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DO CYCLONES AND FOREST FRAGMENTATION HAVE SYNERGISTIC EFFECTS? A BEFORE-AFTER STUDY OF RAINFOREST VEGETATION STRUCTURE AT MULTIPLE SITES

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ABSTRACT

Ecological degradation within areas of remnant forest may be amplified if the effects of fragmentation interact with the effects of other environmental disturbances such as wind storms. We used before-after comparisons to assess the effects of Tropical Cyclone Larry on remnant and continuous rainforest in the Wet Tropics uplands of north-eastern Australia. Vegetation structure was measured three years before the cyclone and six months afterwards, at eight continuous forest sites and eight remnants (6-37 ha), within 20 km of the cyclone's track. The cyclone caused extensive defoliation, felling and breakage of stems and branches (greatest among the trees >100 cm diameter which had around 50% stem loss), and increased litter and woody debris. Cyclone effects were strongly influenced by a site's spatial position (*P* = 0.005, 0.001 in multivariate analyses of overall damage). Maximum damage occurred 10-15 km south of the cyclone track, perhaps because of the additive effects of the west-moving air at the southern eyewall combined with the cyclone's own rapid westward movement. Most fragments were south of the cyclone track, as a consequence of spatially-selective deforestation practices, and therefore showed greatest damage However, once the effects of spatial position were considered, the independent differences in cyclone effects between fragments and continuous forest were lost (*P* = 0.23, 0.41 when north-south distance was included as a covariate in analyses). The expected protection afforded by a continuous forest canopy seems to have disappeared in the face of extremely strong cyclonic winds and down-draughts. Nevertheless, an interaction between fragmentation and disturbance may yet occur, during the period of post-cyclone recovery, due to the effects of landscape context on plant recruitment. For example, there was a higher diversity of exotic seedling germination in fragments, independent of the extent of cyclone damage.

Key words: hurricane, remnant, damage, tree, vine

Running title: Cyclone impacts and forest fragmentation

INTRODUCTION

Patches of remnant vegetation within a cleared matrix of pasture or cropland are expected to undergo a variety of ecological changes, many of which may take many years to develop (Saunders *et al*. 1991). There has been extensive research into the outcomes of habitat reduction and disconnection for the population dynamics of individual species within such remnants. However, an important emerging issue which has received less attention is the way in which disturbances to the physical environment, such as fires or storms, may interact with anthropogenic fragmentation, with the consequence that the effects of these disturbances on patches of remnant vegetation may be significantly greater than their effects on unfragmented vegetation (Laurance and Cochrane 2001, Laurance 2002). If this is the case, then fragments may be more susceptible to disturbance than continuous forest, and less able to recover, resulting in a progressive sequence of changes to their physical and biological characteristics (Tabarelli *et al*. 2004).

Rainforest vegetation is characterised by a distinctive and complex physical structure, including closely-spaced trees whose foliage forms a closed canopy, multiple foliage layers in the subcanopy and understorey; the presence of characteristic forms of plant life such as vines, lianes, large and small epiphytes, palms, and strangler figs, and a thick layer of litter on the ground (Tracey and Webb 1975, Adam 1994). This structure facilitates a humid, relatively cool, ground-level microclimate in which light levels are relatively low. The maintenance of this structure is important to the persistence of the full complement of rainforest biodiversity (Kanowski *et al*. 2003). However, occasional structural damage also plays a role in the maintenance of biological diversity within rainforests. For example, tree-fall gaps (typically created when large trees are felled by wind) are an important component of spatial heterogeneity within rainforests, and may help to maintain plant diversity by providing opportunities for seedling and sapling growth, and for local turnover of plant species (Denslow 1987, Hopkins 1990).

On the other hand, exposure to periodic windstorms (such as cyclones, typhoons and hurricanes) can have more dramatic effects on rainforest vegetation (Boose *et al.* 1994, Franklin *et al*. 2004, Uriarte *et al.* 2004). The cumulative effects of a storm regime may greatly increase the supply of tree-fall gaps (Grove *et al.* 2000, Turton and Seigenthaler 2004), leading to an increased prevalence of microenvironments which favour particular floristic elements such as vines, earlier-successional species and invasive exotic species (Webb 1958, Olsen and Lamb 1986). Eventually this may lead to longer-term changes in forest structure, floristic composition and ecosystem function (Laurance *et al.* 2006).

Within about 30 m of the edges of remnant patches, rainforest vegetation typically responds to increased light availability by developing an increased foliage growth of trees, shrubs and vines which eventually "seals" the edge and reduces the penetration depth of many edge effects (Williams-Linera 1990, Malcolm 1994, Camargo & Kapos 1995). Storm-associated effects of strong lateral winds may penetrate much more deeply (Nelson *et al.* 1994, Laurance 1997, Laurance *et al*. 1998). Depending on this penetration depth, forest fragments could be expected to differ from the interior of continuous forest, by showing greater storm-associated removal and breakage of the trunks, branches and foliage of trees, greater consequent forest-floor litter accumulation, and therefore greater impacts on forest-floor seedlings and shrubs (Laurance *et al.* 1997, Didham 1998). However, despite such logical reasoning it remains poorly understood whether the vegetation of rainforest fragments is actually more extensively damaged in severe storms than that of continuous forest.

The effects of wind storms can be very patchy in space (Webb 1958). Therefore, to test whether fragments are indeed prone to amplified storm damage requires quantitative measurements at independent replicate fragments and continuous forest sites, both before and after a storm. However, the unpredictability of severe storms has largely prevented such studies being undertaken. Here we present the results of a study which compares rainforest structure between fragments and continuous rainforest sites, taken before and after Tropical Cyclone Larry in the Wet Tropics region of north-eastern Australia. We consider the extent of storm-associated damage, how it varies spatially, the potential interactions between storm and fragmentation impacts, and the implications for longer-term change in the structure and floristic composition of fragmented rainforest.

METHODS

Study region, design and sites

The study took place on the Atherton Tablelands, northeast Australia ($17^0$15-$17^0$30’S, $145^0$35’-$145^0$45’E; Fig. 1), an upland (650-850 m a.s.l.) plateau where large tracts of pre-European rainforest occurred in areas with a mean rainfall of 1600-3000 mm per annum. The eastern edge of the plateau is bounded by steeply-sloping areas. The region's geology consists of basalt flows overlying acid-igneous and metamorphic substrates (Laffan 1988). There is a gradient of decreasing rainfall towards the north-west of the region, and the native vegetation varies from eucalypt-dominated open-forest (on drier sites) to a variety of rainforest types, whose differences in structure and floristics are broadly associated with variation in climate, soils and geology, altitude and disturbance history (Tracey and Webb 1975, Tracey 1982). Forest clearing began on the Tablelands in the early part of the 20th century. Deforestation was most intensive during the first two decades (Winter *et al*. 1987), although substantial clearing continued until the 1950s, and smaller-scale clearing and logging on freehold land continued at the time of the present study, albeit at a much-reduced rate. Most of the cleared land at the time of the study supported cattle pasture, as well as areas of low regrowth on abandoned farmland, occasional tree crops and timber plantations and scattered rural dwellings.

Vegetation structure before the cyclone was measured in 2003 at 16 sites (8 fragment, 8 continuous forest) during a broader project aimed at assessing how fragmentation affects the vegetation of rainforest remnants, with a particular emphasis on plant species' density and composition of different plant life-forms and size-classes (S. McKenna unpublished data). The rainforest type at all sites was complex mesophyll to notophyll vine forest of high rainfall on basalt in cloudy uplands, classified as Regional Ecosystem 7.8.2 (EPA 2007), also known as Type 1b Tracey (1982). It occurs at altitudes of 400-900 m, has a tall closed canopy (tree height up to 55 m), and has a high diversity of structural features (e.g., presence of buttresses, variety of stem diameters), life-forms, and tree species, with good representation from the families Lauraceae, Meliaceae, Myrtaceae, Proteaceae, Rutaceae and Sapindaceae.

Fig 1 about here

From over 50 potential fragment sites initially identified (size range 4-40 ha) using maps and aerial photography, eight were considered suitable for the fragmentation study, once screening criteria were applied. Sites were considered unsuitable if they showed any substantial signs of disturbance, including: recent (<10 years ago) selective logging, degradation by cattle, or extensive disturbance associated with invasion by exotic weeds. Sites were also rejected if they had large regrowth components or if they had strong floristic affinities with, or were spatially close to, non-targeted forest types, and if they were too low or too high in elevation, or too steeply sloping. Fragment sizes (to the nearest 0.5 ha) were: 6.0, 6.5, 7.5, 10.5, 18.0, 27.5, 32.0, and 37.0 ha. The adjacent matrix was predominantly grazed pasture, and all fragments were at least 0.6 km (median 0.75 km, maximum 2.2 km) from the nearest forest patch > 5 ha.

All sites in continuous forest were within large tracts whose overall area exceeded 20,000 ha. Site selection criteria included a requirement that base environmental conditions (altitude, geology and soils, climatic regime, disturbance history and vegetation type) were similar between fragments (which were selected first) and continuous sites. Vegetation heterogeneity near to sites in continuous forest was restricted to adjacent rainforest types with broadly similar structural and floristic composition (Regional Ecosystem 7.8.4 /Type 5a or Regional Ecosystem 7.11.1 /Type 2a (Tracey 1982, EPA 2007) to the studied type.

Sites were dispersed across an area of 31 km from north to south, and 17 km from east to west (Fig 1). Because forest-clearing by rural settlers had targeted the level land in the west of the study region, and because there were different forest types in the region's north-west (which was drier) and south-east (which sloped rapidly away to lower altitudes), many fragments lay south-west of the continuous forest sites, and were slightly higher in altitude (fragments $17^0$21’ S to $17^0$33’ S, $145^0$34’E to $145^0$39’E, altitude 710-830 m (average 765 m); continuous forest $17^0$16’ S to $17^0$28’ S, $145^0$39’ E to $145^0$44’ E, altitude 670-790 m (average 705 m). The median distance between fragments was 12 km (range 1-22 km), and the median distance between continuous forest sites was 8 km (range 2-22 km). Two fragments and two continuous forest sites contained gullies with permanent streams.

Pre-cyclone vegetation data were collected in June-September 2003. On Monday 20th March 2006, Category 4 Tropical Cyclone Larry crossed the coastline some 30 km to the east of the study region.) This small but fast-moving, and severe cyclone then traveled westwards, and about one hour later its eye had reached the eastern margin of the study region, moving on an almost exactly east-west trajectory at around $17^0$23’S (Fig 1; see also Turton this volume). A picture of TC Larry's behaviour was obtained from records and analyses compiled by the Australian Bureau of Meteorology (BOM 2007), supplemented by personal communications with P. Otto and R. Falls (BOM meteorologists) to provide further detail, especially concerning revisions to the cyclone track's location made by BOM in early 2008. On the Tableland, the cyclone was considered to be Category 3, with gusts up to 187 km/h recorded at the High Road windfarm (with an average of 93 km/h), and a radius of maximum windspeed estimated from radar to be about 15-20 km (and probably greater to the south than the north). The cyclone crossed the Tableland, a distance of around 30 km, in one hour between 9 am and 10 am. Considerable local variation in wind strength was reported, associated with both variations in wind behaviour (e.g., eddy formation) and local topography, resulting in visibly patchy damage levels (BOM 2007). The study sites were located between 12 km north and 20 km south of the cyclone's track (Fig. 1).

Post-cyclone vegetation data were collected at the study sites in July-October 2006. Between March 2006 and October 2006, the study region continued to receive high rainfall, so that conditions would have been favourable for plant growth, seedling establishment and litter decomposition.

Vegetation measurements

To sample the vegetation, we used a series of transects, each 50 m long, spaced more-or-less evenly across a 3-4 ha area at each site. Before-cyclone surveys used eight transects per site for all attributes, whereas post-cyclone transects used four transects per site for most attributes, and six for a few (Table 1). Because there were fewer after-cyclone transects within each site than before-cyclone transects, the latter were spread more widely across a site's area; some after-cyclone transects overlapped in position with before-cyclone transects, but others differed. The aim was to obtain a representative sample of the site's vegetation within the previously-sampled area, and sites were used as the unit of measurement and replication in all data analyses.

Table 1 about here

Vegetation attributes were sampled using a variety of specific within-transect methods (details in Table 1). In the before-cyclone data, the eight transects (total length 400 m) were the basis for four sets of count data, made along the transects' entire length, as well as plot data from two 5 m radius (78.5 m^2) circular plots per transect. The resulting methods of data collection were: (1) a stem-count area 2 m wide, used for the smallest size-class of woody stemmed plant, 0.5 m tall & < 2.5 cm diameter; (2) a stem-count area 4 m wide, used for older saplings, 2.5-9.9 cm diameter, and also for counts of vines in various diameter classes; (3) a stem-count area 10 m wide, used for trees of four larger size-classes, 10-20, 20-50, 50-100, and >100 cm diameter; (4) a 400 m line along which fallen woody debris intercepts of various diameter classes were counted; (5) two 5 m radius plots at 10 m and 40 m along each transect, used for foliage cover estimates at 5 points per plot and ground cover variables estimated across the whole plot. Stem counts included only those individuals rooted in the sampling area.

After the cyclone (2006), the four types of transect-based data were similar to those in 2003, except that either four or six transects were used, with a total length of either 200 m or 300 m, depending on the diameter of the stems being counted (Table 1). The following variations were made: (1) ground-cover variables and visually-estimated canopy cover were measured within two 5 x 5 m square quadrats per transect, with the addition of tree height, and photographically-estimated canopy cover; (2) damage levels in four categories ranging from defoliation to trunk breakage and tree-fall were scored for all visible stems that had been rooted in the sampling area during the stem counts (fallen stems were also included in the woody debris counts); (3) the frequencies of plant life-forms indicative of response to canopy disturbance (vine towers, vine tangles, scrambler thickets) were obtained by scoring their presence/absence in the 5 x 5 m quadrats; and (4) an index of the number of species of common recently-germinated seedlings of native and exotic plants in each site was obtained, by listing species which showed noticeable germination flushes in each transect (all details in Table 1). All vegetation data were collected by the same observer (SM).

The average distance of transects from the edge of each site ranged from 30 m to 50 m (mean 41 m) within fragments, and 80-260 m (mean 216 m) in continuous forest. The average slope of transects within each site ranged from 2^0 to 12^0 (mean 5.3^0) within fragments, and $2\text{-}14^0$ (mean 6.9^0) in continuous forest. The average topographic position score (based on ridge 4, slope 3, flat 2, gully 1) of transects within each site had a range of 2-3 (mean 2.3) within fragments, and 2-4 (mean 2.6) in continuous forest.

Data analyses

Values of all attributes were either averaged or summed across transects, to give a single site-level measure for each. After the cyclone, foliage cover was measured in two ways: by photograph and by visual estimate (Table 1). These were highly correlated (r=0.94, n=16 sites). Therefore, a comparison between visual estimates in 2003 and 2006 was considered to be robust.

For individual variables which were measured both before and after the cyclone, we tested the statistical significance of year (2003, 2006), site-type (continuous, fragment) and their interaction with two-factor repeated-measures ANOVA (SPSS 2003), in which sites were replicates and time the within-plot factor. For variables which were measured only after the cyclone (2006), fragments were compared with continuous forest sites using t-tests; due to low sample sizes statistical significance was calculated using randomisation (Edgington 1980) with 4999 iterations.

The patterns of overall similarity in the 10 ground cover attributes (which summed to 100%) among all sites before and after the cyclone were visually represented using non-metric multidimensional scaling ordination (MDS) of untransformed data in the software package PRIMER (Clarke and Warwick 2001). Pearson's correlations of each ground cover variable with the ordination axes were used to show each variable as a biplot vector on the ordination.

To summarise the overall cyclone impact on rainforest structure, a principle components analysis (PCA) was conducted on the change between 2003 and 2006 in the site-specific values of seven variables, selected to represent major aspects of cyclone impact: canopy cover; total woody debris cover (all diameter classes) from ground quadrat samples; litter cover from ground quadrat samples; total woody debris intercepts (all diameter classes) from transect counts; the stem density of standing trees (>20 cm diameter, not fallen or snapped); the percent of standing trees (>20 cm diameter) showing any form of damage (foliage loss, branch breakage); and the percent of all trees which showed extreme damage (fallen or snapped). Damage rates in 2003 were taken as zero. Prior to analysis, data points within each variable were range-standardised (the difference between each value and the minimum, divided by the data range), to give equal weighting to all variables. The first PCA axis was then used as a summary measure of cyclone impact for each site.

The sites' distances northward from the southernmost site were used to explore the relationship between spatial separation from the cyclone's core and various measures of vegetation damage, using graphical and correlation analyses. This was meaningful because the cyclone's track across the study region was almost precisely east-west (Fig. 1),

The effect of site-type (continuous, fragment) on the multivariate cyclone-responses of vegetation attributes were tested using NP-MANOVA (Anderson 2001), with 9999 iterations. There were three such analyses: first a two-factor analysis of ground-cover attributes, with site-type and year as independent factors; second a single-factor analysis based on the between-year changes in values of ground-cover attributes in continuous versus fragment sites; and third a single-factor analysis based on the cyclone-associated change in the seven selected overall summary variables, in continuous versus fragment sites. Because the sites' spatial positions on a north-south axis proved to be a highly significant predictor of change in most vegetation variables, the latter two analyses were repeated both with and without the sites' northward distances as a covariate.

Site-type and time were considered to be fixed variables in all analyses. The Euclidean inter-site distance measure was used in all multivariate analyses. Pearson's correlation coefficients were used to explore patterns of association between selected pairs of variables across the 16 sites. The comparative ability of a suite of environmental variables (distance from the cyclone's track, westward distance, distance from forest edge, slope, topographic position score, distance from flowing steams, and patch area) to predict overall cyclone damage (PCA axis 1 values) was explored using all-subsets regression (SAS 1999).

RESULTS

Overall changes in vegetation structure before versus after the cyclone

Across all sites, the cyclone caused large and statistically significant changes in vegetation structure (Table 2). There was a 10% mean net reduction in canopy cover across all sites, in spite of several months' opportunity for post-cyclone growth (mean cover estimates changed from 76% in 2003 to 69% in 2006). At ground level there were mean increases in litter and herbaceous plants: leaf litter cover increased on average by 38%; fine and coarse debris within quadrats by 85% and 61% respectively; fine and coarse debris cover measured from intercept counts by 97% and 84% respectively; and forb cover by 46% (Table 2). There were mean decreases in the cover of exposed soil (61%), rock (43%), and tree boles (23%).

Stem losses were concentrated in the largest (>100 cm diameter) and smaller (<20 cm) diameter classes. The density of standing trees (those whose stems were neither felled nor snapped) decreased significantly in the three smallest and the largest size classes (Table 2), but did not change significantly in the two size classes representing intermediate-sized trees (20-50 cm). Standing tree density was reduced by an average (across all sites) of 28% for trees <20 cm in diameter, by 1% for those 20-50 cm diameter, by 10% for those 50-100 cm diameter, and by 53% for those above 100 cm diameter. For all stems >20 cm diameter, the density reduction was 10%. The density of large vine stems (>2.5 cm stem diameter) decreased on average by 39%, but smaller vines showed no significant change (6%) over time (Table 2).

Table 2 about here

Tree stems still standing unbroken after the cyclone showed considerable signs of damage; this consisted of either the breakage of major branches or the loss of foliage and smaller branches. These damage rates increased progressively with the size of the trees, ranging from 7% in stems

<2.5 cm diameter, to 35%, 45%, 55%, and 72%, in stems 2.5-10, 10-20, 20-50, 50-100 cm diameter, and 95% in stems >100 cm diameter (Table 2). Among all trees >20 cm diameter, 63% showed signs of damage (any level of severity), and 12% had very severe damage (stems snapped or fallen). Among standing stems (not snapped or fallen) 59% of trees >20 cm diameter showed signs of foliage or branch damage.

Interactions between structural change, fragmentation and other factors

Compared with the magnitude of differences between years before and after the cyclone, differences between fragments and continuous forest were small (Table 2). Before the cyclone, fragments differed from continuous forest sites in having a lower canopy cover, lower densities of younger stems (up to 10 cm diameter), and a lower density of ground-level ferns and fern allies.

Ordination of ground cover attributes considered together (MDS, Fig. 2) showed that, while fragments and continuous forest sites were interspersed with one another in the before-cyclone measurements, after the cyclone the fragments were located more towards the "disturbed" end of the first MDS axis, associated in particular with increased litter cover, and a decreased cover of soil and tree boles. Two-factor NP-MANOVA of these data revealed a significant interaction between site-type and time (interaction *P*=0.02, site-type *P*=0.32, time *P*=0.0001). In a single-factor NP-MANOVA based on the change in the 10 ground-cover attributes at each site between 2003 and 2006, site-type had a significant effect (*P*=0.005). However, changes in the values of the dominant ground cover attributes (litter and soil cover) were also significantly correlated with sites' distances along a northward axis perpendicular to the cyclone track (r=0.55 and 0.50 respectively). When this distance was included as a covariate (*P*=0.02) in the NP-MANOVA of change in ground-cover attributes, the effect of site-type was only marginally significant (*P*=0.05).

Fig 2 about here

Changes over time in the density of standing woody stems were generally similar in fragments and continuous forest, although some smaller stems (2.5-20 cm diameter) showed greater decreases in continuous forest sites than in fragments (Table 2). Damage rates to surviving stems (not fallen or snapped) were consistently greater in fragments than in continuous forest (Table 2); a two-factor ANOVA showed significant effects of both stem diameter (five classes; <2.5, 2.5-10, 10-20, 20-50, >50 cm; *P*<0.0001) and site-type (*P*=0.006), with interaction *P*=0.03. However, when the sites' northward distances were included as a covariate in the analysis, site-type was no longer statistically significant (stem diameter *P*<0.0001, site-type *P*=0.23, interaction *P*=0.33, covariate *P*=0.005). Damage rates to all tree size-classes increased from north to south, with the damage to standing stems reaching a maximum around 10-15 km south of the cyclone track (Fig. 3; r-squared values ranged from 0.48 to 0.71 for curvilinear best fits of damage to standing stems in different size-classes, and from 0.20 to 0.72 for rates of extreme damage). Linear correlations between these two damage measures and northward distance were also mostly high (r-squared 0.48 to 0.71, 0.10-

(

Fig 3 about here

The first axis of a principle components analysis based on the change in values of the seven key structural attributes explained 50% of total variation, and was strongly correlated with the change in canopy cover, quadrat debris cover, damage rates to standing trees (>20 cm diameter), and extreme damage rates to trees (Fig. 4). Analysis (NP-MANOVA) of the multivariate difference in these same seven attributes between continuous and fragment site-types gave *P* for site-type of 0.09. When the northward distance was included in the analysis as a covariate, the site-type *P* was 0.41, whereas the covariate was highly significant (*P* = 0.001). The summary level of cyclone damage at a site (as reflected by the first PCA axis) increased in a curvilinear fashion from north to south, and was greatest around 10-15 km south of the cyclone track.

Figs 4 and 5 about here

Only the northward distance emerged as a useful predictor in all-subsets regression analyses using adjusted r-squared and information-theoretic criteria (AIC, BIC) to select the three best predictive models for values of cyclone impact as measured by the first PCA axis. In these analyses, we inspected the three best models obtained from differing numbers of independent variables (1, 2, 3, 4, 5, and 6). Northward distance was the best single-variable predictor of cyclone impact (simple r-squared 0.57), and was also included in 11 of the 15 models with two or more predictors. Predictors selected in the other two best single-variable models were distance from the edge (simple r-squared 0.44) and site area (0.21). Both were highly correlated with the northward distance (r = 0.75, 0.59, respectively). The BIC estimate of the most efficient predictor of the cyclone's effect was the northward distance alone (with adjusted r-squared of 0.54), while AIC selected a four-variable model containing distance from the cyclone's track, westerly distance, distance from forest edge, and slope, with adjusted r-squared of 0.66.

After the cyclone, fragments continued to differ from continuous forest in having a lower canopy cover, lower densities of stems less than 10 cm diameter, and a lower density of ground-level ferns and fern allies (Table 2). Additionally, fragments showed a greater frequency of occurrence of vine tangles and thickets of thorny scramblers (neither were measured in 2003), and a greater number of exotic plant species showing flushes of post-cyclone seedling germination (Table 2). None of these three attributes were significantly predicted by the individual sites' northward distances (Table 3). However, the occurrence of vine tangles and vine towers was significantly greater at sites with lower post-cyclone canopy cover (which in turn was more likely to occur closer to the cyclone's track). Sites with lower post-cyclone canopy cover also had higher numbers of native plant and tree species showing flushes of seedling growth, whereas exotic species' germination showed no significant relationship with canopy cover.

Table 3 about here

DISCUSSION

Cyclone effects on rainforest structure

The cyclone caused large structural changes to both continuous and fragmented rainforest sites, although the amount of damage varied considerably both between and within sites. Major damage included both frequent tree-fall and snapping of tree trunks some metres above ground level, leaving the bottom part of the stem standing. Some fallen trees were still alive at the time of sampling, and this study did not attempt to infer mortality rates. Their mortality may in any case be delayed for some time after the damage occurred, since trees which survived the stress of root loss and exposure during the rainy post-cyclone months could be vulnerable to subsequent dry periods. In the cases where snapped standing tree boles were able to grow from re-sprouts, recovery into the growth form of a large tree would not be possible in the near future. Foliage and branches were lost from a large proportion of the remaining trees, even from smaller-sized individuals, with the consequent deposition of large amounts of leaf litter, and both fine and coarse woody debris on the ground. These changes left quantitatively detectable and consistent signatures, with significant change over time in the measured values of most ground cover and stem density variables, and substantial quantitative damage rates.

The measurements of changes in stem density and of rates of damage enable analyses of relative change across sites in relation to environmental factors. Interpretation of absolute values requires more caution. To measure absolute rates of stem loss individual trees would need to be marked pre-cyclone and then relocated post-cyclone, which was not done in this study. The rainforests in the study region, although considered relatively intact, were generally in a state of post-disturbance recovery even before Cyclone Larry, due to widespread impacts of Cyclone Winifred in 1986 (Laurance 1997), and selective logging of many areas (EPA 2007). Therefore changes in density of standing stems between 2003 and 2006 would also have been affected by: the growth transitions of individuals from smaller to larger size-classes (which may have then been accelerated in some individuals which experienced high moisture and light levels after the cyclone); new recruitment during 2003-2006 into the smallest size-class; and any mortality which may have occurred prior to the cyclone. This has probably led to some under-estimates of cyclone impacts on the density of mid-sized trees. The direct measurement of the percent of stems showing damage would be unaffected by these issues, but small and narrow-stemmed individuals could have been overlooked if they lay beneath areas in which larger stems and branches, tangled in vines, had collectively fallen. This would lead to under-estimates of the numbers of fallen or snapped stems in the smallest size-class.

That said, there are some clear findings which are unaffected by these sampling issues. Complete felling was most frequent among the old forest giants (large trees >100 cm in diameter, with around 50% stem loss), and this size class also showed the highest overall damage levels to standing stems (95%). The observation of differential cyclone impacts on very large individuals is consistent with the findings of many previous studies (Brokaw & Walker 1991, Walker 1991, Reilly 1991, Franklin *et al*. 2004, Pascarella *et al*. 2004, Uriarte *et al*. 2004; Van Bloem *et al*. 2005), although specific patterns of size-specific impact have varied between different studies (Franklin *et al*. 2004). Some studies of cyclone damage elsewhere have also reported that greater damage to trees occurred among species with higher growth rates or those typical of earlier successional stages (Zimmerman *et al*. 1994, Franklin *et al*. 2004, Ostertag *et al*. 2005). Sites dominated by pioneers or early successional species were avoided during site selection in the present study. Therefore, species identity is unlikely to explain the higher damage rates to large trees. The spreading canopy-level crowns of the largest trees would have intercepted the cyclonic winds over larger surface areas than mature but smaller-crowned trees (20-100 cm stem diameter), which were relatively resistant to being toppled, but which still showed high rates of damage. Conditions prior to the cyclone had been moist, and the wet soil would have decreased the resistance of trees to being felled, unlike the drier situation in the Wet Tropics during cyclone Agnes in 1956, when few large trees were uprooted (Webb 1958).

For the smallest size class (diameter <2.5 cm), the felling or breakage of stems is less likely to have been a direct consequence of wind than of the compounding effect of falling branches and stems from the larger trees, entangled with vines, which either carried the smaller trees to the ground or crushed them. Relatively low levels of canopy damage to standing <2.5 cm diameter individuals indicate that the understorey remained relatively sheltered even where winds were severe.

The spatial pattern of variation in damage was striking and its nature unexpected. The level of cyclone damage varied asymmetrically with distance from the cyclone track, being less to the north and much more to the south. Such a pattern may be a consequence of potential wind variation resulting from the addition of the cyclone's rotational windspeed and its speed of forward motion (for example, if the cyclone moved westward at 30 km/hr, with winds rotating clockwise at 90 km/hr, the net wind velocity may be 60 km/hr north of the cyclone's track but 120 km/hr to the south; R. Falls, BOM, personal communication). This simplification neglects the many complexities and patterns of turbulence associated with cyclonic winds, and their interaction with topography (BOM 2007). For example, some sites associated with east-facing slopes to the north of the track may have been relatively sheltered from the cyclone's westerly winds. Nevertheless, our observed 10-15 km radius of worst damage to the south of the cyclone track is reasonably consistent with the Bureau of Meteorology's radar-based estimate of a 15-20 km radius of maximum wind speed on the Tablelands.

Are fragments differentially prone to cyclone damage?

Contrary to expectations, our results indicate that horizontal vegetation continuity provided no protection from cyclone damage. Once the effect of northward position was removed, there was no residual effect of fragmentation on the overall measure of vegetation change. This lack of difference contradicts the extensive, and logical, speculation that small remnants should be more vulnerable than continuous forest areas to the effects of strong winds (e.g., Saunders *et al*. 1991, Laurance 1997, Turton and Seigenthaler 2004, Laurance *et al*. 2006). However, our finding is consistent with the lack of effect reported by other studies of the impact of Cyclone Larry on edges and linear remnants of rainforest in different parts of the Wet Tropics (Grimbacher *et al*. 2008 for the northern Tablelands and Pohlman *et al*. 2008 for the lowlands).

The study design held the environmental conditions and vegetation type as similar as possible between fragments and continuous forest sites (see Methods). Much of the pre-European area of the targeted rainforest type was located on the undulating hills and flats of the southern Atherton Tablelands, which were heavily and selectively cleared for agricultural purposes. Because of the gradients in climate, elevation and soil type which limit its distribution, the remaining continuous forest of this type occurs on more steeply sloping land in the eastern to north-eastern Tablelands. Therefore, Cyclone Larry, when it moved across the region, had greatest impact on the southern Tablelands, in which the remnants were located. These fragments were indeed worse off, but only as a consequence of non-random history; the apparent synergy in the effects of fragmentation and cyclone impact has been due to the spatial co-occurrence of of clearing and cyclone.

Why would fragments not have been more damaged by TC Larry than continuous forest, after the effects of spatial position were factored out? Wind behaviour during cyclones involves not only strength, duration, and direction, but also the occurrence of vertical downwards air movements, and local eddies whose effects interact with topography (BOM 2007). Very strong winds accompanied by down-draughts (conditions expected to occur within the radius of maximum windspeed) may broach the normally-protective effect of the continuous forest canopy. It remains possible that a continuous forest canopy may provide better relative protection from chronic exposure to moderate winds over extended time-periods than from acute exposure to the extremely high windspeeds and turbulence associated with cyclones, especially fast-moving cyclones such as Larry.

Longer-term trajectories in rainforest and fragments: recovery versus degradation

An important short-term impact of the cyclone on vegetation structure was the opening-up of the forest canopy, which occurred because of both widespread defoliation and tree-felling. Progressive recovery of the canopy over some years will depend on both re-foliation by standing trees and the growth of currently-small stems and tree-crowns to replace those lost during the cyclone. In the meantime, we expect that the canopy opening would have a variety of ecological effects, including an increased abundance of plant species and life-forms which, in the understorey of intact rainforest, are limited by shading. These include grasses, many herbaceous species, vines, scramblers (including the lawyer cane *Calamus* spp), and pioneer trees (see also Webb 1958, Olsen and Lamb 1986, Laurance *et al*. 2006). Responses of this type apparent in the present study are the increased occurrence of vine tangles, vine towers and recently-germinated seedlings of native vines and early-successional trees (e.g., species of *Polyscias*, *Melicope*, *Homalanthus* and *Alphitonia*) in sites which had least canopy cover six months after the cyclone. The response of the vines was one of biomass and growth habit alone, as the density of vine stems did not increase after the cyclone. Scramblers, which are likely to be slower-growing, had retained the signature of 2003 canopy openness.

In the absence of further disturbance, these open-canopy opportunists would be expected to decline as the tree canopy recovered. Indeed, contemporary rainforests in the Australian tropics have evolved under a climatic regime in which severe cyclones are likely to recur a number of times within the lifespan of a mature tree (Webb 1958, Turton 2008). However, if repeated disturbance to the canopy becomes too frequent, a vigorous growth of herbaceous ground cover may suppress the recruitment of tree seedlings, and a proliferation of leafy vine tangles and towers would not only suppress seedling recruitment but also may smother existing saplings and smaller trees, slowing or reversing their growth, and potentially leading to dramatic changes in the structure and composition of the forest.

Such a stunted forest situation was described by Webb (1958) for lowland rainforests adjacent to the study region, which he termed "cyclone scrubs". This region appears especially "cyclone-prone", and has experienced several severe cyclones during the past 150 years (Turton 2008). The type of rainforest targeted for the present study is floristically very species rich, and includes many threatened plant species, but its biodiversity is considered by management agencies to be under threat (EPA 2007). This study's results suggest a currently-unresolved tension between a tendency for recovery through post-cyclone tree growth and germination versus a tendency for vine proliferation and herbaceous growth, in both fragments and continuous forest.

Most previous cyclones have decreased considerably in strength before reaching the inland Atherton Tablelands, but the possibility of increased cyclone severity with anticipated global climate change (Hughes 2003) raises the prospect that further areas will take on the attributes of "cyclone scrubs", especially since logging has provided episodes of canopy damage in the relatively recent past. Even if the tree canopy prevails, post-cyclone germination recorded in this study was dominated by early-successional species. Since at least some early-successional tree species may be relatively vulnerable to cyclone damage in the Wet Tropics (Bruce *et al*. 2008, Curran *et al*. 2008), repeated disturbance by cyclones may cause a shift in floristic composition away from mature-phase species.

These processes would affect both fragments and continuous rainforest. However, there is, additionally, a significant potential for interaction between fragmentation and cyclone effects in terms of pathways of post-cyclone recovery or degradation. Fragmentation is likely to affect several processes which govern plant regeneration: the local supply of plant propagules; frugivore-mediated seed dispersal processes, and predator-mediated seed and seedling survival. The increasing anthropogenic establishment of exotic plants in the matrix surrounding the fragments will provide an altered species mix of propagules. This tendency is already apparent in the present study, with fragmentation having the only detectable statistical effect on the diversity of common exotic germinants (so far, mainly herbaceous). Frugivore-assisted dispersal is likely to be especially important in post-cyclone recovery processes within rainforests (Olsen and Lamb 2006, Hjerpe and Hedenas 2001, Franklin *et al*. 2004). A fragmentation-induced deficit of vertebrate frugivores most capable of dispersing large-seeded plants could reduce recruitment of mature-phase trees (Moran *et al*. 2004), while reforestation plantings using fleshy-fruited exotic plants may, in future, add more strongly invasive trees whose dispersal into remnant patches is aided by fragmentation-tolerant frugivores (Kanowski *et al*. 2005, Buckley *et al*. 2006). Herbivore and seed-predator populations are also known to have strong influences on plant recruitment, and to be affected by rainforest fragmentation, in Australia (Harrington *et al*. 1997, 2001, Wahungu *et al*. 2002).

CONCLUSIONS

It seems clear from this and other studies of Cyclone Larry's effects on rainforest vegetation that the extent to which a site was fragmented by land clearing had little influence on its vulnerability to short-term impact from the strong, patchy and turbulent cyclonic winds. However, longer-term recovery trajectories in fragments are likely to diverge from those in continuous rainforest due to altered processes of seed dispersal and recruitment. The outcome of these processes is unpredictable with current knowledge, therefore longer-term monitoring is desirable, both to increase scientific understanding, and to inform the process of forest management. A better understanding of the interaction between cyclone effects and fragmentation would enable a better-targeted choice of mitigating measures. For example, using revegetation to enlarge remnant forest patches or to create corridor linkages between them is unlikely to reduce the risk of short-term cyclone impact, although often desirable for other reasons (perhaps including post-cyclone recovery).

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Table 1. Attributes measured at each site and their sample sizes in 2003 and 2006. The last four columns are numbers of measurements per transect (tran) and per site.

Variable	Description	Measurement method	Unit	/tran 2003	/site 2003	/tran 2006	/site 2006
Canopy:							
tree height	Height of tallest tree	Rangefinder and clinometer measurement in 5 X 5 m plot	m	0	0	2	8
cover photo	Cover of foliage & branches >2m.	Projected foliage cover from digital photograph[1]	%	10	80	2	8
cover estimate	Cover of foliage & branches >2m.	Projected foliage cover visually-estimated[1]	%	0	0	2	8
Ground:							
cover	10 ground-cover attributes	Visual estimate % cover of features within 0.5 m of the ground[2]	%	2	16	2	8
debris counts	2 coarse woody debris attributes	Counts of line-intercept with debris in 5 diameter categories[3]	no./50 m	1	8	1	4
Stems (dbh)[4]:							
trees <2.5 cm	Woody stem density <2.5 cm	Count of woody stems <2.5 cm dbh in 50 m by 2 m transect	no./ha	1	8	1	4
trees 2.5-10 cm	Woody stem density 2.5-10 cm	Count of woody stems 2.5-10 cm dbh in 50 m by 4 m transect	no./ha	1	8	1	4
trees 10-20 cm	Woody stem density 10-20 cm	Count of woody stems 10-20 cm dbh in 50 m by 10 m transect	no./ha	1	8	1	4
trees 20-50 cm	Woody stem density 20-50 cm	Count of woody stems 20-50 cm dbh in 50 m by 10 m transect	no./ha	1	8	1	4
trees 50-100 cm	Woody stem density 50-100 cm	Count of woody stems 50-100 cm dbh in 50 m by 10 m transect	no./ha	1	8	1	4
trees >100 cm	Woody stem density >100 cm	Count of woody stems >100 cm dbh in 50 m by 10 m transect	no./ha	1	8	1	6
damage rates	6 woody stem damage attributes	No. of damaged stems (in 4 damage levels) in each diameter class[5]	no./ha	1	8	1	4 or 6
Vines/ scramblers:							
vine densities	2 vine density attributes	Count of vine stems <2.5 and >2.5 cm dbh, in 50 m by 4 m transect[6]	no./ha	1	8	1	6
vine towers/tangles	2 attributes: vine towers, tangles	Frequency in 5X5 m plots[7]	count 0-8	0	0	2	8
scrambler thickets	Thorny scrambler thickets	Frequency in 5X5 m plots[7]	count 0-8	0	0	2	8
New seedlings	2 attributes (native, exotic species)	Number of common germinant species, native and exotic[8]	no. of spp.	0	0	1	1

[1] Canopy cover in 2003 was estimated at 5 points within 2 circles of 5 m radius (78.5 m2); in 2006 3 canopy variables were measured once in each of two 5x5 m squares

[2] Ground cover in 2003 was estimated in 2 circles of 5 m radius (78.5 m2); in 2006 in two 5x5 m squares: % of area occupied by each of: graminoid (grasses, sedges), fern (including fern allies), seedling (native rainforest seedlings), forb (other herbaceous plants), tree boles (including buttresses and vine stems), litter (leaves and twigs < 2.5 cm diameter), soil, rock (>= 2 mm smallest dimension), fine woody debris (2.5-10 cm diameter), coarse woody debris (>= 10 cm diameter). Cover of these attributes summed to 100%.

[3] Wood pieces > 1 m long on the ground, in classes 2.5-10 and >10 cm diameter used in analyses (field counts 2.5-10, 10-20, 20-50, 50-100, >100 cm)

[4] Stems were only counted if >0.5 m high; dbh is diameter at 1.3 m above ground.

[5] Structural damage to live plants: 1 = defoliation and smaller branches broken; 2 = larger branches broken, 3 = trunk snapped; 4 = tree pushed over at >45° angle or uprooted.

[6] Vine densities - climbing plants' stems; size classes were <2.5, 2.5-10, >10 diameter at 1.3 m above ground.

[7] Vine life form attributes and thorny scramblers were measured in 2006 only, present/absent in each of two 5x5 m squares; "vine towers", columns over and smothering trees, "vine tangles" dense masses of interwoven vine stems; "thorny scrambler thickets" thickets of spiny vines/shrubs, including *Calamus*, *Lantana*, *Rubus*.

[8] A list of common recently-germinated seedlings was made in each transect; these were compiled to yield a list for each site.

Table 2. Mean values of vegetation attributes in continuous forest (C) and fragment (F) site-types (S-t; N=8 of each), before the cyclone (B: 2003) and 3-6 months after it (A: 2006). "% diff" is the mean of the changes across sites[1]. "N" indicates measurement not made or comparison not possible.

	Before		After		ANOVA results[2]			Before	After	%diff
Attribute[1]	C	F	C	F	Time	S-t	TXS-t	C&F	C&F	C&F
Canopy cover (%)	77	75	72	65	B**	C*	ns	76	69	-10
Tallest tree height (m)	N	N	24	25	N	ns	N	N	25	N
Quadrat ground cover (%):										
Litter	43.0	39.7	52.5	58.7	A***	ns	AF**	41	56	38
Debris 2.5-10 cm	5.2	4.6	9.0	8.4	A***	ns	ns	4.9	8.7	85
Debris >10 cm	4.0	3.6	6.1	5.8	A**	ns	ns	3.8	5.9	61
Soil	26.7	33.1	13.2	8.7	B***	ns	BF**	30	11	-61
Rock	3.6	4.4	2.0	2.1	B***	ns	ns	4.0	2.1	-43
Tree boles	6.1	5.6	4.3	4.5	B***	ns	ns	5.8	4.4	-23
Seedlings	4.5	4.0	4.5	4.3	ns	ns	ns	4.2	4.4	8
Graminoids	2.3	2.2	2.9	3.2	ns	ns	ns	2.2	3.0	32
Forbs	2.0	2.5	2.7	3.8	A*	ns	ns	2.3	3.2	46
Ferns	2.6	0.4	2.8	0.5	ns	C**	ns	1.5	1.6	4
Intercept debris counts (no. per 50 m line intercept):										
2.5-10 cm dbh	10.6	11.3	19.0	21.8	A***	ns	ns	11	20	97
> 10 cm dbh	4.5	4.7	6.6	8.9	A**	ns	ns	4.6	7.7	84
Standing tree[3] densities (no. per hectare):										
< 2.5 cm dbh	18259	10345	12563	8369	B***	C**	BC*	14302	10466	-25
2.5-10 cm dbh	3875	3245	2389	1634	B***	C*	ns	3560	2012	-44
10-20 cm dbh	568	449	396	361	B***	ns	BC**	508	378	-25
20-50 cm dbh	261	214	260	214	ns	ns	ns	238	237	1
50-100 cm dbh	79	76	66	71	ns	ns	ns	77	69	-10
>100 cm dbh	6.3	7.5	2.5	3.7	B***	ns	ns	6.9	3.1	-53
Standing tree[3] damage %:										
< 2.5 cm dbh	0.0	0.0	4	10	B	F**	N	0	7	7
2.5-10 cm dbh	0.0	0.0	22	48	B	F***	N	0	35	35
10-20 cm dbh	0.0	0.0	30	60	B	F**	N	0	45	45
20-50 cm dbh	0.0	0.0	41	68	B	F*	N	0	55	55
50-100 cm dbh	0.0	0.0	64	80	B	ns	ns	0	72	72
>100 cm dbh	0.0	0.0	88	100	B	ns	ns	0	95	95
Special life forms (no. per hectare (density) or frequency score):										
Vine density <2.5 cm	5769	3419	4538	3719	ns	C*	ns	4594	4128	-6
Vine density >2.5 cm	427	314	220	178	B***	ns	ns	371	199	-39
Vine tower	N	N	0.3	1.0	N	ns	N	N	0.6	N
Vine tangle	N	N	0.4	1.9	N	F*	N	N	1.1	N
Scrambler thicket	N	N	0.3	2.8	N	F*	N	N	1.5	N
Germination (no. of abundant recently-germinated seedling species in four transects each 50 X 10 m):										
Native	N	N	3.6	5.8	N	ns	N	N	4.7	N
Exotic	N	N	0.8	2.8	N	F*	N	N	1.8	N

[1] Units of measurement for attributes are given in Table 1. % diff =100(after-before)/ before.

[2] Results of either two-factor repeated-measures ANOVA or t-tests (by randomisation, for variables measured only in 2006): letters show the time (B or A) or site-type (C or F) for which values were greatest;* P<0.05, **P<0.01, ***P<0.001.

[3] Standing trees were live stems not fallen or snapped (i.e. damage levels 0-2); damage % is the % of these stems showing removal of major or minor branches and leaves (levels 1 or 2).

Significance levels are not given for percent tree damage comparisons over time because all damage levels "before" were taken as zero. Trees < 2.5 cm diameter were >0.5 m tall.

Table 3. Relationships between vegetation attributes relevant to post-cyclone responses to disturbance and potential causal agents (distance from the cyclone's track and canopy cover before and after the cyclone). Values are Pearson's r, across 16 sites, * *P*<0.05, ***P*<0.01.

	Vine tangle	Vine tower	Scrambler thicket	Exotic germinants*	Native germinants*	Tree germinants*	Canopy 2006	Canopy 2003
Northwards distance	-0.48	-0.39	-0.36	-0.22	-0.40	-0.49	0.74**	0.36
Canopy 2003	-0.18	-0.31	-0.55*	-0.38	-0.19	-0.18	0.15	
Canopy 2006	-0.59*	-0.73**	-0.22	-0.42	-0.52*	-0.63**		

* 30 native species in total, comprising 13 trees (mainly species considered characteristic of early successional stages), 8 vines, two scramblers; 9 exotic species in total, comprising 2 vines, no trees. The remaining species were mainly low-growing herbaceous plants.

Figure legends

Figure 1. Map of the Atherton Tablelands showing study sites (continuous forest numbered 1-8; fragments numbered 9-16), and the path of Cyclone Larry. In the northwest section of the map the rainforest areas are continuous with large areas of eucalypt forest (not mapped).

Figure 2. Multidimensional scaling ordination plot of variation among sites in 10 ground cover characteristics, before (2003: squares) and after (2006: circles) the cyclone; C continuous forest (shaded symbols) and F forest fragments (open symbols). Vector locations and lengths indicate the pattern and strength of association of each variable with the ordination space; FWD, CWD: woody debris 2.5-10 cm, >10 cm diameter respectively.

Figure 3. Damage to woody stems at 16 sites within different diameter (cm) classes, and in relation to the sites' positions on a northward axis perpendicular to the cyclone track. (a) % of standing stems (not fallen or snapped) showing damage to branches or foliage; (b) % of all stems extremely damaged (fallen or snapped). Lines were fitted in Microsoft Excel with third-order polynomial.

Figure 4. The pattern of similarity in cyclone effect on vegetation structure at 16 rainforest sites, from principle components analysis. Attributes (and their absolute correlations with Axis 1) were the changes between 2003 (pre-cyclone) and 2006 (post-cyclone) in: canopy cover (0.89), litter cover (0.41), debris intercept count (0.24), debris quadrat cover (0.92), standing stem density (>20cm diameter; 0.30), % of standing trees damaged (0.88), % of all trees with extreme damage (0.92); see Table 1 for details). Bracketed numbers on the graph are the percent of total variation explained by each axis.

Figure 5. The relationship between overall cyclone effect at 16 rainforest sites (from principle component analysis of change in vegetation structure, see Figure 4) and their positions on a northward axis perpendicular to the cyclone track (vertical dotted line shows track's position). Line of best fit is a third-order polynomial.

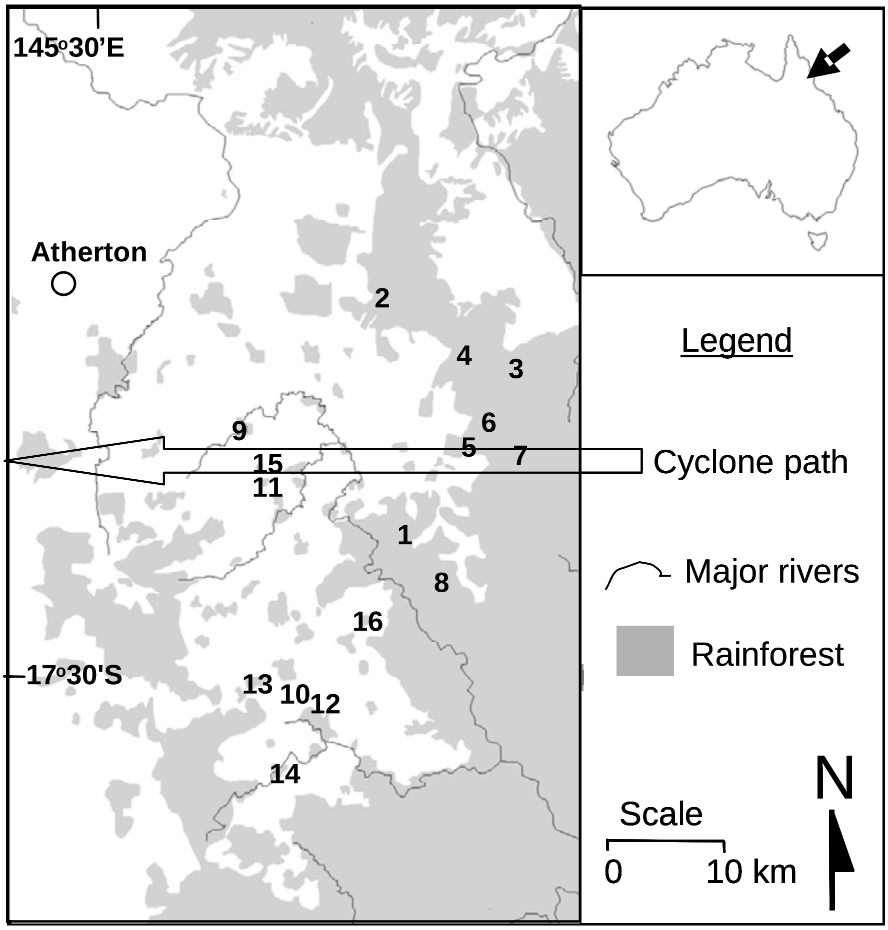

145°30'E
Atherton
2
4
3
6
9
5
7
15
11
1
8
16
17°30'S
13
10
12
14
Legend
Cyclone path
Major rivers
Rainforest
Scale
0
10 km
N

Figure 1.

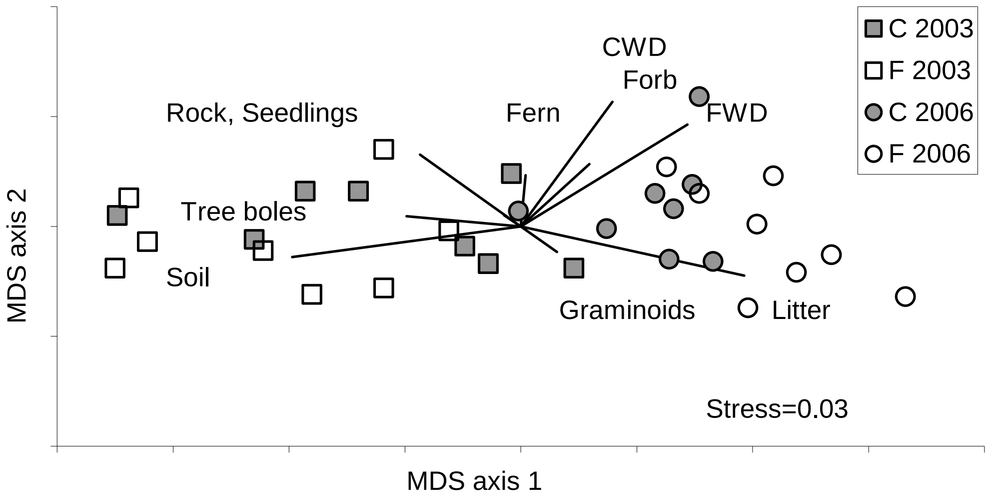
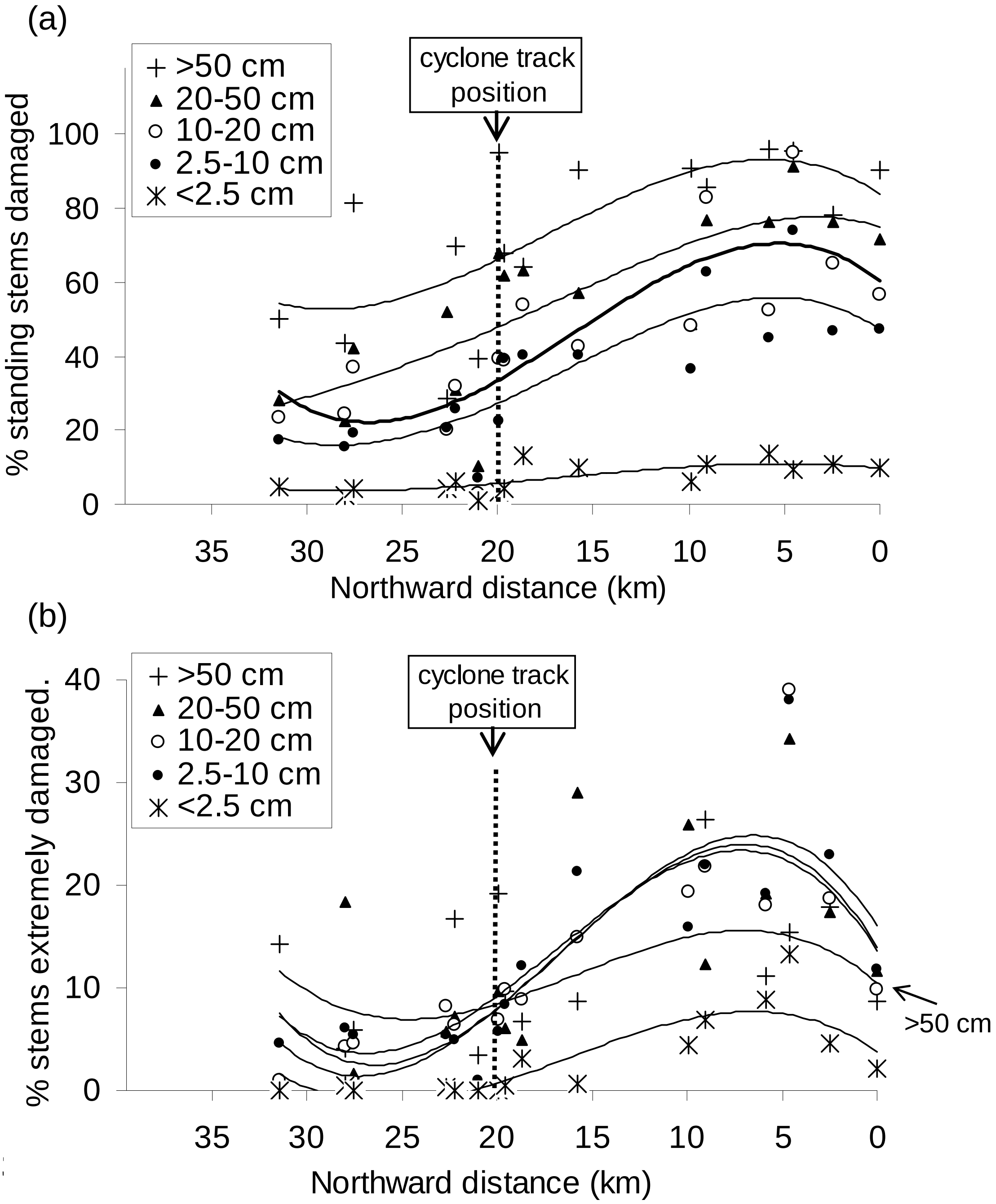

■ C 2003
□ F 2003
● C 2006
○ F 2006
CWD
Forb
Rock, Seedlings
Fern
FWD
Tree boles
Soil
Graminoids
Litter
Stress=0.03
MDS axis 2
MDS axis 1

Figure 2.


(a)
+ >50 cm
▲ 20-50 cm
○ 10-20 cm
● 2.5-10 cm
✳ <2.5 cm
cyclone track position
% standing stems damaged
100
80
60
40
20
0
35
30
25
20
15
10
5
0
Northward distance (km)
(b)
+ >50 cm
▲ 20-50 cm
○ 10-20 cm
● 2.5-10 cm
✳ <2.5 cm
cyclone track position
% stems extremely damaged.
40
30
20
10
0
35
30
25
20
15
10
5
0
>50 cm
Northward distance (km)

Figure

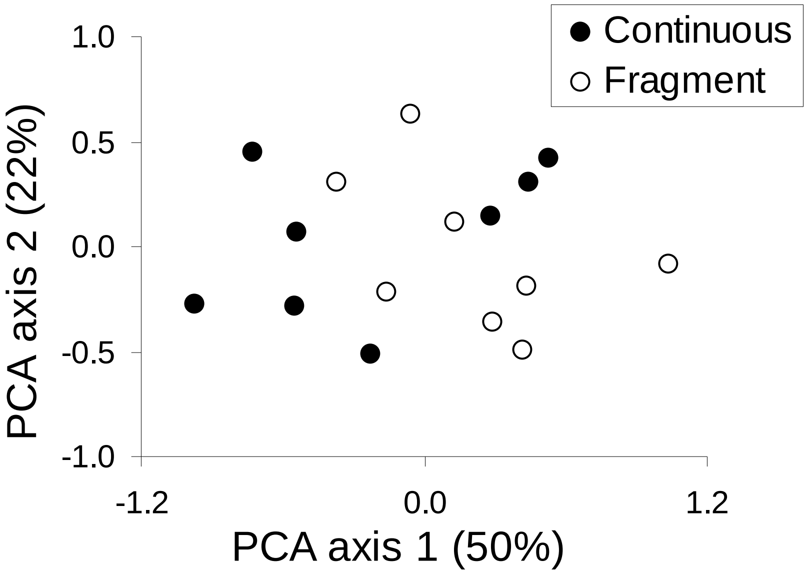

● Continuous
○ Fragment
1.0
0.5
0.0
-0.5
-1.0
PCA axis 2 (22%)
-1.2
0.0
1.2
PCA axis 1 (50%)

Figure 4.

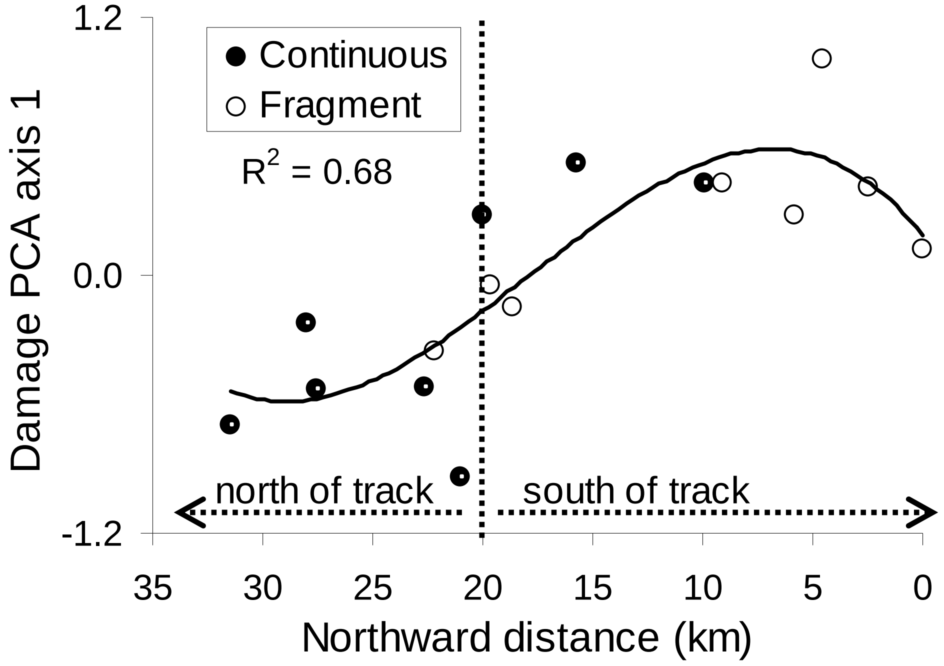

1.2
0.0
-1.2
Damage PCA axis 1
● Continuous
○ Fragment
R^2 = 0.68
north of track
south of track
35
30
25
20
15
10
5
0
Northward distance (km)

Figure 5.