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Impacts of cyclone Larry on the vegetation structure of timber plantations, restoration plantings and rainforest on the Atherton Tableland, Australia.

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Running title: Cyclone impacts on replanted rainforest

ABSTRACT

We examined the impact of severe cyclone 'Larry' on the vegetation structure of monoculture and mixed species timber plantations, restoration plantings and reference sites in upland rainforests on the Atherton Tableland, north Queensland, Australia. Sites were initially assessed in 2000 and resurveyed in 2006, six to eight months after the cyclone traversed the region. In both surveys, timber plantations had a relatively open canopy, grassy understorey and few shrubs or small-sized trees; whereas restoration plantings had a relatively closed canopy, an understorey of bare ground, leaf litter and rainforest seedlings, a high density of small-diameter trees and a moderate representation of special life forms characteristic of rainforest. Cyclone damage varied with tree size, site-type, proximity to the cyclone and stem density. First, the proportion of trees that were severely damaged by the cyclone (major branches broken, stem snapped or pushed over) increased with the diameter of trees across all site types. Second, damage to larger-sized trees (>10 cm dbh, >20 cm dbh) was proportionally highest in monoculture plantations, intermediate in mixed species plantations and rainforest, and lowest in restoration plantings. Third, within site-types, damage levels decreased with distance from the cyclone track and with stem density. There was no evidence that topographical position influenced damage levels, at least for timber plantations. We tentatively attribute the high levels of damage experienced by timber plantations to their relatively open structure and the large size of stems in plantations. Restoration plantings generally escaped severe damage by the cyclone, but their continued development towards rainforest conditions may require a coordinated monitoring and maintenance program to address the potential threat of weed invasion.

Key words: hurricane, rain forest, restoration, timber plantations, Wet Tropics

INTRODUCTION

There has been considerable investment in reforestation in north Queensland since the declaration of the Wet Tropics World Heritage Area in 1988, in an attempt to create an alternative source of supply for the timber industry and restore degraded land (Catterall *et al.* 2005; Erskine *et al.* 2007). In total, around 2000 ha of monoculture and mixed-species timber plantations and 1000 ha of restoration plantings have been established on cleared land in the region, in addition to larger areas of monoculture plantations established by conversion of rainforest in previous decades (Vize *et al.* 2005; Catterall & Harrison 2006). The timber plantations typically comprise one or a few species of local and exotic timber trees, selected primarily for their growth rates and market value, established at around 1000 stems per ha and subsequently thinned and pruned (Bristow *et al.* 2005; Lamb *et al.* 2005). The restoration plantings comprise a diverse range of locally-occurring rainforest trees planted at higher densities (3-5000 stems per ha), with little subsequent management (Goosem & Tucker 1995; Freebody 2007).

In all reforestation schemes, efforts have been made to match species to environmental conditions, particularly soil type, rainfall and altitude. In the case of restoration plantings, this is to ensure that species are planted within their former range (Goosem & Tucker 1995); in the case of timber plantations, to promote high rates of survival and growth (Bristow *et al.* 2005). Resistance to cyclone damage has not been an important consideration in species selection or other aspects of the design of reforestation projects, even though cyclones are a recurrent feature of the region (Webb 1958).

72
73 Little is known of the impacts of cyclones (a term used generically in the present paper
74 for cyclones, hurricanes and typhoons) on replanted sites anywhere in the tropics. There
75 is a substantial literature on the effects of cyclones on secondary and old growth forests,
76 especially in the Neotropics, but it is difficult to extrapolate from this literature to
77 predict the impacts of cyclones on replanted sites. On the one hand, replanted sites
78 might be expected to be severely damaged by cyclones, because both timber plantations
79 and restoration plantings are comprised predominantly of fast-growing tree species,
80 considered especially vulnerable to cyclone damage (Zimmerman *et al.* 1994; Franklin
81 *et al.* 2004; Ostertag *et al.* 2005). Most replanted sites are also small and surrounded by
82 cleared land (Catterall & Harrison 2006), which would be expected to increase their
83 exposure to damaging winds (Laurance 1997). On the other hand, young replanted sites
84 have few large trees and are low in stature, factors which may reduce their vulnerability
85 to cyclone damage compared with older forests (Brokaw & Walker 1991; Pascarella *et*
86 *al.* 2004; Uriate *et al.* 2004; Van Bloem *et al.* 2005).

87
88 The present study describes the impact of cyclone Larry on the vegetation structure of
89 monoculture and mixed species timber plantations, restoration plantings and rainforest
90 reference sites on the Atherton Tableland, north Australia. It examines factors
91 associated with variation in damage levels including proximity to the cyclone path, site
92 type, tree size, stem density and landscape context. Understanding the factors which
93 affect the impacts of cyclones on replanted sites is important for subequatorial regions,
94 given the continuing interest in reforestation for environmental and economic purposes
95 (Lamb *et al.* 1997; Lugo 1997) and the high probability of exposure to cyclones within

the life of a project. Severe damage may not only reduce the economic and biodiversity values of existing replanted sites, but also reduce investment in future reforestation schemes.

METHODS

Study area and sites

The study was conducted at sites on the Atherton Tableland, north Queensland, Australia (17° – 17°30' S, 145°30 – 145°45 E); an upland plateau heavily cleared for agriculture in the late 19th and early 20th centuries. Replanted sites were 11 – 21 years old in 2006, and included monoculture timber plantations (planted with hoop pine *Araucaria cunninghamii*), mixed species cabinet timber plantations (planted with local and exotic rainforest trees, and eucalypts from various localities) and diverse 'ecological restoration' plantings of local rainforest trees. Rainforest reference sites were matched for altitude, soil type and rainfall with replanted sites. All sites were located on basaltic soils 500 – 850 m above sea level with mean rainfall 1300 – 3000 mm per annum. Sites were located 1 - 24 km from the track of cyclone Larry, which crossed the Atherton Tableland just south of the township of Malanda in March 2006. On average, all site-types were a similar distance from the cyclone track. Site attributes are summarised in Table 1; further details are provided in Kanowski *et al.* (2003) and Catterall *et al.* (2004).

Surveys of vegetation structure and cyclone damage

Vegetation structure was initially assessed at all sites prior to the cyclone in 2000 (Kanowski *et al.* 2003). Post-cyclone surveys were conducted from September to

November 2006, six to eight months after cyclone Larry, using the methodology published in Kanowski and Catterall (2007). In both periods, surveys were conducted on a 100 m x 10 m plot at each site (sometimes split into two sections), with detailed assessments conducted at five or six quadrats evenly spaced along the transect. Plots sampled the same general area of study sites in both survey periods. The topographical position of each plot was categorised in the field as upper, mid or lower slope.

Attributes assessed in both survey periods included canopy cover and height, the density of live trees in four diameter classes (2.5 – 10, 10 – 20, 20 – 50, >50 cm), measured at 1.3 m above the ground ('dbh'); the frequency of special life forms characteristic of rainforest (slender vines <5 cm diameter, robust vines >5 cm diameter, hemi-epiphytes, epiphytes, strangler figs, thorny scrambler thickets); the frequency (2000) or proportional ground cover (2006) of grass; and counts of woody debris in two size classes: fine (2.5 – 10 cm diameter) and coarse (>10 cm diameter). The 2006 surveys also assessed the density of shrubs (1 – 2 m), small-sized trees (<2.5 cm diameter), and dead trees (in same size classes as for live trees); the proportional ground cover of herbs, scramblers and vines, tree seedlings, leaf litter and bare soil; and cyclone damage to living trees (on a three point scale: 1 = defoliation and smaller branches broken; 2 = larger branches broken, 3 = trunk snapped, pushed over or uprooted). For analysis, categories 2 and 3 were combined as 'severe' damage.

Analyses

Comparisons of vegetation structure and levels of cyclone damage between different site-types were made with ANOVA, on log-transformed (count) or arcsine-square root

transformed (proportional) data. Least significant difference (LSD) tests were used to compare site-types when the overall ANOVA result was significant. Two-way repeated measures ANOVA was used to examine variation in structural attributes between the pre- and post-cyclone surveys, with sites as subjects, site-type as a between-subject factor and year as a within-subject factor. All attributes surveyed in both periods were included in analyses, except for grass cover (measured differently in each period), and special life forms (many zero values, especially in the first survey period). Two-way repeated measures ANOVA was used to examine variation in cyclone damage across tree diameter classes at sites, with sites as subjects, site-type as a between-subject factor and diameter class as a within-subject factor.

To investigate the factors associated with cyclone damage (considered as the proportion of trees (i) >10 cm dbh, and (ii) >20 cm dbh suffering severe damage) at a site, the following analyses were conducted. ANCOVA was used to examine variation in cyclone damage with distance north of the cyclone track, with site-type as a fixed factor. Regression was used to examine variation in cyclone damage with stem density and distance from the cyclone track, regardless of site-type. The effect of topographical position on levels of cyclone damage was explored for timber plantations only (pooled across monoculture and mixed species plantations), as the confounding of topographical position with site-type meant it was not informative to examine this relationship across all site-types. On average, sites in each topographical position were a similar distance from the cyclone track (8, 7 and 7 km, for upper, mid and lower slope categories, respectively), after the exclusion of one upper slope site 20 km from the cyclone track.

Due to small sample sizes ($n = 3$ for each category), these data were not subjected to statistical analysis.

Multivariate analysis (hybrid non-metric multidimensional scaling: Faith *et al.* 1987) was used to explore overall patterns of similarity in vegetation structure between site-types and survey periods, based on the Gower similarity metric calculated from log- or arcsine-transformed data. These analyses were based on all 15 attributes assessed in both survey periods: canopy cover and height, the density of trees by diameter (four classes); the frequency of special life forms (six classes); grass cover (range standardised within each survey period for this analysis); and counts of woody debris (two classes). Multivariate analysis was performed using the program PATN (Belbin & Collins 2004).

RESULTS

Structural attributes of sites

Timber plantations and restoration plantings differed considerably in structure in both survey periods (Tables 2, 3). Timber plantations had a relatively open canopy, an understorey of grasses, herbaceous weeds or scramblers, and few shrubs, small-sized trees (<10 cm dbh) or special life forms characteristic of rainforest, apart from slender vines. In contrast, ecological restoration plantings had a relatively closed canopy, an understorey comprised of bare soil, leaf litter and seedling recruits, a high density of small-diameter trees and a moderate representation of special life forms, including hemi-epiphytes and epiphytic ferns. Restoration plantings resembled rainforest sites in the density of smaller-sized trees, canopy cover and seedling cover in the understorey;

but rainforests were taller, had more large trees (>50 cm dbh), a larger basal area of trees, more coarse woody debris and more special life forms than replanted sites.

Replanted sites had generally increased in height, canopy cover, the density of trees – 50 cm dbh, tree basal area and the abundance of woody debris between 2000 and 2006 (Table 3). Consequently, despite the impact of cyclone Larry, all replanted site-types were generally more ‘rainforest-like’ in 2006 than in 2000 (Fig. 1). In both survey periods, restoration plantings more closely resembled rainforest than monoculture or mixed species timber plantations (Table 2, Fig. 1).

Cyclone damage to sites

Cyclone damage varied between trees of different size-classes, between site-types and between sites within site-types. First, the proportion of trees that were severely damaged by the cyclone (major branches broken, stem snapped or pushed over) increased with the size of trees across all site types (size class: $F_{3, 20} = 25.8$, $P < 0.001$; site-type $F_{3, 22} = 1.51$, $P = 0.24$; interaction $F_{9, 66} = 1.58$, $P = 0.14$; Fig. 2). On average, across all site-types, 27% of trees >10 cm dbh were severely damaged by the cyclone, compared with only 5% of smaller-sized trees (<10 cm dbh).

Second, damage levels varied between site-types. On average, 52% of trees >10 cm dbh in monoculture plantations were severely damaged by the cyclone, compared with 27% in mixed species timber plantations, 14% in ecological restoration plantings and 27% in reference rainforest ($F_{3, 26} = 7.26$, $P = 0.001$). The proportion of trees >20 cm dbh that were severely damaged by the cyclone in each site type followed a similar trend,

although differences between site-types were marginally significant ($F_{3,26} = 2.44$, $P = 0.087$).

Third, cyclone damage varied considerably between sites within most site-types. The proportion of trees >10 cm dbh that were severely damaged by the cyclone ranged from 43 – 61% in monoculture plantations, 4 – 45% in mixed species timber plantations, 3 – 34% in ecological restoration plantings and 7 – 60% in rainforests. Within site-types, cyclone damage tended to decrease with distance north of the path of the cyclone and stem density. In an ANCOVA model, with site-type as a factor, the proportion of severely damaged trees >10 cm dbh decreased with distance north of the cyclone track (site-type $F_{3,25} = 9.15$, $P < 0.001$; distance $F_{1,25} = 7.19$, $P = 0.013$). There was a similar, but only marginally significant, trend for stems >20 cm dbh (site-type $F_{3,25} = 2.64$, $P = 0.074$; distance $F_{1,25} = 3.18$, $P = 0.087$) (Fig. 3). In regression models which included the distance of sites north of the cyclone track, the proportion of severely damaged trees decreased with stem density, both for stems >10 cm dbh ($R_{2,27} = 0.57$, $P = 0.005$) and stems >20 cm dbh ($R_{2,27} = 0.56$, $P = 0.007$) (Fig 4). For timber plantations, there was no evidence that levels of cyclone damage were related to topographical position (Fig. 5).

DISCUSSION

Cyclone Larry brought damaging winds to replanted sites on the Atherton Tableland that had not experienced an event of similar magnitude since establishment. In part, damage to replanted sites was determined simply by proximity to the path of the cyclone, that is, by chance. However, damage levels also varied between different types of reforestation. Timber plantations were more severely damaged by the cyclone than

restoration plantings; and amongst timber plantations, damage levels were higher in monocultures than mixed species plantations. These differences in damage levels among site-types were not confounded by proximity to the cyclone path. In the following paragraphs, we discuss potential reasons for the observed patterns of damage and their implications for the management and design of reforestation projects.

The effects of cyclones on different types of reforestation have not previously been examined. However, several studies from the Caribbean have reported severe cyclone damage to timber plantations (Tanner *et al.* 1991; Fu *et al.* 1997). The susceptibility of plantations to cyclones has been attributed to their relatively open structure, a consequence of their establishment in widely-spaced rows and subsequent pruning and thinning operations, which allows strong winds to deeply penetrate stands (Lugo 1997). Unlike timber plantations, restoration plantings are generally planted at high densities and are not subjected to pruning or thinning. The restoration plantings surveyed in the present study comprised dense stands of small-diameter trees, often with a well-developed understorey of seedlings and saplings. This type of forest structure may generally be resistant to wind damage, as reported for low-statured, multi-stemmed tropical forests in the Caribbean and elsewhere (Van Bloem *et al.* 2005).

Other factors which may have contributed to higher damage levels in plantations than restoration plantings include landscape context and the biogeographical origin of species used in replanted sites. First, all but one of the restoration plantings surveyed in this study were established on the lower slopes of valleys, a location which would generally be expected to provide some shelter from cyclones (Webb 1958; Unwin *et al.*

1988; Reilly 1991; Grove *et al.* 2000). However, the protection afforded by topography is contingent on the orientation of potential shelters to the direction of destructive winds. In some cases, valleys can act as funnels for intense cyclonic winds, increasing damage levels (Reilly 1991; Grove *et al.* 2000). In the present study, there was no evidence that topographical location influenced damage levels in timber plantations; hence it is difficult to argue that restoration plantings escaped severe damage because they were located in sheltered parts of the landscape.

Second, restoration plantings utilised locally-occurring species, whereas timber plantations have sourced many species and provenances of trees from outside north Queensland. For example, provenances of hoop pine used in plantations in Queensland were largely from subtropical Australia, with some material from New Guinea (Nikles & Robson 2005; Killin 2006), while mixed species plantations included a number of species and provenances from subtropical and temperate Australia (Bristow *et al.* 2005; Lott *et al.* 2005). It is possible that locally-occurring trees may be better adapted to withstanding cyclonic winds than species from outside the subequatorial cyclone belt, because of natural selection for resistance (or resilience) to cyclone damage in regions exposed to recurrent cyclones (Lugo & Scatena 1996).

Implications for the design and management of timber plantations

In the last two decades, there has been considerable interest in expanding the area of monoculture and mixed species timber plantations in north Queensland (Vize *et al.* 2005; Killin 2006), coincident with a period of reduced cyclone activity (Nott *et al.*

2007). However, cyclone Larry has dampened confidence in the future of timber plantations in the region (M. Bristow, pers. comm., 2006).

For those still interested in establishing timber plantations in north Queensland, an important question is how to reduce the risk of cyclone damage (Harrison 2006). Our data and more general observations (Webb 1958; Unwin *et al.* 1988) suggest that some risk is simply unavoidable, given that sites close to the path of the cyclone are likely to experience high levels of damage, regardless of their composition or structure. Plantations grown on long rotations may be at high risk of a direct hit at some stage of the rotation, given the return interval of severe cyclones to the region and the extent of severe damage associated with each event (Webb 1958; Unwin *et al.* 1988). In fact, the likelihood of a direct hit is probably greater than implied by recent history, given the long-term frequency of very large, intense cyclones in the region (Nott *et al.* 2007) and the potential for an increase in the frequency of severe cyclones with global warming (Walsh *et al.* 2001).

If the risks of a direct hit are considered tolerable, it may be possible to reduce the extent of cyclone damage to plantations by careful location and design. In Australia, one strategy would be to locate plantations away from the coast, where destructive winds are usually most intense (Webb 1958). Within a region, the location of plantations in topographically sheltered locations would also be expected to reduce the likelihood of exposure to damaging winds. For example, some mahogany plantations surveyed by Van Bloem *et al.* (2005), which had been established in valleys, did not experience the high levels of cyclone damage reported for timber plantations elsewhere in the

Caribbean. However, our data demonstrate that the protection afforded by location and topography is not absolute.

Plantations could also be designed to reduce the potential exposure of trees to damaging winds. For example, plantations could be surrounded by windbreaks of denser restoration plantings (Tucker *et al.* 2004). Alternatively, plantations themselves could be stocked at higher rates, and subjected to reduced silvicultural management (thinning, pruning), to increase stand density and wind resistance. However, changes to the silviculture of plantations will affect their establishment costs, maintenance requirements and the value of timber they produce (Keenan *et al.* 2005). Furthermore, at the scale of individual trees, wind resistance is influenced by form (e.g., the ratio of diameter: height), which can improve as a result of thinning (Canham *et al.* 2001).

While the current plantation estate in north Queensland is based largely on native and exotic conifers, the experience of the last two decades has demonstrated that many local rainforest trees can be grown in plantations (Tucker *et al.* 2004; Bristow *et al.* 2005). Increased use of locally-occurring trees (or species from other subequatorial regions) which have evolved in an environment subject to recurrent cyclones might help reduce cyclone damage to timber plantations. It is very likely that the growth rates and merchantability of local species could be improved through breeding programs and silvicultural treatment (Keenan *et al.* 2005; Nikles & Robson 2005), although there may be a fundamental trade-off between growth-rates and wind resistance in trees (Canham *et al.* 2001; Ostertag *et al.* 2005).

334 **Implications for restoration projects**

335 The last two decades have seen significant investment in restoration plantings in north
 336 Queensland (Catterall & Harrison 2006). In general, restoration plantings on the
 337 Atherton Tableland were not severely damaged by cyclone Larry, an outcome we
 338 tentatively attribute to their design (high density plantings of local trees) and youth (few
 339 large trees). Further, some impacts of the cyclone may have had a positive effect on the
 340 value of restoration plantings for biodiversity. For example, the cyclone greatly
 341 increased the volume of woody debris in restoration plantings, a structural element often
 342 poorly developed on replanted sites, but that provides habitat for a range of specialised
 343 fauna (Grove & Tucker 2000; Kanowski *et al.* 2003, 2006).

344
 345 The long-term development of restoration plantings towards rainforest conditions will
 346 require the dispersal and subsequent recruitment of rainforest trees and shrubs to planted
 347 sites, and their persistence over repeated cycles of disturbance (Tucker & Murphy 1997;
 348 Catterall *et al.* 2007). By 2006, all restoration plantings surveyed had recruited some
 349 rainforest species, but most had also recruited a range of exotic plants. These included
 350 light-demanding herbs and scramblers, which would not be expected to persist after
 351 canopy closure, as well as more shade-tolerant trees and shrubs including privets
 352 (*Ligustrum lucidum*, *L. sinense*), guavas (*Psidium guajava*, *P. cattleianum*) and
 353 camphor laurel (*Cinnamomum camphora*). Even before cyclone Larry, the recruitment
 354 of exotic plants had raised concerns about the long-term ecological trajectory of
 355 restoration plantings (Wardell-Johnson *et al.* 2005). The loss of canopy cover resulting
 356 from cyclone Larry is likely to stimulate the growth of existing recruits, including
 357 exotics. If restoration plantings are to remain on the desired developmental trajectory

towards rainforest conditions, they may require significant intervention over the next few years to control exotic plants, coupled with an appropriate monitoring program.

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Table 1. Attributes of replanted sites and upland rainforest on the Atherton Tableland, north Queensland.

Site type	No. of sites	Age in 2006 (years)	No. of species planted [†]	Distance (mean, range) from cyclone (km)	Topographical location of sites [‡] (U, M, L)	Most common tree genera [§]
Monoculture plantations	5	12 - 16	1	9 (5 – 12)	1, 2, 2	<i>Araucaria, Agathis</i>
Mixed species plantations	5	12 - 14	6 - 15	8 (2 – 20)	3, 1, 1	<i>Eucalyptus, Elaeocarpus, Flindersia, Homalanthus, Alphitonia, Blepharocarya, Agathis, Melicope, Castanospermum</i>
Restoration plantings	10	11 - 21	20 - 40	8 (2 – 24)	1, 0, 9	<i>Acacia, Alphitonia, Flindersia, Elaeocarpus, Homalanthus, Blepharocarya, Alstonia, Melicope, Darlingia, Cardwellia, Aleurites, Grevillea, Guioa, Syzygium</i>
Rainforest	10	n/a	n/a	11 (1 – 17)	5, 2, 3	<i>Argyrodendron, Endiandra, Cryptocarya, Flindersia, Aglaia, Syzygium, Brombya,</i>

Citronella, Daphnandra, Castanospermum,
Acronychia, Beilschmiedia, Mallotus,
Castanospora, Doryphora, Tetrasyandra, Litsea

[†] Typical values from Catterall *et al.* (2004). [‡] Number of sites in the following locations: U = upper slope; M = mid slope; L = lower slope.

[§] Genera listed in order of decreasing abundance in nine 10 x 10 m plots per site, pooled across sites. Only taxa comprising at least 2% of stems >10 cm dbh are listed.

Table 2. Vegetation structure (mean, SE) of replanted sites and upland rainforest on the Atherton Tableland, north Queensland in 2006.

Site-types as for Fig. 1. Site types with the same letters do not differ significantly in values of a particular attribute.

Category	Attribute	Site type				ANOVA	<i>P</i>
		P	CT	ER	F	<i>F</i> _(3, 26)	
Ground cover	Grass and herbs (%)	30 (8.4) c	34 (11.0) c	9 (3.4) b	1 (0.7) a	12.77	<0.001
	Scramblers and vines (%)	11 (3.5) b	1 (0.3) a	1 (0.3) a	8 (0.7) b	10.64	<0.001
	Tree seedlings (%)	1 (0.4) a	2 (1.1) a	8 (1.9) b	7 (2.1) b	4.92	0.008
	Leaf litter (%)	41 (5.6)	47 (7.6)	53 (5.3)	55 (4.0)	1.10	0.37
	Bare soil (%)	12 (3.1) a	15 (2.2) ab	26 (5.3) b	12 (2.2) a	3.24	0.038
Canopy	Canopy cover (%)	47 (4.1) a	68 (3.3) b	80 (3.2) c	80 (1.7) c	19.39	<0.001
	Canopy height (m)	15 (0.7) a	20 (1.1) b	20 (1.0) b	30 (1.4) c	28.88	<0.001
Trees and shrubs	Shrubs (1-2 m) (stems ha ⁻¹)	1053 (483) b	960 (694) a	3303 (607) b	4263 (903) b	8.22	0.001
	Trees <2.5 cm dbh (stems ha ⁻¹)	833 (282) b	727 (597) a	1650 (360) b	1920 (259) b	4.74	0.009
	Trees 2.5-10 cm dbh (stems ha ⁻¹)	233 (103) a	460 (290) a	1890 (187) b	1873 (184) b	12.28	<0.001
	Trees 10-20 cm dbh (stems ha ⁻¹)	150 (86) a	290 (66) b	772 (79) b	408 (45) b	9.97	<0.001

	Trees 20-50 cm dbh (stems ha ⁻¹)	363 (30) b	253 (32) ab	205 (35) a	242 (28) ab	3.08	0.045
	Trees > 50 cm dbh (stems ha ⁻¹)	0 (0) a	0 (0) a	12 (6) a	80 (14) b	15.28	<0.001
	Basal area trees (m ² ha ⁻¹)	28 (2.0) a	23 (2.3) a	33 (3.3) a	63 (7.3) b	11.43	<0.001
	Basal area dead trees (m ² ha ⁻¹)	0 (0) a	1 (0.6) ab	2 (0.3) b	8 (3.0) c	10.28	<0.001
Woody debris	Fine (2.5–10 cm diam.)	5 (0.8) a	10 (3.5) ab	10 (1.1) b	16 (2.4) b	6.53	0.002
	Coarse (>10 cm diam.) (m ³ ha ⁻¹)	5 (1.0) a	13 (7.2) a	11 (2.4) a	72 (15.1) b	18.96	<0.001

Table 3. Variation in structural attributes of replanted sites and upland rainforest on the Atherton Tableland, north Queensland, between 2000 and 2006. The table presents the results of repeated measures ANOVA (see text). Data from 2006 include all living trees, regardless of cyclone damage. Site-types as for Fig. 1.

Attribute	Survey		Site-		Interacti		Interpretation
	period		type		on		
	$F_{(1, 26)}$	P	$F_{(3, 26)}$	P	$F_{(3, 26)}$	P	
Canopy cover	2.42	0.13	78.0	<0.001	18.7	<0.001	Increase in replanted sites, especially P, CT; decrease in F
Canopy height	25.6	<0.001	60.6	<0.001	14.5	<0.001	Increase in replanted sites; decrease in F
Trees 2.5-10 cm dbh	0.015	0.91	57.1	<0.001	1.01	0.41	
Trees 10-20 cm dbh	0.89	0.35	7.91	0.001	1.66	0.20	
Trees 20-50 cm dbh	17.5	<0.001	2.59	0.075	5.88	0.003	Increase in replanted sites, especially P; decrease in F
Trees >50 cm dbh	0.01	0.95	47.2	<0.001	5.45	0.005	Increase in ER, decrease in F
Basal area trees	10.0	0.004	25.2	<0.001	14.9	<0.001	Increase in replanted sites, especially P; decrease in F
Fine woody debris	41.2	<0.001	5.04	0.007	1.04	0.39	Increase in all sites
Coarse woody debris	5.71	0.024	38.9	<0.001	1.53	0.23	Increase in all sites

Figure captions

Fig. 1. Ordination of replanted sites and upland rainforest on the Atherton Tableland, north Queensland, by vegetation structure. Site-types: triangles = monoculture plantations (P); squares = mixed species plantations (CT); diamonds = restoration plantings (ER); circles = rainforest (F). Open symbols = 2000; closed symbols = 2006. The ellipses show the area of ordination space within 1 SD of the centroids of each site-type in each survey period. Arrows show the movement in ordination space of centroids of site-types between 2000 and 2006. Stress = 0.12

Fig. 2. Proportion of trees (mean, SE) in different size classes severely damaged by cyclone Larry in replanted sites and upland rainforest on the Atherton Tableland, north Queensland. Site-types as for Fig 1.

Fig. 3. Relationship between distance from the cyclone track and the proportion of severely damaged trees in replanted sites and upland rainforest on the Atherton Tableland, north Queensland. (a) stems >10 cm dbh; (b) stems >20 cm dbh. Site-types: triangles = monoculture plantations; squares = mixed species plantations; diamonds = restoration plantings; circles = rainforest.

Fig. 4. Relationship between stem density and the proportion of severely damaged trees in replanted sites and upland rainforest on the Atherton Tableland, north Queensland. (a) stems >10 cm dbh; (b) stems >20 cm dbh. Site-types: triangles = monoculture plantations; squares = mixed species plantations; diamonds = restoration plantings; circles = rainforest.

Fig. 5. Relationship between topographical position and the proportion of severely damaged trees in timber plantations on the Atherton Tableland, north Queensland.

Diamonds = stems >10 cm dbh; open squares = stems >20 cm dbh. Data pooled across monoculture and mixed-species plantations, with one site distant from the cyclone excluded (see text).

Fig. 1. Ordination of replanted sites and upland rainforest on the Atherton Tableland, north Queensland, by vegetation structure. Site-types: triangles = monoculture plantations (P); squares = mixed species plantations (CT); diamonds = restoration plantings (ER); circles = rainforest (F). Open symbols = 2000; closed symbols = 2006. The ellipses show the area of ordination space within 1 SD of the centroids of each site-type each survey period. Arrows show the movement in ordination space of centroids of site-types between 2000 and 2006. Stress = 0.12

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