

Temporal and spatial variation in an Australian tropical rainforest

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Abstract This study describes the floristics and structure of a 0.95-ha lowland tropical rainforest plot at the Australian Canopy Crane Research Facility at Cape Tribulation, Queensland. Five years of post-cyclonic change in forest floristics and structure following the passage of Tropical Cyclone ‘Rona’ in February 1999 are examined. Local and regional variation in tropical rainforest is examined in comparison with other lowland plots established nearby and mid-elevation plots located elsewhere in north Queensland at Eungella, Paluma and the Atherton Tablelands. These plots are placed in a broader Australasian context along with lowland rainforest plots at Baitabag and Oomsis, Papua New Guinea. The 2005 survey found 680 stems of 82 species ≥ 10 cm d.b.h. on the crane plot, an increase of 30.3% in stems and 16.4% of species in the 5 years since the previous survey. The most abundant families were Meliaceae, Euphorbiaceae, Lauraceae, Myrtaceae and Apocynaceae and the most abundant species were *Cleistanthus myrianthus*, *Alstonia scholaris*, *Myristica insipida*, *Normanbya normanbyi* and *Rockinghamia angustifolia*. Temporal floristic and structural variation suggests that the crane site remains in an active stage of post-cyclonic recovery. Local spatial variability in floristics and structure at Cape Tribulation exceeded the variation exhibited by a single plot over a period of 5 years, despite the impact of Cyclone Rona. This finding suggests a high degree of temporal stability within this stand of rainforest despite frequent catastrophic disturbances. The rainforests of Cape Tribulation constitute a relatively unique floristic community when observed in an Australasian context. Variation in rainforest community composition across the region shows the importance of biogeographical connections, the impacts of local topography, environmental conditions and disturbance history.

Key words: Cape Tribulation, cyclone, floristics, structure, tropical rainforest.

INTRODUCTION

There has been a globally synchronous warming in tropical forest regions of $0.26 \pm 0.05^\circ\text{C}$ per decade over at least the last 30 years (Malhi & Phillips 2004). Associated with this increase in temperature there has been an observed increase in stored biomass in these forests (Phillips *et al.* 1998; Phillips *et al.* 2002; Baker *et al.* 2004; but see Clark 2002). Much of the evidence for this increased biomass has come from the monitoring of up to 17 large-scale forest plots, most 25–50 ha in size, and from many smaller forest plots across the tropical world. To date there is little comparable baseline information from Australia’s tropical rainforests let alone data on the way they are changing.

Some evidence suggests that Australian tropical forests may be responding differently to climatic extremes than other rainforests. A recent study in the Wet Tropics bioregion showed that flowering and seedling recruitment behaviour in Australian species did not match expectations generated from studies in the neotropics (Connell & Green 2000). In another recent Australian study (Edwards & Krockenberger 2006), seedling survival across the 2002 El Niño event was extremely low; 64% of the individuals and 30% of the species that were recorded in 2001 were no longer present at the end of 2002. Those species that were removed were among the rarest in the community. These estimates are much greater than that reported from previous work in Panama, where most seedlings survived an El Niño drought (Engelbrecht *et al.* 2002).

In this study we describe the floral composition of almost 1 ha of lowland rainforest beneath the arc of

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Accepted for publication December 2006.

the Australian canopy crane near Cape Tribulation in North Queensland and monitor how this had changed over a 5-year period (from 2000 to 2005). This site was heavily impacted by Category 3 Tropical Cyclone Rona in February 1999 and our surveys in 2000 and 2005 provide an opportunity to assess how the floristics of this site have changed post cyclone. Elsewhere, Stork (2007) and Ticehurst *et al.* (2007) present further analysis of the impact of Cyclone Rona on the crane area and surrounding forest.

The floristics of the canopy crane are also compared with a series of seven other rainforest plots, some located relatively close to the crane plot and others on a latitudinal gradient from 5° to 21°S. This analysis provides some measure of the variation in vegetation structure and floristics in tropical forests in the Australasian region.

METHODS

Vegetation survey

The Cape Tribulation Canopy Crane Research Facility is located in lowland tropical rainforest at 16°06'20"S 145°26'40"E and at approximately 50 m elevation. It lies within a semi-enclosed coastal basin formed by ridges running east-west to an upland massif (Grove *et al.* 2000). In 1998, a Leibherr 91EC industrial T-crane was established on the site to facilitate canopy access by researchers (Stork & Cermak 2003; Stork 2007). Installation was carried out by helicopter in order to minimize canopy disturbance. In 2000, a circular vegetation plot was established directly below the 55 m radius of the crane jib, encompassing an area of 0.95 of a hectare (Cape Tribulation Survey 2000). All stems with a diameter at breast height (d.b.h) of 10 cm or more were tagged, numbered and mapped. Their diameters were measured at 1.3 m from the ground on the uphill side of the bole. Tree heights were obtained by locating the crane gondola at the top of each tree and dropping a tape measure to the ground beside each stem. These stems were identified by consultant botanists and by staff at the research facility and the taxonomic work of Henderson (2002) should be consulted for all species authorities. This survey methodology was repeated in 2005 and new recruits to the ≥10 cm size class were included in the survey (Cape Tribulation Survey 2005).

Additional 1-ha plots were established elsewhere near the crane plot (Thompson Creek) and in other tropical forests in the region (see Table 1). In most cases, a standard 100 m × 100 m plot was established with markers delineating each 10 m × 10 m quadrat within the plot. All stems with a d.b.h. ≥5 cm were tagged and numbered. The diameter of each tagged

individual was measured at 1.3 m from the ground on the uphill side of the bole. Each individual was then surveyed for height, identified to species and its position within the plot mapped. All individuals were counted in the quadrats where they were rooted, regardless of the projection of the crown. Any coppice stems with a d.b.h. ≥ 5 cm were included as separate individuals. Where trees possessed buttress roots, the d.b.h. was measured directly above these roots. If an irregularity occurred in the bole at 1.3 m, the d.b.h. was measured directly below this point.

These plots form part of a larger comparative study of rainforest plots on a transect stretching from south-east Queensland to southern Vietnam. Some of these results have been published (Laidlaw *et al.* 2000, submitted; Small *et al.* 2004). For others (including several of those described in this paper) the results are hitherto unpublished (but see Laidlaw 1999). In the comparative analyses presented here, we have screened these data to produce information only on those stems with diameters ≥10 cm so that the results will be comparable with data from the crane plot.

Analysis

For each plot we have calculated values for both family, generic and species richness (the simple taxon count, *s*), species evenness, and the Shannon Index value (*H'*). For evenness and diversity we used the standard formulae found in Magurran (1988). We calculated basal areas, family importance values (FIV) and an individual value index (IVI) for each species. We calculated the FIV's using the formula of Mori *et al.* (1983), namely

$$\text{FIV} = \text{relative diversity} \\ + \text{relative density} + \text{relative dominance}$$

where: relative diversity = number of species in the family/the plot total
 relative density = number stems in the family/the plot total
 relative dominance = basal area of the family/plot total basal area.

The IVI values were calculated using the formula of Cottam and Curtis (1956), namely

$$\text{IVI} = (\text{relative density} + \text{relative dominance} \\ + \text{relative frequency}) \times 100$$

where: relative frequency = number of times a species occurs/total quadrats
 relative density = number stems of the species/the plot total
 relative dominance = basal area of the species/plot total basal area.

Table I. Floristic and structural data for one hectare vegetation plots in Queensland and Papua New Guinea

Lowland rainforest, Queensland, Australia				
	Cape Tribulation Crane Plot 2000	Cape Tribulation Crane Plot 2005	Cape Tribulation Thompson Creek	Noah Creek
Location	16°06'20"S, 145°26'40"E	16°06'20"S, 145°26'40"E	16°06'20"S, 145°26'40"E	16°08'32"S, 145°25'47"E
Elevation (m asl)	50	50	50	50
Stems ≥ 10 cm dbh	522	680	861	974
Species ≥ 10 cm dbh	73	82	118	166
Basal area (m ²)	39.84	38.03	32.67	–
Shannon Diversity (H')	3.49	3.59	3.64	4.15
Evenness (E)	0.81	0.81	0.76	0.81
Genera richness	57	63	76	125
Family richness	32	34	35	62
FIV1 [†]	Meliaceae	Meliaceae	Lauraceae	–
FIV2	Euphorbiaceae	Euphorbiaceae	Euphorbiaceae	–
FIV3	Lauraceae	Lauraceae	Arecaceae	–
FIV4	Myrtaceae	Myrtaceae	Myrtaceae	–
FIV5	Apocynaceae	Apocynaceae	Proteaceae	–
IV1 [‡]	<i>Cleistanthus myrianthus</i>	<i>Cleistanthus myrianthus</i>	<i>Macaranga subdentata</i>	–
IV2	<i>Alstonia scholaris</i>	<i>Alstonia scholaris</i>	<i>Licuala ramsayi</i>	–
IV3	<i>Normanbya normanbyi</i>	<i>Myristica insipida</i>	<i>Normanbya normanbyi</i>	–
IV4	<i>Myristica insipida</i>	<i>Normanbya normanbyi</i>	<i>Cleistanthus myrianthus</i>	–
IV5	<i>Acmena graveolens</i>	<i>Rockinghamia angustifolia</i>	<i>Endiandra microneura</i>	–
Mid-elevation rainforest, Queensland, Australia				
	Eungella	Paluma	Atherton Tableland	
Location	21°01'04"S, 148°36'42"E	18°57'17"S, 146°10'50"E	17°06'00"S, 145°37'05"E	
Elevation (m asl)	720	1000	686	
Stems ≥ 10 cm dbh	1194	1064	687	
Species ≥ 10 cm dbh	40	68	92	
Basal area (m ²)	55	64.87	49.57	
Shannon Diversity (H')	2.87	3.59	3.73	
Evenness (E)	0.78	0.85	0.82	
Genera richness	28	48	61	
Family richness	19	27	27	
FIV1	Lauraceae	Lauraceae	Lauraceae	
FIV2	Myrtaceae	Myrtaceae	Elaeocarpaceae	
FIV3	Elaeocarpaceae	Elaeocarpaceae	Monimiaceae	
FIV4	Arecaceae	Icacinaceae	Myrtaceae	
FIV5	Cunoniaceae	Rutaceae	Euphorbiaceae	
IV1	<i>Archontophoenix alexandrae</i>	<i>Apodytes brachystylis</i>	<i>Sloanea australis</i>	
IV2	<i>Cryptocarya</i> sp.1	<i>Cryptocarya leucophylla</i>	<i>Daphnandra repandula</i>	
IV3	<i>Elaeocarpus largiflorens</i>	<i>Acmena resa</i>	<i>Litsea lefeana</i>	
IV4	<i>Sloanea macbrydei</i>	<i>Sloanea macbrydei</i>	<i>Beilschmiedia bancroftii</i>	
IV5	<i>Cryptocarya densiflora</i>	<i>Brackenridgea nitida</i>	<i>Syzygium trachyphloium</i>	
Lowland rainforest, Papua New Guinea				
	Oomsis		Baitabag	
Location	6°41'S, 146°48'E		5° 08' S, 145° 47' E	
Elevation (m asl)	65		100	
Stems ≥ 10 cm dbh	484		453	
Species ≥ 10 cm dbh	97		111	
Basal area (m ²)	27.54		26.35	
Shannon Diversity (H')	3.96		4.13	
Evenness (E)	0.86		0.88	
Genera richness	64		74	
Family richness	37		36	
FIV1	Moraceae		Rubiaceae	
FIV2	Meliaceae		Meliaceae	
FIV3	Myristicaceae		Moraceae	
FIV4	Ulmaceae		Sapotaceae	
FIV5	Lauraceae		Euphorbiaceae	
IV1	<i>Medusanthra laxiflora</i>		<i>Pimelodendron amboinicum</i>	
IV2	<i>Celtis latifolia</i>		<i>Pouteria lobianum</i>	
IV3	<i>Ficus</i> sp.		<i>Horsfieldia irya</i>	
IV4	<i>Myristica globosa</i>		<i>Pometia pinnata</i>	
IV5	<i>Myristica subululata</i>		<i>Erythrospermum candidum</i>	

[†] Family Importance Value ranked from 1 to 5.[‡] Individual Value Index ranked from 1 to 5.



Fig. 1. Location of Australasian 1-ha rainforest plots.

The pattern analysis program PATN (Belbin 1993) was used to determine the relationship among all eight survey sites based on tree species ≥ 10 cm d.b.h. A Bray-Curtis dissimilarity dendrogram based on quantitative data was produced to examine community variation between the crane site and other lowland plots established nearby, mid-elevation plots located elsewhere in north Queensland (Eungella, Paluma and the Atherton Tablelands) and lowland rainforest plots established at Baitabag and Oomsis, Papua New Guinea (Fig. 1).

RESULTS

Summaries of the results from all four lowland sites surveyed in the Daintree Region (three at Cape Tribulation, including the 2000 and 2005 surveys at the crane site and Thompson Creek, and one at Noah Creek) are presented in Table 1 together with those from the three other tropical Queensland plots

(Eungella, Paluma and the Atherton Tableland) and the two lowland plots for New Guinea (Oomsis and Baitabag). More detailed results from the 2005 survey of the crane plot are presented as Appendix I.

Cape tribulation surveys 2000 and 2005

The first Cape Tribulation survey (Year 2000) was 18 months after the passage of Cyclone Rona. At this time, approximately 16% of stems ≥ 10 cm under the canopy crane had been recorded as dead, some of which were killed by the cyclone's passage (Grove *et al.* 2000). These dead stems are not included in the following analyses. In 2000, the Cape Tribulation crane plot supported 522 stems ≥ 10 cm d.b.h. These stems were from 32 families, 57 genera and 73 species of trees. Shannon Index was 3.49 with an evenness of 0.81. The five most important families were Meliaceae, Euphorbiaceae, Lauraceae, Myrtaceae and Apocynaceae. The most important species were *Cleistanthus myrianthus* (Euphorbiaceae), *Alstonia scholaris* (Apocynaceae), *Normanbya normanbyi* (Arecaceae), *Myristica insipida* (Myristicaceae) and *Acmena graveolens* (Myrtaceae).

The reassessment of the Cape Tribulation crane plot in 2005 showed that the stem count had increased by 30.3% (158 individuals, Table 1). Shannon Index increased slightly to 3.59 but the evenness remained the same (0.81). An additional 12 species, 11 genera and two families were recorded in 2005 that were not present in 2000. Two of the 'new' species were the non-strangling figs *Ficus copiosa* ($n = 1$) and *Ficus variegata* ($n = 3$). Two species (*Dysoxylum latifolium* (Meliaceae) and *Polyosma hirsuta* (Grossulariaceae)) recorded in 2000 and originally represented by only one individual, were no longer present in 2005. Despite these changes, the Bray-Curtis index of dissimilarity was extremely low at 0.15. The most important families (FIV) did not change between measurements although species importance values (IVI) did change due to shifts in species abundances. Twenty-eight species (33.7%) were recorded only as singletons and six species (7.2%) as doubletons in 2005. This is very similar to the survey in 2000 where there were 27 (36.9%) were singletons and four species (5.5%) were doubletons.

In 2000, the mean diameter of trees ≥ 10 cm d.b.h. was 0.25 m (\pm SE 0.008). The two largest individuals were a *Dysoxylum papuanum* (Meliaceae) 1.49 m and a *Syzygium sayeri* (Myrtaceae) 1.45 m. The mean height of trees ≥ 10 cm d.b.h. was 15.9 m (\pm SE 0.27) and the tallest individual in 2000 was a *Cryptocarya mackinnoniana* at 32.6 m. The total basal area of the plot was 39.84 m². In 2005, the mean d.b.h. of trees ≥ 10 cm d.b.h. on the crane plot was 0.22 m (\pm SE 0.56). The individual with the largest d.b.h. was a *Ficus destruens*

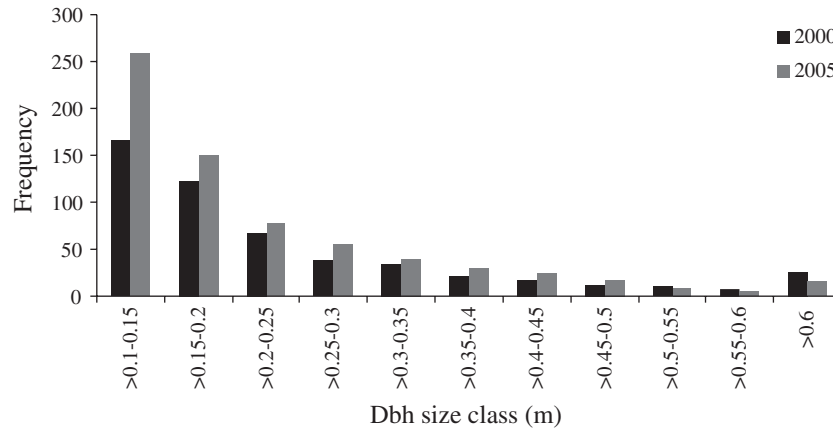


Fig. 2. D.b.h. size classes of individuals surveyed at Cape Tribulation in 2000 and 2005.

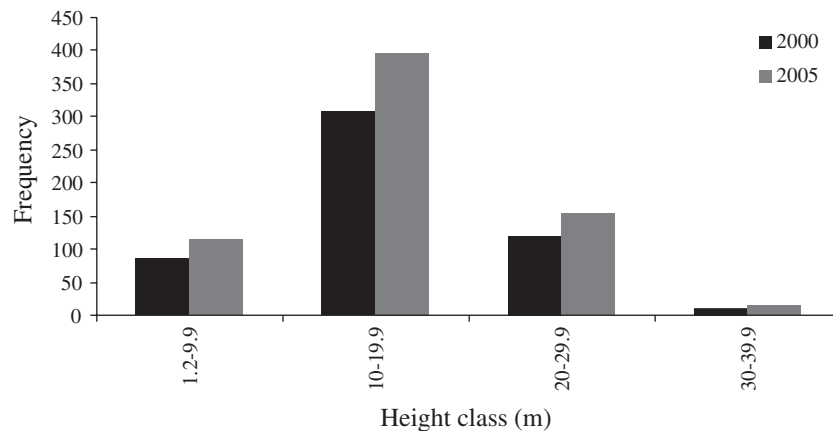


Fig. 3. Height classes of individuals surveyed at the Cape Tribulation crane site in 2000 and 2005.

(Moraceae) 1.34 m. The largest non-fig individual was a blackbean, *Castanospermum australe* (Fabaceae) 1.26 m. The two largest individuals recorded in 2000 were no longer present in the 2005 survey. The mean height of trees ≥ 10 cm d.b.h. was 15.85 m (\pm SE 0.23). The tallest individual was an *Argyrodendron peralatum* (Sterculiaceae) at 34.6 m. The large *C. mackinnoniana* recorded in 2000 was not located in 2005. The basal area of the plot decreased by 1.81 m² to 38.03 m² (Table 1).

The frequency of stems in all d.b.h. size classes ≥ 10 cm and ≤ 50 cm d.b.h. increased from 2000 to 2005 (Fig. 2). The greatest increases were in the 10–15 cm d.b.h. size class. Individuals with a d.b.h. of over 50 cm decreased. The frequency of individuals in all height classes increased between 2000 and 2005 (Fig. 3). The greatest increase was in the 10–19.9 m size class.

The structural changes in species represented by 10 or more individuals ($n = 16$) across the two surveys has been examined. The mean d.b.h. increased in some species, and decreased in others (Fig. 4a). Decreases

may have been due to the delayed loss of large individuals as a result of Cyclone Rona, or by other mortality factors. Two-sample *T*-tests assuming unequal variances found that none of the changes in mean d.b.h. was significant. Changes in the mean heights of the same 16 species were also examined and again responses varied from species to species (Fig. 4b). A two-sample *T*-test assuming unequal variances found only one significant result. The black palm, *N. normanbyi* (Arecaceae) was found to have increased significantly in height ($t = 3.46$, d.f. = 97, $P < 0.001$) from a mean of 15.24 (\pm SE 0.59) to a mean of 17.93 (\pm SE 0.49).

A comparison of the abundances of the same 16 key species between 2000 and 2005 were made. A majority of species were found to have increased in abundance (Fig. 4c). The greatest increases were by *C. myrianthus* (Euphorbiaceae), *M. insipida* (Myristicaceae) and *Rockinghamia angustifolia* (Euphorbiaceae). Three species declined in abundance: *A. graveolens*, *Cardwellia sublimis* and *D. papuanum* – all canopy species. The basal area of these 16 key species was examined

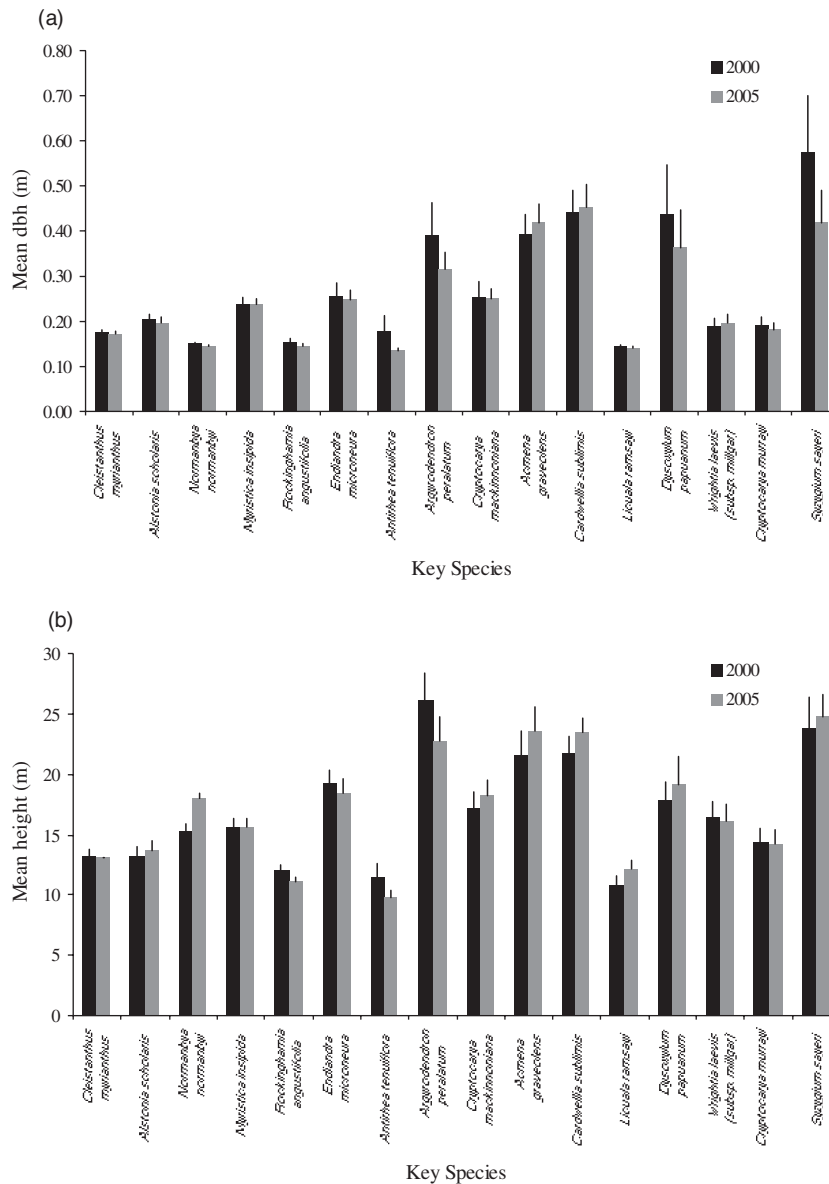


Fig. 4. (a) Mean d.b.h. of species represented by 10 or more individuals surveyed at Cape Tribulation in 2000 and 2005. (b) Mean height of species represented by 10 or more individuals surveyed at Cape Tribulation in 2000 and 2005. (c) Abundance of species represented by 10 or more individuals surveyed at Cape Tribulation in 2000 and 2005. (d) Basal area of species represented by 10 or more individuals surveyed at Cape Tribulation in 2000 and 2005.

and again showed some variability in response (Fig. 4d). Although a majority of species increased in basal area, five species lost total basal area. These were *Antirhea tenuiflora*, *A. graveolens*, *C. sublimis*, *D. papuanum* and *S. sayeri*. For *A. graveolens*, *C. sublimis* and *D. papuanum* this is readily explained by the concomitant drop in the number of individuals on the plot. This is not the case for the remaining two species. The mean height and d.b.h. of *A. tenuiflora* (Rubiaceae) decreased along with the total basal area suggesting that the species has suffered some mortality of its larger individuals, but the species is now recovering as

evidenced by increased numbers in the smaller size classes. *Syzygium sayeri* (Myrtaceae), however, experienced a decrease in the mean d.b.h., an associated decrease in total basal area for the species, but an increase in mean height and abundance. This suggests either a rapid reach for the canopy by midstorey individuals, or, possibly, an error in the initial height survey.

Local variation in vegetation in the region of the crane plot is evident in our comparisons of the 2000 data with that from a 2001 survey made by Griffith University (Thompson Creek). The 2000 crane site

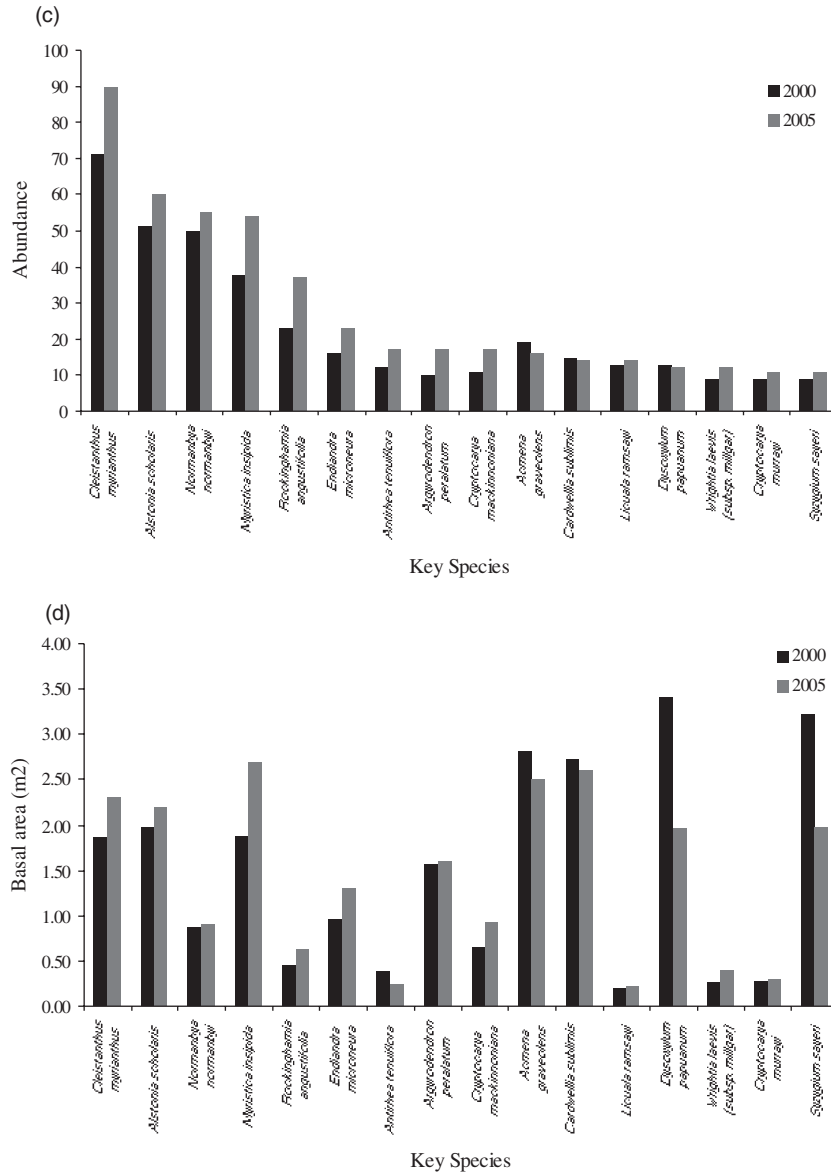


Fig. 4. Continued

data were used in order to minimize the time difference between the two datasets. Although separated only by a small creek line, the two plots are quite different in character. The Thompson Creek plot supported 339 more stems, three more families, 19 more genera and 45 more species ≥ 10 cm d.b.h. than the crane plot (Table 1). The Bray-Curtis index of dissimilarity between the two plots was 0.62. Despite this, the Thompson Creek plot had a considerably lower total basal area (32.67 m²), 7.17 m² less than the crane plot. The Thompson Creek plot was more diverse, with a Shannon Index of 3.64, although less even (0.76). The most important families on the Thompson Creek plot were Lauraceae, Euphorbiaceae, Arecaceae, Myrtaceae and Proteaceae, three of which were also

important on the crane plot. The most important species were *Macaranga subdentata* (Euphorbiaceae), *Licuala ramsayi* (Arecaceae), *N. normanbyi* (Arecaceae), *C. myrianthus* (Euphorbiaceae) and *Endiandra microneura* (Lauraceae). Forty-four species (37.3%) were recorded only as singletons and 20 species (16.9%) were recorded as doubles.

Over half of the species recorded on the crane plot in 2005 (57.3%) are endemic to Australia and 56.1% are endemic to Queensland. More specifically, 45.1% of species are endemic to Northern Queensland (Cook and North Kennedy pastoral districts) and 20.7% of species are endemic to Cape York (Cook pastoral district). Many species are shared with our neighbouring regions: 40.2% with New Guinea, 20.7% with

Melanesia, 19.5% with Malesia, 0.09% with Asia, 0.04% with the Pacific Islands and 0.01% with New Zealand/Antarctica (Henderson 2002). Three species ≥ 10 cm d.b.h. are listed as rare under the Nature Conservation (Wildlife) Regulation 2006. These are *C. myrianthus* (Euphorbiaceae) ($n = 90$), *Pseuduvaria froggattii* (Annonaceae) ($n = 1$) and *Austromuellera trinervia* (Proteaceae) ($n = 5$). All three species are restricted to Cape York, however, *C. myrianthus* also occurs in Malesia and Papua New Guinea (Henderson 2002). As this species is the most dominant recorded on the crane site, it should be considered as a survey plot of high conservation value.

Other North Queensland plots

The most direct comparison with the two Cape Tribulation plots is that from Noah's Creek, a refugial lowland forest about 11 km due south of Cape Tribulation. We have limited data from that plot but it is evident from the results summarized in Table 1 that this is a much richer site both in terms of its family, generic and species richness than either of the two Cape Tribulation plots. There were almost 60 additional species and almost twice as many families found within the Noah Creek hectare than at the richest of the more northerly plots. This accords with its 'special' status as a supposed glacial refugium and suggests, furthermore, that it may be much more protected from cyclonic depredations than the Cape Tribulation sites.

The other three tropical plots are all at higher elevations than the Cape Tribulation plots and are all at more southerly latitudes. In terms of species richness they show a gradual northerly increase from 40 species at the most southerly site, Eungella (which is also at the highest elevation) to 92 species at the Robson Creek site on the Atherton Tablelands. This gradual northerly enrichment continues when the richer of the two Cape Tribulation plots is added. These patterns are reflected with only minor modifications in the values of generic and family richness. The crane plot is richer than all but the Atherton Tablelands plot (and, we note above, appears to be on an increasing temporal trend in that regard). When relative abundance is considered, the trends are not so clear. Shannon Index values are clearly lower at the Eungella plot and higher at the Noah Creek plots, but hover around the 3.6 mark for all other plots.

The dominant families differ markedly across plots. All three upland plots (Eungella, Paluma and the Atherton Tablelands) feature Lauraceae, Myrtaceae and Elaeocarpaceae in their top four ranked families. In contrast the two Cape Tribulation plots, although including Lauraceae and Myrtaceae in their top-ranking families, add Euphorbiaceae (which also ranks Number 5 on the Atherton Tablelands plot). As would

be expected with these widely separated plots, there is no overlap among the top-ranked species.

Basal area at each of the southerly plots exceeds that recorded in either of the Cape Tribulation sites.

The Papua New Guinea plots

The two lowland plots from Papua New Guinea are remarkably similar in measures of diversity and structure to the Cape Tribulation plots (see Laidlaw *et al.* submitted) with an average species richness value of 104 (cf. 105 for the Cape Tribulation sites), a generic richness value of 69 (cf. 70 for Cape Tribulation) and a family richness value of 36.5 (cf. 34 for Cape Tribulation). Shannon Index and evenness values were also very similar. Basal area at the Papua New Guinea sites was even lower than at the Cape Tribulation sites, almost certainly because of historical human use of the sites for shifting agriculture.

The most important families in the Papua New Guinea sites showed some overlap with one or other of the Cape Tribulation sites (e.g. Meliaceae, Lauraceae, Euphorbiaceae) but also include other families that are much less important in the Australian sites (e.g. Ulmaceae). Again we had no expectation that important species would be shared and these expectations were born out.

Site classification

The Bray-Curtis (BC) dissimilarity metric based on quantitative data showed that the Papua New Guinea plots shared very few species with the Australian plots (BC = 1), although there was overlap between the two (Baitabag and Oomsis, BC = 0.73). Of the Australian plots, Eungella and Paluma shared several species (BC = 0.82) but shared few species with the more northerly plots (BC = 1). The crane plot and the Thompson Creek plot were the most closely related (BC = 0.59), and both were closely associated with the Noah Creek plot (BC = 0.70). Atherton fused with the Daintree plots (Cape Tribulation, Noah Creek and Thompson Creek) at a Bray-Curtis dissimilarity of 0.89 (Fig. 5).

DISCUSSION

Recently, Graham (2006) described the basic structure of 20 0.5 ha rainforest plots that were established between 1971 and 1980 and have been resurveyed several times since. Unfortunately, data on the changes to the floristics of the site during that time have not yet been published and are unavailable for comparison. In this respect we believe that our study is probably unique

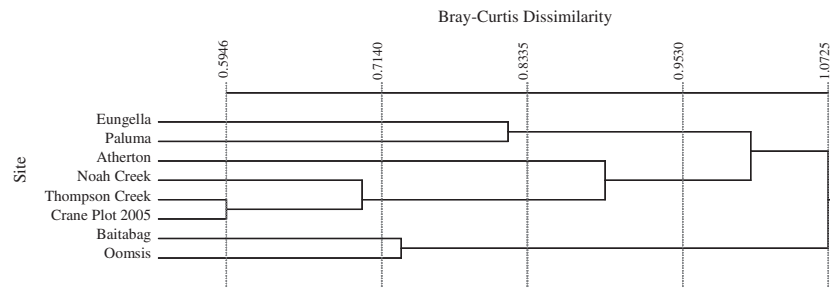


Fig. 5. Bray-Curtis dissimilarity dendrogram of Australasian rainforest survey plots based on floristic composition (d.b.h. ≥ 10 cm).

in Australian rainforest studies being the first published account of such floristic changes over a 5-year period.

It is clear from the comparison of the two surveys of the crane plot that the site is still in a very active stage of post-cyclonic recovery. Several large trees, apparently healthy in 2000 did not appear in the survey in 2005. This could represent 'normal' processes of ageing and mortality but it seems more likely to us that these represented delayed mortality following the 1999 cyclone. These losses no doubt explain why the overall basal area for trees on the site has remained almost unchanged through this period even though there has been substantial recruitment of smaller stems (total stems: 2000, 522; 2005, 680). Turton and Stork (in press) analysed the frequency and intensity of tropical cyclones crossing the wet tropical coast (Cooktown–Ingham) over the period 1858–2006 according to the Australian Cyclone Severity Scale. Their data suggest that a weak cyclone (Australian System: Category 1–2) is likely to cross the wet tropical coast with a frequency interval of about 5 years, compared with a frequency of about 15 years for a moderate to severe cyclone (Category 3) and about 75 years for a very severe cyclone (Category 4–5). Coastal areas are much more heavily and frequently damaged than inland areas. It is likely therefore that the Daintree lowlands are constantly being affected by cyclones and therefore in a constant state of recovery.

How representative is the crane site of the local vegetation? The Thompson Creek (2000) site is only a few metres to the north of the crane site and was selected to provide details on vegetation that would be useful to future work using the crane without compromising work on the actual crane site through generating human 'traffic' during the survey. Yet at the time of the survey this site appears to be quite different with 861 stems >10 cm d.b.h. of 118 species compared with the 522 stems of 73 species on the crane site itself. There are several possible explanations for this. First it has a different general aspect to the crane site (south-east rather than east-north-east), which may, in turn have led to a differential impact at the time of Cyclone Rona. Furthermore, it has a section that includes an

area of disturbance approaching a forest edge and this may have led to a greater representation of secondary species within the inventory (and also no doubt accounts in part for the lower basal area on the Thompson Creek plot). Ticehurst *et al.* (2007) have shown that the impact of Cyclone Rona on the crane site and surrounding area was very variable with some areas heavily impacted and others, some just a few metres away, much less so. One consequence of the patchy impact of cyclones has been to produce an exceptional ecological heterogeneity within the forest. This no doubt acts, on a larger scale, in a way comparable to within-forest intermediate disturbance regimes. The mosaic of patches of forest exhibiting various degrees of post-cyclonic recovery is no doubt a strong contributory factor to the overall ecological diversity of the Daintree lowland ecosystems.

This having been said, it is also evident that some forest patches are much less cyclone-prone than others. The Noah Creek site is much more diverse than either of the Cape Tribulation sites and exhibits little evidence of disturbance. This is no doubt due in part to local topography that may 'steer' cyclone paths around the valley. We have little doubt that this is one reason why the Noah Creek valley (and others such as Oliver and Cooper Creek) have maintained their status as postglacial vegetation refuges over millennia. Comparable areas showing few signs of recent cyclonic impact are also apparent north of Cape Tribulation where there are to be found areas with trees of truly impressive basal area (e.g. Emagen Creek).

The Bray-Curtis dissimilarity metric shows clearly that at the species level the two Cape Tribulation sites group together and are progressively more distant 'sisters' to the Noah Creek site and Atherton Tablelands site (Fig. 5). This 'North Queensland' grouping represents a set of sites which, to varying degrees, share considerable numbers of tree species. The other two groupings are the two more southerly Queensland sites (Paluma and Eungella) and the two New Guinea sites (Baitabag and Oomsis). Again this reflects varying degrees of co-occurrence of species within a grouping. Very few species are shared *cross* groupings. The most

parsimonious explanation for the patterns seen in the dendrogram (Fig. 5) is simply that intersite distance gradually diminishes the number of shared species between sites.

Other patterns emerge at the supra-species level. In analyses at the generic level (Kitching *et al.* 2004) it was demonstrated that the Thompson Creek site at Cape Tribulation showed lower values for a so-called Gondwanic Index in which genera from families with stereotypical Australian distributions were compared with a set with Papuanian distributions. The mid-elevation sites of Atherton Tableland and Eungella showed high values (indicating a greater representation of 'Australian' genera), the New Guinean sites an even lower value indicating a (not unexpected) pre-eminence of genera from Papuanian families. These vegetation patterns were also reflected in pattern analyses of Diptera and underscores the existence of biogeographical connections between lowland rainforest in Australia and New Guinea.

The Daintree lowland rainforests are of such high biological significance that it will be of considerable value to continue resurveys of the trees on the crane plot at 5-year intervals so that the processes of post-cyclonic recovery can be further monitored and interpreted. The current vegetation data on the crane site is based on a survey using a 10-cm d.b.h. cut-off. We have data from the Thompson Creek plot down to a 5-cm cut-off. It will be valuable to resurvey the crane plot at least to the level of 5 cm d.b.h and a recomparison with the Thompson Creek plot made. It would be of considerable value in understanding tree demographics if a subset of 10 × 10 m plots on both the crane and Thompson Creek sites were surveyed for seedlings at least of the dominant species. This would allow genuine population dynamic interpretations to be made for key species during post-disturbance recovery.

Given the very clear regional heterogeneity of vegetation it will require more information before better interpretations of forest dynamics can be made in the Daintree lowlands. This area is of immense conservation and iconic value and we recommend strongly that a network of perhaps 10 1-ha plots be established between the Daintree and the Bloomfield of which the crane plot is part. Thanks to the efforts of our botanical colleagues, the state of our taxonomic knowledge is now such that these plots could be established with relatively little effort.

Finally, it is noteworthy that nowhere in the Australasian region are there long-term forest dynamic plots larger than 1 ha. The utility of 25–50 ha forest dynamic plots has been well demonstrated (Hubbell & Foster 1983) and addresses some of the problems in highly patchy forests. The creation of a 25- or 50-ha lowland rainforest plot in the Daintree would allow comparisons with the 17 others that have been created in other parts of the tropical world.

ACKNOWLEDGEMENTS

The authors wish to thank staff and volunteers involved in vegetation surveys conducted at Cape Tribulation in 2000, 2001 and 2005. Sincerest thanks go to the late Richard Cooper, Martin Frieberg, Guy Vickerman, Karen Hurley, Griffith University and James Cook University volunteers, DIWPA participants, The Queensland National Parks and Wildlife Service, staff of the Australian Canopy Crane and The Rainforest CRC.

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APPENDIX I

Species (d.b.h. \geq 10 cm d.b.h) recorded on the Cape Tribulation crane plot in 2005

Species	Family	Abundance
<i>Acmena graveolens</i>	Myrtaceae	16
<i>Acmenserma claviflorum</i>	Myrtaceae	3
<i>Aglaia tomentosa</i>	Meliaceae	1
<i>Alstonia scholaris</i>	Apocynaceae	60
<i>Antirhea tenuiflora</i>	Rubiaceae	17
<i>Archidendron ramiflorium</i>	Mimosaceae	1
<i>Archontophoenix alexandreae</i>	Arecaceae	5
<i>Argyrodendron peralatum</i>	Sterculiaceae	17
<i>Austromuellera trinervia</i>	Proteaceae	5
<i>Brombya platynema</i>	Rutaceae	8
<i>Canarium vitiense</i>	Burseraceae	1
<i>Canthium</i> sp. (Whitfield Range)	Rubiaceae	3
<i>Cardwellia sublimis</i>	Proteaceae	14
<i>Castanospermum australe</i>	Fabaceae	8
<i>Celtis paniculata</i>	Ulmaceae	1
<i>Chisocheton longistipitatus</i>	Meliaceae	1
<i>Citronella smythii</i>	Icacinaeae	1
<i>Cleistanthus myrianthus</i>	Euphorbiaceae	90
<i>Cryptocarya grandis</i>	Lauraceae	7
<i>Cryptocarya hypospodia</i>	Lauraceae	1
<i>Cryptocarya mackinnoniana</i>	Lauraceae	17

Appendix I Continued

Species	Family	Abundance
<i>Cryptocarya murrayi</i>	Lauraceae	11
<i>Doryphora aromatica</i>	Monimiaceae	3
<i>Dysoxylum alliaceum</i>	Meliaceae	7
<i>Dysoxylum arborescens</i>	Meliaceae	8
<i>Dysoxylum oppositifolium</i>	Meliaceae	2
<i>Dysoxylum papuanum</i>	Meliaceae	12
<i>Dysoxylum parasiticum</i>	Meliaceae	8
<i>Dysoxylum peltigrewianum</i>	Meliaceae	9
<i>Elaeocarpus grandis</i>	Elaeocarpaceae	5
<i>Elaeocarpus bancroftii</i>	Elaeocarpaceae	1
<i>Emmanosperma cunninghamii</i>	Rhamnaceae	1
<i>Endiandra insignis</i>	Lauraceae	1
<i>Endiandra leptodendron</i>	Lauraceae	9
<i>Endiandra microneura</i>	Lauraceae	23
<i>Endiandra sankeyana</i>	Lauraceae	1
<i>Eupomatia laurina</i>	Eupomatiaceae	1
<i>Fagraea cambagei</i>	Gentianaceae	2
<i>Ficus copiosa</i>	Moraceae	1
<i>Ficus destruens</i>	Moraceae	1
<i>Ficus variegata</i>	Moraceae	3
<i>Ganophyllum falcatum</i>	Sapindaceae	1
<i>Garcinia warrenii</i>	Clusiaceae	3
<i>Gardenia ovularis</i>	Rubiaceae	1
<i>Gillbeea adenopetala</i>	Cunnoniaceae	6
<i>Gmelina fasciculiflora</i>	Lamiaceae	1
<i>Gomphandra australiana</i>	Icacinaeae	3
<i>Lepidozamia hopei</i>	Zamiaceae	1
<i>Licuala ramsayi</i>	Arecaceae	14
<i>Litsea lefeana</i>	Lauraceae	4
<i>Macaranga subdentata</i>	Euphorbiaceae	2
<i>Mallotus mollissimus</i>	Euphorbiaceae	9
<i>Medicosma fareana</i>	Rutaceae	3
<i>Musgravea heterophylla</i>	Proteaceae	8
<i>Myristica insipida</i>	Myristicaceae	54
<i>Myristica globosa</i> ssp. <i>muelleri</i>	Myristicaceae	1
<i>Neonauclea glabra</i>	Rubiaceae	1
<i>Niemeyera prunifera</i>	Sapotaceae	7
<i>Normanbya normanbyi</i>	Arecaceae	55
<i>Palaquium galactoxylon</i>	Sapotaceae	5
<i>Polyscias australiana</i>	Araliaceae	2
<i>Pouteria obovoidea</i>	Sapotaceae	3
<i>Premna serratifolia</i>	Lamiaceae	1
<i>Prunus turneriana</i>	Rosaceae	1
<i>Pseuduvaria froggattii</i>	Annonaceae	1
<i>Rhodamnia sessiliflora</i>	Myrtaceae	1
<i>Rockinghamia angustifolia</i>	Euphorbiaceae	37
<i>Semecarpus australiensis</i>	Anacardiaceae	4
<i>Siphonodon membranaceus</i>	Celastraceae	1
<i>Synima cordierorum</i>	Sapindaceae	6
<i>Syzygium cormiflorum</i>	Myrtaceae	3
<i>Syzygium erythrocalyx</i>	Myrtaceae	5
<i>Syzygium gustavioides</i>	Myrtaceae	8
<i>Syzygium kuranda</i>	Myrtaceae	3
<i>Syzygium sayeri</i>	Myrtaceae	11
<i>Tetrasynandra laxiflora</i>	Monimiaceae	3
<i>Toechima erythrocarpum</i>	Sapindaceae	3
<i>Toona ciliata</i>	Meliaceae	1
<i>Trema tormentosa</i> var. <i>viridis</i>	Ulmaceae	1
<i>Viticipremna queenslandica</i>	Lamiaceae	2
<i>Wrightia laevis</i> (ssp. <i>millgar</i>)	Apocynaceae	12
<i>Xanthophyllum octandrum</i>	Xanthophyllaceae	6

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