheil, 1998), China (Guo-Hui et al., 1998, Li et al., 1998), Malaysia (Condit et al., 1998), Taiwan (Sun et al., 1998), Indonesia (Abdulhadi et al., 1998), Thailand (Condit et al., 1996), the Philippines (Pipoly & Mudulid, 1998), Papua New Guinea (Oatham & Beehler, 1998) and the Solomon Islands (Burslam et al., 1998). This paper presents the methodology and results of the floristic and structural survey of all individual trees ≥5cm diameter at 1.3m (dbh) within this permanent reference hectare. A full account of the methods used in both the vegetation and arthropod surveys is available as a manual from the authors (Kitching et al., 1999).

#### SITE DESCRIPTION

The study site is located near the Queensland-New South Wales border (28°13'S, 153°07'E) at an altitude of 900m, on a ridge running north-north-west from the main spine of the McPherson Range. This forms the northern caldera rim of the extinct Mt. Warning shield volcano (Stevens, 1977) and receives an average

annual rainfall of 1660mm (Clewett et al., 1994). The region is formed from Tertiary volcanic rocks that are primarily basaltic (Stevens, 1977). The structural type of the predominant vegetation is complex notophyll vine forest (CNVF, Webb et al., 1984) described floristically as being within Argyrodendron trifoliolatum-A.actinophyllum-Caldeluvia paniculosa tall closed-forest alliance (McDonald & Whiteman, 1979). This alliance consists, however, of two floristic associations described by McDonald & Whiteman (1979). The Argyrodendron spp. association is found below 800m altitude whilst the Caldcluvia paniculosa - Cryptocarya erythroxylon - Dysoxylum fraserianum -Geissois benthamii association occurs at altitudes between 800m and 1000m. Despite being at an altitude higher than that described for the former association, species reported from both associations were found on the study plot. This may suggest that the plot lies within a transition zone between these two floristic associations.

Floristically, Lamington National Park falls within a cross-over region between humid sub-tropical and warm temperate regions sometimes known as the McPherson-Macleay botanical overlap (Burbidge, 1960; Graham *et al.*, 1977). The diverse habitats represented within Lamington National Park allow both tropical and temperate species to be represented (Graham *et al.*, 1977).

McDonald and Thomas (1990) recently enumerated the flora of Lamington National Park, but species continue to be discovered in this biologically diverse area (e.g. *Bulbophyllum lamingtonense* described by Jones, 1993). What is lacking, however, are published data on the relative abundances of specific taxa or detailed descriptions of vegetation associations in the area (but see McDonald & Whiteman, 1979). The establishment of the permanent reference plot described in this paper begins to address this situation. Other plots are planned to characterise further the remarkable flora of Lamington National Park.

#### **METHODS**

A one hectare plot was laid out in plan design in an area of rainforest that did not exhibit any significant disturbance related to the 1983 storm which had caused widespread damage to nearby rainforest (Olsen & Lamb, 1988). The axes of the plot were aligned along the compass points and the western margin of the plot utilised as the

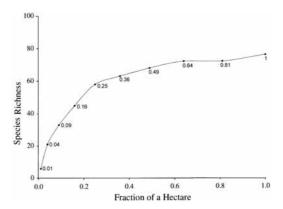


FIG. 1. Species discovery curve for individual trees ≥5cm diameter at 1.3m from the ground, obtained by considering nested quadrats of increasing size within the study hectare.

'straight' edge from which parallel easterly traverses were undertaken with regular checks to ensure the plot remained more or less square in plan view.

The hectare was subdivided into  $10\text{m} \times 10\text{m}$  grids delineated by wooden pegs at the four corners of each  $100\text{m}^2$  grid cell. Within individual grid cells, all stems greater than 5cm dbh were identified and their girth measured to the nearest cm at 1.3m above ground on the uphill side of each stem. Where a tree's trunk occurred within a quadrat but its crown did not, it was included. Any coppice stems that were greater than 5cm in diameter were included as separate individuals. Where trees possessed buttresses, the girth was measured directly above the buttress roots by using a ladder or by estimating the diameter directly from the ground.

Epiphytes and lianas were prized from the trunk at the point of measurement (without removal or unnecessary damage) to allow for greater accuracy of girth measurement. These girth measurements were later transformed into diameter measurements. The position of each individual within the grid cell was then plotted to the nearest 10cm along both x and y axes and the height estimated to the nearest 2m. The height data have not been included in the analyses presented here. Once the structural features of the trees had been noted, each individual was identified to species. Where trees could not be identified in the field, voucher samples and blazes were taken and notes were made on bark texture. This information was then used in the field station to finalise identification.

TABLE 1. The abundance, relative density, relative dominance, relative frequency and importance value indices (IVI) of all species on the study hectare, in order of family importance (FIV). Formulae for calculation of relative density, relative dominance and IVI are presented in the text. Names follow Henderson (1997), in which volume authorities for the names can be found.

Family	Species	Abundance	Relative Density	Relative Dominance	Relative Frequency	IVI
Sterculiaceae	Argyrodendron trifoliolatum	75	5.924	14.113	101.351	121.389
	Argyrodendron actinophyllum	33	2.607	11.269	44.595	58.470
	Brachychiton acerifolius	4	0.316	0.110	5.405	5.831
Euphorbiaceae	Baloghia inophylla	132	10.427	4.797	178.378	193.602
	Actephila lindleyi	136	10.742	1.257	183.784	195.783
Cunoniaceae	Pseudoweinmannia lachnocarpa	37	2.923	9.224	50.000	62.147
	Caldcluvia paniculosa	64	5.055	7.361	86.486	98.902
	Geissois benthamii	11	0.869	1.148	14.865	16.882
Rutaceae	Acronychia octandra	34	2.686	3.892	45.946	52.524
	Halfordia kendack	14	1.106	1.495	18.919	21.520
	Acronychia suberosa	34	2.686	1.162	45.946	49.794
	Flindersia australis	3	0.237	0.717	4.054	5.008
	Pentaceras australis	9	0.711	0.463	12.162	13.336
	Acronychia pubescens	18	1.422	0.246	24.324	25.992
	Sarcomelicope simplicifolia	1	0.079	0.229	1.351	1.660
	Acronychia laevis	5	0.395	0.029	6.757	7.181
	Microcitrus australis	1	0.079	0.003	1.351	1.434
Lauraceae	Litsea reticulata	7	0.553	4.779	9.459	14.791
	Cinnamomum oliveri	3	0.237	0.994	4.054	5.285
	Cinnamomum virens	43	3.397	0.938	58.108	62.443
	Cryptocarya erythroxylon	4	0.316	0.525	5.405	6.246
	Cryptocarya obovata	3	0.237	0.504	4.054	4.795
	Endiandra muelleri	10	0.790	0.116	13.514	14.419
	Cryptocarya foveolata	2	0.158	0.092	2.703	2.952
	Neolitsea australiensis	1	0.079	0.007	1.351	1.438
Sapindaceae	Sarcopteryx stipata	17	1.343	0.682	22.973	24.998
	Arytera divaricata	3	0.237	0.368	4.054	4.659
	Diploglottis australis	2	0.158	0.180	2.703	3.040
	Elattostachys nervosa	4	0.316	0.131	5.405	5.852
	Jagera pseudorhus	1	0.079	0.014	1.351	1.444
	Mischocarpus anodontus	1	0.079	0.011	1.351	1.442
	Cupaniopsis flagelliformis var. australis	2	0.158	0.008	2.703	2.869
	Harpullia alata	1	0.079	0.006	1.351	1.436
	Guoia semiglauca	1	0.079	0.004	1.351	1.434
	Rhysotoechia bifoliolata	1	0.079	0.003	1.351	1.434
Rubiaceae	Randia benthamiana	146	11.532	1.682	197.297	210.512
	Psychotria simmondsiana	2	0.158	0.010	2.703	2.870
Moraceae	Ficus watkinsiana	5	0.395	12.602	6.757	19.754
	Streblus brunonianus	1	0.079	0.005	1.351	1.435
Monimiaceae	Doryphora sassafras	54	4.265	1.479	72.973	78.717
	Wilkiea huegeliana	29	2.291	0.129	39.189	41.609
	Wilkiea austroqueenslandica	4	0.316	0.035	5.405	5.757
Proteaceae	Orites excelsa	54	4.265	3.683	72.973	80.921
	Stenocarpus sinuatus	6	0.474	0.383	8.108	8.965
	Stenocarpus salignus	5	0.395	0.053	6.757	7.205

TABLE 1. cont.

Family	Species	Abundance	Relative Density	Relative Dominance	Relative Frequency	IVI
Myrtaceae	Syzygium crebrinerve	7	0.553	0.880	9.459	10.892
	Austromyrtus sp. Upper Mudgeeraba Creek	24	1.896	0.273	32.432	34.601
	Austromyrtus acmenoides	3	0.237	0.110	4.054	4.401
	Decaspermum humile	3	0.237	0.036	4.054	4.327
	Acmena smithii	4	0.316	0.031	5.405	5.753
	Rhodamnia sp.	1	0.079	0.021	1.351	1.451
Ebenaceae	Diospyros pentamera	43	3.397	3.529	58.108	65.034
Meliaceae	Dysoxylum rufum	1	0.079	0.089	1.351	1.519
	Synoum glandulosum	1	0.079	0.045	1.351	1.476
	Dysoxylum fraserianum	18	1.422	0.009	24.324	25.755
Araucariaceae	Araucaria cunninghamii	7	0.553	3.790	9.459	13.802
Grossulariaceae	Quintinia verdonii	16	1.264	0.273	21.622	23.158
	Polyosma cunninghamii	1	0.079	0.006	1.351	1.436
Verbenaceae	Premna lignum-vitae	13	1.027	1.871	17.568	20.465
Cyathenaceae	Cyathea leichhardtiana	27	2.133	0.493	36.486	39.113
Mimosaceae	Archidendron grandiflorum	8	0.632	0.159	10.811	11.602
	Acacia melanoxylon	1	0.079	0.037	1.351	1.467
Winteraceae	Tasmannia insipida	10	0.790	0.058	13.514	14.362
Rhamnaceae	Emmenosperma alphitonioides	15	1.185	0.807	20.270	22.262
Pittosporaceae	Pittosporum rhombifolium	2	0.158	0.147	2.703	3.008
	Citriobatus lancifolius	1	0.079	0.007	1.351	1.438
Celastraceae	Denhamia celastroides	12	0.948	0.088	16.216	17.252
Oleaceae	Notelaea johnsonii	10	0.790	0.133	13.514	14.437
Akaniaceae	Akania bidwillii	5	0.395	0.064	6.757	7.216
Flacourtiaceae	Scolopia braunii	4	0.316	0.065	5.405	5.786
Eupomatiaceae	Eupomatia laurina	3	0.237	0.018	4.054	4.309
Alangiaceae	Alangium villosum subsp. polysmoides	1	0.079	0.010	1.351	1.441
Araliaceae	Polyscias elegans	1	0.079	0.009	1.351	1.440
Elaeocarpaceae	Sloanea woollsii	1	0.079	0.003	1.351	1.433

All botanical names used in this paper follow Henderson (1997) and this work should be consulted for information on the taxonomic authorities associated with each name.

### **RESULTS**

SPECIES COMPOSITION AND FLORISTICS. A total of 1266 stems were recorded from the plot comprising 74 species. A species discovery curve constructed by adding the species encountered in nested quadrats of increasing size is presented (Fig. 1). The plot of the number of species 'known' against quadrat size describes a curve which is clearly converging upon an asymptote, suggesting that a majority of the target neighbourhood flora was 'captured' by the selected hectare.

An estimate of the total regional flora was made from McDonald & Thomas (1990). A total of 51 families containing 188 tree species displayed life forms and habitat requirements which could allow them to be detected by our survey. Based on this assessment, approximately 40% of the regional rainforest tree flora of the park was recorded on this single hectare and an extrapolation of the species discovery curve (Fig. 1) suggests that the actual target flora within the immediate vicinity of the plot was approaching 43% of this regional estimate.

For comparative purposes, we have calculated standard diversity measures (Magurran 1988) for the plot, as follows. The Shannon diversity index combines a measure of richness (s) with evenness via the formula:

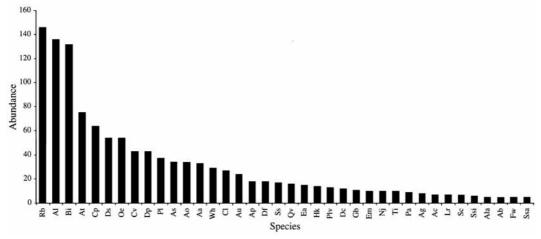


FIG. 2. Ranked abundance levels of all trees with five or more individuals on the hectare plot. Key: Rb = Randia benthamiana, Al = Actephila lindleyi, Bi = Baloghia inophylla, At = Argyrodendron trifoliolatum, Cp = Caldcluvia paniculosa, Ds = Doryphora sassafras, Oe = Orites excelsa, Cv = Cinnamomum virens, Dp = Diospyros pentamera, Pl = Pseudoweinmannia lachnocarpa, As = Acronychia suberosa, Ao = Acronychia octandra, Aa = Argyrodendron actinophyllum, Wh = Wilkiea huegeliana, Cl = Cyathea leichhardtiana, Au = Austromyrtus sp. (upper Mudgeeraba Creek), Ap = Acronychia pubescens, Df = Dysoxylum fraserianum, Ss = Sarcopteryx stipata, Qv = Quintinia verdonii, Ea = Emmenosperma alphitonioides, Hk = Halfordia kendack, Plv = Premna lignum-vitae, Dc = Denhamia celastroides, Gb = Geossois benthamii, Em = Endiandra muelleri, Nj = Notelaea johnsonii, Ti = Tasmannia insipida; Pa = Pentaceras australe, Ag = Archidendron grandiflorum, Ac = Araucaria cunninghamiana, Lr = Litsea reticulata, Sc = Syzygium crebrinerve, Ssi = Stenocarpus sinuatus, Ala = Acronychia laevis, Ab = Akania bidwillii, Fw = Ficus watkinsiana, Ssa = Stenocarpus salignus.

$$H' = -\Sigma p_i \ln p_i$$

where  $p_i$  = the proportional abundance of the i<sup>th</sup> species. Shannon diversity for this plot was 3.39.

Evenness, the ratio of H' to  $\boldsymbol{H}_{\scriptscriptstyle max},$  was calculated as:

$$E = H'/\ln s$$

Application of this formula to our data gave an evenness value of 0.79.

An Importance Value Index (IVI) was calculated for each species recorded on the hectare plot. This is based on the formula of Cottam and Curtis (1956) and uses the relative density, relative dominance and the relative frequency of each species to give an index of species importance. The relative dominance of each species will be discussed in terms of structure rather than included in the floristic results here. Using the formula of Cottam & Curtis (1956), viz.:

IVI = (relative density + relative dominance + relative frequency) × 100 where:

Relative diversity = number of trees of a species/total number of trees

Relative dominance = total basal area of a species/total basal area for all species

Relative frequency = number of times a species occurs/total number of quadrats

where basal area (m<sup>2</sup>) for each species =  $[\pi \times (dbh/2)^2]$ .

Table 1 presents the abundance levels, relative densities, relative dominance, relative frequency and IVI values of species on the plot organised by family importance. The most important species were Argyrodendron trifoliolatum (Sterculiaceae), Randia benthamiana (Rubiaceae), Actephila lindleyi, Baloghia inophylla (both Euphorbiaceae) and Caldcluvia paniculosa (Cunoniaceae) together contributing 42.7% of the total IVI. The stand was dominated numerically by Randia benthamiana, Actephila lindleyi, Baloghia inophylla, Argyrodendron trifoliolatum and Caldcluvia paniculosa, constituting 43.44% of all individuals recorded.

Only 16 species (21.6%) of the 74 species from within the plot are represented by 20 or more individuals. These species account for 965 stems or 76.2% of all those recorded from within the hectare. The majority of species were represented by few individuals with 40 of the 74 species

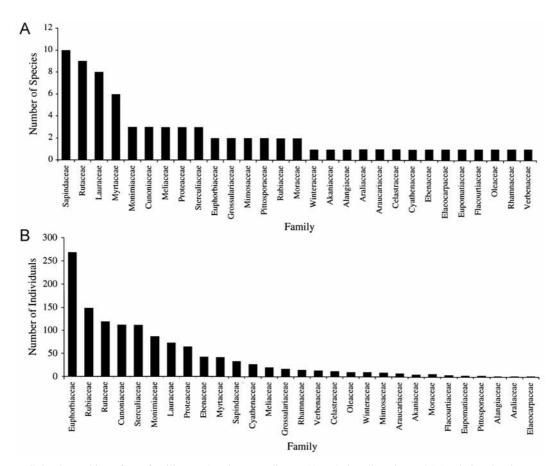


FIG. 3. The ranking of tree families on the plot according to (A) relative diversity and (B) relative density.

(54.1%) recorded from the plot represented by five or fewer individuals and 30 species (40.5%) with three or fewer individuals. This highly asymmetric species/abundance distribution is characteristic of rainforest plant (and other biotic) assemblages in general with a few abundant species and an extended tail of 'rare' taxa (Fig. 2). There is clearly a high level of species heterogeneity.

Turning from an assessment of individual species to the family level, we have calculated 'family importance values' (FIV) using the formula of Mori *et al.* (1983), *viz.*:

FIV = Relative Diversity + Relative Density + Relative Dominance where:

Relative Diversity = number of species in family/total number of species

Relative Density = number of stems in family/total stems on the plot

Relative Dominance = basal area of family/total basal area for all families.

A total of 29 families were recorded from the plot at Lamington National Park. The families with the highest FIV values were the Sterculiaceae, Euphorbiaceae, Cunoniaceae, Rutaceae and Lauraceae, which contributed approximately 51% of the total FIV. These families also represent 54% of all stems recorded. Although Sterculiaceae was not the most abundant family, the large size of individuals within this family, such as Argyrodendron actinophyllum, resulted in them being the most important family. The designation of the forest as an Argyrodendron actinophyllum-A. trifoliolatum-Caldcluvia paniculosa alliance is a consequence of this.

The most diverse families as identified by the relative diversity values were the Sapindaceae,

TABLE 2. Families of trees occurring on the study hectare, ranked in descending order of their Family Importance Value (FIV). Component values of relative dominance, relative diversity and relative density are presented. See text for formulae and method of calculation.

Family	FIV	Relative Domi- nance	Relative Diversity	Relative Density	
Sterculiaceae	37.921	25.020	4.054	8.847	
Cunoniaceae	30.306	17.405	4.054	8.847	
Euphorbiaceae	29.814	5.942	2.703	21.169	
Rutaceae	29.647	8.085	12.162	9.400	
Lauraceae	24.384	7.807	10.811	5.766	
Sapindaceae	17.501	1.381	13.514	2.607	
Rubiaceae	16.054	1.661	2.703	11.690	
Moraceae	15.546	12.369	2.703	0.474	
Proteaceae	13.231	4.043	4.054	5.134	
Myrtaceae	12.752	1.326	8.108	3.318	
Monimiaceae	12.622	1.617	4.054	6.951	
Ebenaceae	8.212	3.464	1.351	3.397	
Meliaceae	7.624	1.990	4.054	1.580	
Araucariaceae	5.624	3.720	1.351	0.553	
Grossulariaceae	4.319	0.273	2.703	1.343	
Verbenaceae	4.215	1.836	1.351	1.027	
Cyathenaceae	3.968	0.484	1.351	2.133	
Mimosaceae	3.606	0.192	2.703	0.711	
Rhamnaceae	3.328	0.792	1.351	1.185	
Pittosporaceae	3.091	0.152	2.703	0.237	
Celastraceae	2.386	0.086	1.351	0.948	
Oleaceae	2.272	0.131	1.351	0.790	
Winteraceae	2.198	0.057	1.351	0.790	
Akaniaceae	1.809	0.063	1.351	0.395	
Flacourtiaceae	1.731	0.063	1.351	0.316	
Eupomatiaceae	1.606	0.018	1.351	0.237	
Alangiaceae	1.440	0.010	1.351	0.079	
Araliaceae	1.439	0.009	1.351	0.079	
Elaeocarpaceae	1.433	0.003	1.351	0.079	

Rutaceae, Lauraceae and Myrtaceae (Fig. 3A). Relative density measures identify the Euphorbiaceae, Rubiaceae, Rutaceae, Cunoniaceae and Sterculiaceae as having the highest values. These families made up 60% of all individuals on the plot (Fig. 3B). These indices are summarised in Table 2.

STRUCTURE. The structural variability across the plot was high with little obvious pattern discernible based upon size class alone. The canopy components of the plot are spatially distributed more or less evenly across the plot, ensuring near total canopy cover at the time of the survey, with the only obvious canopy gap

apparent on the eastern boundary. A topographic map of the plot was produced in 1995 and was digitised using MapInfo™ GIS software (Fig. 4). The (00,00) datum point on this map is located at 900m elevation and shows contours 0.5m apart running downslope from the datum. A thematic map of the distribution of all stem and graduated symbols representing their relative dbh sizes is presented (Fig. 4). The distribution of stems on the plot was found not to differ significantly from a Poisson distribution. This site has never experienced commercial logging and the more or less even distribution of the larger stem classes appears to reflect this.

The stand structure on the plot was dominated by subcanopy elements with almost half of all stems found within the size classes of less than 10cm dbh (Fig. 5). The most abundant species on the plot - Randia benthamiana, Actephila lindleyi and Baloghia inophylla, fall into this category. The first two of these species are exclusively understorey shrubs or small trees (Fig. 6A-B) whereas B. inophylla occasionally participates in the canopy (Fig. 6C). The individuals with girths greater than 40cm dbh are those considered most likely to contribute substantively to the canopy in volume and canopy cover. Of this set of size classes, there are a total of 137 stems on the plot. Only four species have more than five individuals with girths ≥40cm dbh (Argyrodendron trifoliolatum (25 individuals, Fig. 6D), A. actinophyllum (18 individuals), Caldeluvia paniculosa (8 individuals, Fig. 6E) and *Pseudoweinmannia* lachnocarpa (12 individuals) and these are the major elements of the canopy. With the exception of Pseudoweinmannia lachnocarpa, this conforms to the floristic description of the forests in this area utilised by McDonald and Whiteman (1979).

The total basal area supported on the plot at 1.3m from the ground was 70.6m². Argyrodendron trifoliolatum (Sterculiaceae) was the most dominant species in terms of basal area followed by Ficus watkinsiana (Moraceae) and Argyrodendron actinophyllum (Sterculiaceae). The basal area of Ficus watkinsiana, however, generally includes that of the species over which the fig had grown, giving perhaps a false indication of the relative importance of F. watkinsiana. If this species is set aside then the two Argyrodendron species are the highest ranked in terms of basal area. The most dominant families in terms of basal area were Sterculiaceae, Cunoniaceae, Moraceae and

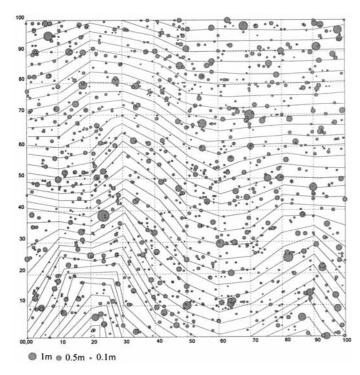


FIG. 4. The dispersion of all stems recorded on the study hectare showing dbh size classes.

Rutaceae, which collectively contributed approximately 55% of the total basal area whilst representing only 27% of all stems reflecting, as already indicated, their pre-eminence in the larger size classes on the plot.

## DISCUSSION

Three general aspects of our results are of particular interest. The first relates to the adequacy of the methodology we have used for assessing floristics and structure within a forest of this type. The second takes our results for this particular plot and compares them with other rainforest plots. Lastly, we discuss the appropriate form for further work to assess the floristic and dynamic aspects of forests within subtropical south-east Queensland and elsewhere.

METHODOLOGY. It is obvious that a full appreciation of the diversity and dynamics of the tree species on any forest plot will ideally include all age classes of the species concerned. From our perspective, this would add the seedlings and saplings below 5cm diameter at 1.3m height and the subterranean seeds that either await

germination or whose shoots have not yet emerged above the ground. If this were possible within a hectare plot, this would undoubtedly add to the species list we have generated from sampling only individuals greater than 5cm dbh. We suspect, however, that this addition would be small and the practical problems associated with such a complete study are legion.

We regard the current scale of our study as adequate although minimal. To capture the characteristics of the forest in anything less than one hectare is simply not a credible proposition. The selection of such a scale would actually become a liability were the study to be extended to include younger age classes. A proper survey of the seedlings within a forest may be done in several different ways using smaller quadrats or transects (e.g. Connell et al., 1984; Hubbell et al., 1990; Lieberman et al., 1990; Lieberman, 1996) but would not be done, in general, by block survey of a hectare. Similarly,

study of the seed stocks within a forest requires an entirely different set of techniques and sampling design (e.g. Garwood, 1989; Graham & Hopkins; 1990, Schupp, 1990). The addition of both seedlings and seeds would considerably increase the identification hurdles within the study.

Like most ecological field studies, ours has been a minimal approach reflecting available financial resources, people-power and return per unit effort. It is evident that we have achieved a much clearer impression and appreciation of the forest than could have been the case using the more commonly used 10cm dbh cut-off. Had we applied such a cut-off to our data we would have encountered only 688 stems of 59 species.

In terms of the age-structure of the trees, and in consequence our appreciation of species' dynamics, we accept that the younger age-classes are missing from the study. This still allows comparative assessment, species to species, plot to plot, location to location, so long as the same dbh cut-off is used.

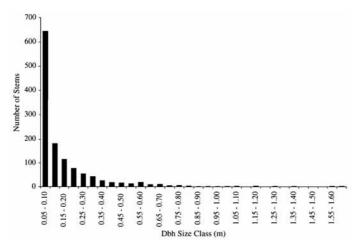


FIG. 5. Size distribution (diameter at 1.3m) for all trees on the study hectare

Finally, in the consideration of methodology, we emphasise the fact that the results presented here represent the outcomes from the study of a single hectare. Although one hectare vegetation plots reflect the diversity and dynamics of the forest within the wider region, they can give no information on the representativeness or variability of the forest of which this hectare is just one small part. The survey results do, however, provide a base for more extensive work (currently in progress) using a larger number of smaller plots. We comment further on this point below.

COMPARATIVE ASSESSMENT. In trying to place our survey results in a wider context, three types of comparisons are relevant: with other Australian rainforest plots, with rainforest plots elsewhere at similar latitudes and with plots elsewhere at different latitudes. Key results from selected surveys in these regions are presented in Table 3 alongside those from the Lamington site.

Within Australia, results for a number of plots are relevant. In other work we have established a series of six plots from Lamington to Cape Tribulation. Data from two of these are readily available and have been partly published by Kitching *et al.* (1998). These are located on the Atherton Tablelands at 17°S and 686m elevation, and at Noah Creek at 16°S and 30m elevation. The survey of the Noah Creek plot was carried out by Andrew Small. The results from the three Australian sites are comparable in terms of the number of stems ≥5cm dbh on each hectare, but show the expected latitudinally related increase

in species and family diversity from the subtropical to the tropical sites. There is more than double the number of species and families on the lowland tropical hectare than on the Lamington plot. This having been noted, we also observe that some subtropical sites north of Lamington have a lower species richness, probably because they represent either smaller patches of rainforest overall, or are at higher elevations (unpublished results from Conondale Ranges and Eungella National Park). We also note that the family diversity at the Noah Creek site is exceptionally high due to the presence of several highly endemic taxa that occur virtually nowhere else in the

region (Kitching et al., 1998). There are many explanations available in the literature for the observed south to north increase in species richness most recently exercised under the general name of 'Rapaport's Rule' (Gaston & Blackburn, 1996; Gaston et al., 1998). This 'rule' describes the observation that the latitudinal ranges of organisms increased with increasing latitude (Stevens, 1989). This, in turn, provides an explanation for the frequently observed decrease in species richness with increase in latitude. The simplest explanation for this phenomenon is that the more extreme environments of the higher latitudes demand that organisms evolve higher tolerance ranges in order to cope with the more variable climates, leading in turn to greater overall ranges and lower species richness. Our tree data from within Australia support, in general, the existence of such a pattern. The increasing equability and predicability of the more tropical sites provides the simplest explanation as to why the observed levels of species richness exist, but this underlying pattern is almost certainly modified by altitude (Rahbek, 1997), substrate and nearness to other biogeographic regions (the highly diverse rainforests of Papuasia in this

Two subtropical rainforest plots at similar latitudes to the Lamington site are also examined in Table 3. The first of these, a 1.1ha plot is located in Dorrigo National Park, 6kms from Dorrigo in New South Wales (Nadolny, 1991). This plot supported a slightly higher stem density

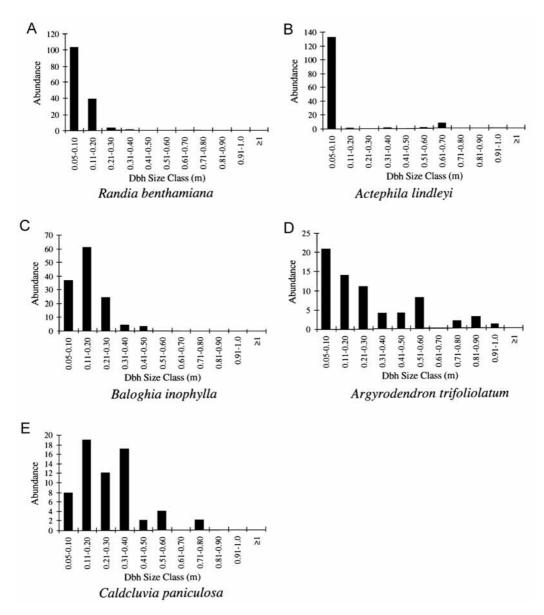


FIG. 6. Size distribution (diameter at 1.3m) for the five most abundant species on the plot.

than the Lamington plot but lower species, genera and family richness as well as a lower Shannon diversity. Of particular interest is a 4.4 ha plot established at Gambubal, approximately 35km east of Warwick and at an altitude of 1100m (Howell, 1996). Despite this site being at both a similar latitude and altitude to the current study site, both the stem density and species richness were considerably lower than those of the

Lamington plot. The Lamington plot supported approximately the same numbers of genera and families despite being less than one quarter of the size of the Gambubal plot. The Shannon diversity of this plot was also considerably lower than that of Lamington. All three of these sites are contained within the MacPherson-Macleay botanical overlap (Burbidge 1960), however, the Lamington plot displays a much higher species

TABLE 3. Summary of results from key rainforest plot studies compared with results from the Lamington plot. \*Species richness and stem densities are as per one hectare, other results are as per 4.4 hectares. \*\*Actual cut-offs used were >1 cm, >4 cm, >8 cm; number of stems is as per one hectare; taxon densities are as per 3 hectares. \*\*\*Results represent one hectare taken from the 50ha Barro Colarado site and stem and taxon densities are reduced accordingly; stem density. Cut-offs were >1cm, >4cm, >8cm; 5cm taxon densities were inferred; numbers of families and Shannon diversity values were derived from the 50 ha plot. References: Gambubal - Howell (1996); Dorrigo - Nadolny (1991); Atherton and Noah Creek - Kitching et al. (in press); China (1) - Kong et al. (1998); China (2) - Li et al. (1998); Taiwan - Sun et al. (1998); Panama - Foster & Hubbell (1990); Ecuador - Valencia et al. (1994).

Australian Forests						
Location	Lamington (this paper)	Gambubal*	Dorrigo	Noah Creek	Atherton	
Latitude	28°S	28°S	30°S	16°S	17°S	
Altitude (m amsl)	600	1100	700	30	686	
Plot Size (ha)	1	4.4	1.11	1	1	
Diameter cutoff (cm)	5	10	10	5	5	
No. of stems ≥1cm	=	-	-	-	-	
No. of stems ≥5cm	1266	-	-	-	1207	
No. of stems ≥10cm	688	599	761	_	569	
No. of species ≥1cm	-	-	-	-	-	
No. of species ≥5cm	76	-	-	169	113	
No. of species ≥10cm	59	40	37	-	83	
No. of genera ≥1cm	-	-	-	-	-	
No. of genera ≥5cm	63	-	-	-	77	
No. of genera ≥10cm	49	49	32	-	58	
No. of families ≥1cm	-	-	-	-	-	
No. of families ≥5cm	29	-	-	60	34	
No. of families ≥10cm	25	27	26	-	26	
Shannon (H') ≥1cm	-	-	-	-	-	
Shannon (H') ≥5cm	3.41	-	-	4.26	3.92	
Shannon (H') ≥10cm	3.28	2.78	2.81	-	3.66	

	Sub-Tropical Forests			Tropical Forests			
Location	China (1)	China (2)	Taiwan**	Brunei	Panama***	Ecuador	
Latitude	33°N	18°N	22°N	4°N	9°N	0°	
Altitude (m amsl)	300	825	320	50	150	260	
Plot Size (ha)	1	1	3	1	1	1	
Diameter cutoff (cm)	1	10	1	5	1	5	
No. of stems ≥1cm	3974	-	12203	-	4710	-	
No. of stems ≥5cm	-	-	4324	1021	1248	1561	
No. of stems ≥10cm	467	669	1725	423	554	693	
No. of species ≥1cm	87	-	118	-	176	-	
No. of species ≥5cm	-	-	102	279	125	473	
No. of species ≥10cm	39	153	89	194	95	307	
No. of genera ≥1cm	-	-	78	-	-	-	
No. of genera ≥5cm	-	-	-	107	-	187	
No. of genera ≥10cm	-	89	-	89	-	138	
No. of families ≥1cm	43	-	41	-	56	-	
No. of families ≥5cm	-	i	-	49	-	54	
No. of families ≥10cm	26	51	-	41	48	46	
Shannon (H') ≥1cm	2.92	-	-	-	1.6	-	
Shannon (H') ≥5cm	-		-	5.01	-	-	
Shannon (H') ≥10cm	2.51	4.39	-	4.94	1.3	-	

diversity suggesting that factors such as topography, rainfall and in particular, logging history may be responsible for differences in site floristics. The Gambubal plot was extensively logged 40 years ago (O'Donnell, 1993). To our knowledge, the Lamington plot has never been logged.

Subtropical rainforest at latitudes comparable with the Lamington site elsewhere in the world are few. Taking a broad interpretation of 'subtropical' (from 18° to 33° from the equator), there are three Chinese plots of interest. These are from the Dinghushan Reserve, Guangdong Province (Kong et al., 1998), from the island of Hainan (Li et al., 1998) and from Taiwan (Sun et al., 1998). Strictly speaking both the Hainan and Taiwanese sites fall within the Tropic of Cancer VØ⊕3 ⊕30 ∇r |Ø≪2⊕>« ΘØ⊕0 \⊖000 ⊕30 ≥10cm line in Table 3), whereas the Taiwan site has considerably higher values, perhaps reflecting its high level of typhoon impact (Sun et al., 1998). Species richness (for stems ≥10cm) at the Dinghushan site is only a little more than half that of the Lamington site despite being at a lower altitude (300m compared with 600m), although the number of families represented is virtually the same. Both of the more tropical sites, in Hainan and Taiwan, are, in general, richer in species and families, as would be expected. The Taiwanese site is similar in richness to an Australian Atherton Tablelands site. The Hainanese site is exceptionally rich with 153 species of 51 families ≥10cm dbh, comparable with the lowland forest of Far Northern Queensland and some of the more equatorial sites elsewhere. We have been unable to obtain comparable subtropical data from, for example, Chile, southern Brazil, or the Ryukyus, but these would be obvious further comparators.

Finally, it is of interest to place the current results in the context of equatorial forest sites – the richest known sites globally. We have already compared the Lamington results with the Noah Creek plot in lowland tropical Australian forest which has more than twice the numbers of both species and families. The richest one-hectare plot surveyed to date is in Ecuadorian Amazonia (Valencia *et al.*, 1994) in which a remarkable 473 species of tree ≥5cm dbh were recorded. These were of 187 genera and 54 families compared with the Lamington figures of 63 and 29 respectively. The Ecuadorian site is more than

twice as rich as the Noah Creek site, the richest Australian site surveyed to date and more than one and a half times richer than the Brunei site (Kitching *et al.*, 1998) which, with 279 species, is probably the richest Old World site surveyed to date. Table 3 also includes data from the well known 50ha plot on Barro Colorado island in Panama. With about 125 species of over 50 families per hectare (on average) this site is intermediate in richness, perhaps reflecting its Mesoamerican and island situation.

In summarising these comparative results, it appears that the latitude and size of the forested region within which a plot lies are the two critical variables in determining tree diversity, both within a continent and globally.

FUTURE WORK. Plot work of the sort described in this paper inevitably raises the question, how representative of the regional vegetation is the chosen plot? Without duplicating the plot many times (an impractical option) this question remains challenging. We have, however, surveyed subsequently a further two  $25m \times 25m$  plots in the vicinity of the Lamington hectare, which resulted in very few additional species of tree being identified. Full results from these studies will be published as part of a wider treatment in due course. In addition, we have established a second one hectare plot in comparable rainforest in the Conondale Ranges at about 26.5° S. An enlarged set of rainforest sites within the subtropical zone in Australia, perhaps each 25m × 25m, is desirable and would be essential to pick up the variation reflecting nuances of altitude, substrate type, forest patch size and ecological history.

Placing the Lamington site within a wider context of more or less undisturbed rainforest sites within Australia and elsewhere is part of our on-going research programme. As has been discussed in part already, we have established strictly comparable sites in the Conondale Ranges, at Eungella, Paluma, the Atherton Tablelands and Cape Tribulation. Surveys at selected sites in Papua New Guinea are also underway. We have no plans for a mid-Cape York site, although one would clearly be desirable, as would sites in rainforest remnants south of Queensland. Each of the sites we survey is completed as a central one-hectare plot with two 'satellite' quarter hectares. Our extended transect links with sites in Borneo and further north in Asia. The entire system of plots provides a baseline of biodiversity assessment against which the biota of other more or less disturbed sites can be compared.

#### **ACKNOWLEDGEMENTS**

The initial plant survey at Lamington was carried out during an Earthwatch expedition in 1993. We thank Earthwatch (Australia) for providing the support for that work and the Earthwatch volunteers who participated in that survey. Further voluntary field assistance was provided by Griffith University undergraduates to whom we are also grateful. The O'Reilly family provided their usual hospitality to the team and Mr Peter O'Reilly (Snr) assisted with tree identification. We would also like to thank W. J. F. McDonald and one anonymous referee for their valuable comments on earlier drafts. The topographic map of the plot was engineered by Mr Brian Watson. The research was carried out under a permit issued by the Queensland National Parks and Wildlife.

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