Do edge effects increase the susceptibility of rainforest fragments to structural damage resulting from a severe tropical cyclone?

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Abstract If changes in the structural characteristics of rainforest at edges are caused by wind, then physical damage from a tropical cyclone might be greatest at edges or in small fragments that have a high proportion of edge. We tested whether this was true of a fragmented rainforest landscape impacted by a category 4 severe tropical cyclone in March 2006. Six structural variables (canopy cover, canopy height, cover of ground vegetation, leaf litter, stem density and counts of woody debris) were surveyed at 18 rainforest sites (six small linear remnants, and both edges and interiors of six large remnants) on the Atherton Tableland in north-eastern Queensland, Australia. Data collected 7 and 12 months after the passage of Cyclone Larry were compared with an identical survey conducted 4 years prior to the cyclone. The cyclone had large effects across many components of forest structure. However, sites within 30 m of forest edges in small and large remnants were not impacted more than the interiors of large remnants. It is likely that the high wind intensity from severe tropical cyclones overrides the modest wind protection provided by surrounding forest. The cyclone’s effects were highly patchy at local scales (0.5–1.0 km), leading to an increase in among-site variation in forest structure and the disappearance of significant spatial autocorrelation among large remnant edge-interior site pairs which had existed prior to the cyclone. The main effect of Cyclone Larry at these study sites was to increase the spatial heterogeneity of forest structure at local scales.

Key words: canopy cover, edges, hurricane, spatial autocorrelation, wind damage.

INTRODUCTION

Cyclones, hurricanes or typhoons are intense tropical storms with strong rotating winds that can reach over 350 km h\(^{-1}\) (McGregor & Nieuwolt 1998). Roughly 80 such storms form across the world each year (Lugo et al. 2000), with some of these causing repeated disturbances to tropical rainforests of the Caribbean (Lugo et al. 2000), islands in the Western Pacific (Franklin et al. 2004), parts of south-east Asia (Mabry et al. 1998) and the Wet Tropics of north-eastern Australia (Webb 1958; Turton 2008; Turton & Stork 2008).

Tropical rainforests are structurally complex ecosystems that sustain a diverse and specialized biota (Kikkawa 1990; Reagan & Waide 1996; Kanowski et al. 2003; Catterall et al. 2004). The upper canopy provides unique resources and shading which buffers the microclimate below (Walsh 1996), creating strong vertical abiotic and biotic gradients (Turton & Siegenthaler 2004; Stork & Grimbacher 2006). Tropical cyclones can cause substantial damage to the structure of rainforests, disrupting such microclimatic gradients (Turton 1992; Bellingham et al. 1996; Turton & Siegenthaler 2004), which can affect the rainforest biota for many years afterwards (Zimmerman et al. 1996; Vandermeer & de la Cerda 2004). When strong cyclonic winds meet rainforest trees, the resulting damage can range from partial to complete defoliation, branch loss and even toppling and uprooting of entire trees (Bellingham 1991; Tanner et al. 1991; Bellingham et al. 1992; Imbert et al. 1996; Lugo et al. 2000). This damage can occur at a range of spatial scales, and can be influenced by topography and distance from cyclone track (Boose et al. 1994; Everham & Brokaw 1996; Mabry et al. 1998; Lugo et al. 2000; Caterall et al. 2008). Different vegetation types, successional stages and individual plant species have been shown to vary in their ability to resist wind damage (Everham & Brokaw 1996; Imbert et al. 1996; Franklin et al. 2004; Ostertag et al. 2005).

Rainforest fragmentation is another form of disturbance that can affect the plants, animals and physical structure of rainforests, in both positive and negative*Corresponding author.

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ways (Laurance et al. 2002; Nascimento & Laurance 2004). Although there are several sometimes synergistic factors driving fragmentation effects (Ewers & Didham 2006), edge effects are thought to cause some of the strongest changes to rainforest plant and animal communities and to key processes that maintain forest diversity (Murcia 1995; Didham et al. 1996; Laurance et al. 2002). The increased amount of edge resulting from forest fragmentation has been associated with increased tree mortality and damage, which is thought to be the result of increased windthrow and microclimate changes near forest edges (Laurance 1991; Laurance et al. 1998; Nascimento & Laurance 2004). Therefore, it has been suggested that rainforest vegetation in fragmented landscapes may be more vulnerable to wind damage resulting from cyclones (Laurance 1997; Laurance & Curran 2008). The quantification of cyclone impacts on rainforest ecosystems is most accurate and informative when pre-cyclone data exist (Tanner et al. 1991). However, we are not aware of any previous study that has directly compared the extent of cyclone-induced structural damage between forest edges and interiors using before–after measurements.

The present study uses pre-cyclone data on vegetation structure that were collected in March 2002 as part of a study examining edge and fragmentation effects on beetle assemblages inhabiting 18 fragment sites on the Atherton Tableland in north-eastern Australia (Grimbacher et al. 2006). A severe tropical cyclone, Cyclone Larry, traversed the study landscape on 20 March 2006 (Turton 2008). Two further surveys quantifying rainforest structural integrity were conducted approximately 7 and 12 months post-cyclone, using the same methodology that was applied in 2002, at the same sites.

**METHODS**

**Study area and design**

The Atherton Tablelands (17°–17°30’S, 145°30’–145°45’E) is a plateau about 700–850 m above sea level, 25–50 km from the coast, with (mostly) fertile, basalt-derived soils (Nix 1991). Across the landscape a strong spatial gradient in climate (particularly precipitation) creates complex vegetation patterns (Tracey & Webb 1975). Much of the upland rainforest inhabiting the Atherton Tablelands was converted to pasture 80–100 years ago, producing a landscape mosaic of rainforest remnants of varying sizes scattered in a matrix that consists mainly of pasture (Winter et al. 1987; Catterall et al. 2004).

Structural attributes were measured at 18 forest sites across the Atherton Tablelands (see Grimbacher et al. 2006) for map and further details). Sites were spread across an area spanning 27 km in a north-south direction and 17 km in an east-west direction. Cyclone Larry tracked in a westerly direction, roughly along latitude 17°23’S once it reached the Atherton Tablelands (Turton 2008). At this point in space and time it was estimated to be a category 3 cyclone (Turton 2008). The track almost perfectly bisected the north-south spread of rainforest sites, with the most northern and southern sites being 15 and 11 km respectively from the cyclone track.

There were six replicate sites in each of three habitat categories: small rainforest remnants, edges of large rainforest remnants and the interiors of these large rainforest remnants. At each site field measurements were conducted along a 100 m transect. Transects at the edges of large remnants and those in the small remnants were both within 30 m of the forest-pasture ecotone. The six small remnants (0.75–4.8 ha) were linear in shape (50–80 m wide) with transects positioned along their midlines, 20–30 m from the nearest edge. The six large remnants (40–400 ha) were rounder in shape, and each contained an edge transect and an interior transect. Edge transects were located approximately 30 m from, and parallel to, a remnant’s edge, and interior transects were positioned over 200 m from the edge, and away from tree fall gaps. The distance between edge and interior sites within a remnant was maximized (500–1000 m) by spatially offsetting them as far as possible, although they remained essentially paired. Sites in large and small remnants were interspersed across the landscape as far as possible.

Most post-cyclone surveys could be conducted on the original transects established in 2002. However, at some sites this was not possible due to vigorous sting ing tree (Dendrocnide spp.) growth and hazardous forest debris, so transects were positioned as close as possible to the original location.

**Field measurements**

Seventeen structural variables were quantified at each site (Table 1) prior to Cyclone Larry in March 2002, and on two occasions post-Cyclone Larry in October 2006 and March 2007. At ten equidistant points along the 100 m transect, a 5-m rope was laid perpendicular to the transect line, alternately to its right and left, to mark the diameter of a circular quadrat (2.5 m radius). Within each quadrat, canopy cover, canopy height, ground cover and leaf litter cover were estimated visually. Leaf litter dry weight was quantified by weighing leaf litter collected from five 0.25-cm² quadrats within a site (total area 0.3125 m²). The density of living woody stems was quantified by counting the number of stems above 2 m high in each of six size classes (Table 1), within each quadrat. Woody debris was mea-
Table 1. Summary of structural attributes measured at each site

<table>
<thead>
<tr>
<th>Structural variable and unit</th>
<th>Method</th>
<th>No.†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (%)</td>
<td>Visual estimation of vegetation cover &gt; 2 m within circular quadrat (2.5 m radius).</td>
<td>10 (av.)</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>Visual estimation of canopy height (upper layer).</td>
<td>10 (av.)</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td>Visual estimation of vegetation cover ≤ 2 m within circular quadrat (2.5 m radius).</td>
<td>10 (av.)</td>
</tr>
<tr>
<td>Leaf litter – cover (%)</td>
<td>Visual estimation of leaf litter covering the ground (excluding area taken by trees) within circular quadrat (2.5 m radius).</td>
<td>10 (av.)</td>
</tr>
<tr>
<td>Leaf litter – volume (g/0.0625 m²)</td>
<td>Dry weight of leaf litter (excluding woody debris) from 0.0625 m².</td>
<td>5 (tot.)</td>
</tr>
<tr>
<td>Woody stems (stems/ha)</td>
<td>Counts of all living stems within circular quadrat (2.5 m radius), in size classes; (≤3, 3–5, 5–10, 10–20, 20–50, &gt;50 cm d.b.h.).</td>
<td>10 (av.)</td>
</tr>
<tr>
<td>Woody debris (counts/5 m)</td>
<td>Counts of all woody debris contacts made with 5 m rope, in size classes; (≤3, 3–5, 5–10, 10–20, 20–50, &gt;50 cm).</td>
<td>10 (av.)</td>
</tr>
</tbody>
</table>

†The number of sampling points along a 100 m transect. av., averaged; tot., total.

sured by counting the number of wood contacts with the 5-m rope, within six diameter size classes (Table 1).

Data analysis

The multiple (five or ten) within-site measurements obtained for each structural variable were averaged to create a single value for each site and for each sampling occasion. In order to reduce the overall complexity and possibly redundant variables, the two measures of leaf litter, the six size class counts for stem density and the six size class counts for woody debris were condensed into three separate variables. To obtain an overall measure of leaf litter, the leaf litter cover and dry weight values were each range-standardized (site value minus minimum value)/(maximum minus minimum) and then averaged. A similar procedure was separately applied to the stem density and woody debris size class data. This procedure of range-standardizing each size class and then averaging across them allowed each size class to make an equal relative contribution. The resulting six structural variables were then (re)range-standardized. In condensing the number of variables we acknowledge that some more subtle patterns may be obscured (e.g. responses of separate size classes for stem density). However, we feel that this is appropriate considering that the intensity of sampling, although adequate to get an overall measure of cyclone damage, may not have been sufficient to accurately quantify patterns among individual size classes.

To assess the patterns among the 18 rainforest sites and three sampling occasions, we analysed the six structural variables using non-metric multidimensional scaling ordination (Plymouth Marine Laboratory 2002) and permutational multivariate analysis of variance (PERMANOVA; Anderson 2005). Both analyses used the Euclidean distance measure of pairwise dissimilarity between sites. To relate the patterns in the ordination to specific aspects of forest structure, correlations were performed between each axis and each of the six structural variables.

The effects of year (cyclone) and site type (fragmentation) were tested with a two-way factorial PERMANOVA, with 4999 permutations. Because distance from cyclone track could be an important factor influencing degree of cyclone damage (Boose et al. 1994; Caterall et al. 2008), spatial position (eastings and northings) were added to the model as covariates. The north–south measure accounted for variation in site distances from the cyclone track, but it was also deemed important to include an east–west spatial measure because Cyclone Larry lost some intensity as it moved inland (Turton 2008). Post hoc pairwise tests were conducted with 4999 permutations to identify differences among groups. Because the study design uses repeated-measures (in which sites are subjects), which cannot be accounted for within the factorial PERMANOVA analyses, the potential interaction between fragmentation and cyclone impact was also investigated by conducting single-factor PERMANOVAs to examine differences among site types for: (i) structural attributes in each year separately; and (ii) the change in structural attributes between years (2002–2006 and 2002–2007). Structural change was measured as the post-cyclone value minus pre-cyclone value of each of the six attributes at each site. Difference among years in the pre- and post-cyclone structural variability of sites grouped by site type was tested with permutational analysis of multivariate dispersions (PERMDISP; Anderson 2004). This analysis calculated the distance of observations to their site centroids and then compares the average of these distances among year groups.

Spatial autocorrelation in structural attributes was explored by calculating bivariate correlation coefficients in overall structure between the paired edge and interior sites across the large remnants (n = 6), with
RESULTS

The full PERMANOVA model showed that the effect of year was the strongest and was highly statistically significant \((F = 14.71, \text{d.f.} = 2, P < 0.001)\). The effect of site type was also significant \((F = 4.62, \text{d.f.} = 2, P < 0.001)\), but there was no interaction \((F = 0.71, \text{d.f.} = 4, P = 0.79)\). Spatial position in the landscape (the covariates) was also statistically significant \((F = 3.32, \text{d.f.} = 1, P = 0.002)\). Pairwise tests showed that each of the 3 years was significantly different from each other \((P < 0.001\) for each comparison). The effect of year can be graphically seen in Figure 1a where there is little overlap among years. Nevertheless, some sites showed limited structural damage after the cyclone, and were clustered among or near the pre-cyclone group in the ordination (Fig. 1a). In this ordination, axis 1 was significantly \((P < 0.001)\) positively correlated with canopy cover, canopy height and stem density, and negatively correlated with ground cover, all structural variables directly or indirectly impacted by the cyclone (Table 2). However, interpreting the patterns in Figure 1a is complicated by the fact that several variables were correlated with each axis, and three variables were correlated with both axes. For example, canopy cover was positively correlated with axis 1 but negatively correlated with axis 2. Some variables such as canopy cover, suggested a degree of post-cyclone recovery (e.g. mean canopy cover values for each year were 2002 = 72%, 2006 = 52% and 2007 = 61%). However, in the ordination, the 2007 sites did not cluster closer to the 2002 sites. A likely reason was that another variable, ground cover, with the strongest correlation to axis 1 \((r = -0.85)\), showed a response time lag. The mean ground cover values in 2002 = 9%, 2006 = 12% and 2007 = 18% show that understory plant growth took some time to respond to the increased light that was able to penetrate the cyclone-damaged canopy. Thus in the short amount of time since the passage of Cyclone Larry, some variables show a degree of recovery, while others are still responding and changing to the initial disturbance.

The structural variability of sites grouped by site type increased after the passage of Cyclone Larry, with the standard deviations of site values being much larger in the post-cyclone years regardless of site type (Fig. 1b). The PERMDISP analysis showed that sites grouped by site type, significantly differed in their variability among years \((F = 5.79, \text{d.f.} = 2, P = 0.007)\). Pairwise tests showed that the 2002 site grouping was significantly less variable than either the 2006 grouping \((P = 0.008)\) or the 2007 grouping \((P = 0.003)\) while the 2006 and the 2007 site groupings were not significantly different \((P = 0.55)\). The effects of site type were not significant \((F = 0.01, \text{d.f.} = 2, P = 0.99)\) and there was no site type by year interaction \((F = 1.03, \text{d.f.} = 4, P = 0.40)\).

**Table 2.** Correlation coefficients between structural variables and ordination axes

<table>
<thead>
<tr>
<th>Structural variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover</td>
<td>0.40**</td>
<td>-0.35*</td>
</tr>
<tr>
<td>Canopy height</td>
<td>0.75***</td>
<td>-0.46***</td>
</tr>
<tr>
<td>Ground cover</td>
<td>-0.85***</td>
<td>0.02</td>
</tr>
<tr>
<td>Leaf litter</td>
<td>0.25</td>
<td>0.83***</td>
</tr>
<tr>
<td>Stem density</td>
<td>0.72***</td>
<td>0.31*</td>
</tr>
<tr>
<td>Woody debris</td>
<td>-0.12</td>
<td>-0.18</td>
</tr>
</tbody>
</table>

\(\ast P < 0.05, \ast\ast P < 0.01, \ast\ast\ast P < 0.001\)
For sites grouped by fragmentation in the full PERMANOVA model, interiors and small remnants were significantly different ($P < 0.001$), edges and interiors were marginally different ($P = 0.043$), but edges and small remnants were not significantly different from each other ($P = 0.21$). However, these results were not apparent in the ordination plot (Fig. 1b). Also, the two-factor PERMANOVA may have overestimated the effect of site type because it could not incorporate the repeated-measures nature of the data.

When separate one-way PERMANOVA's were performed for each year, further differences emerged. Spatial position was significant in 2002 ($F = 2.39$, d.f. $= 1$, $P = 0.01$) but not in 2006 ($F = 1.67$, d.f. $= 1$, $P = 0.13$) or 2007 ($F = 1.73$, d.f. $= 1$, $P = 0.13$), while site type was marginally significant in 2002 ($F = 2.12$, d.f. $= 2$, $P = 0.044$) and 2007 ($F = 2.26$, d.f. $= 2$, $P = 0.047$) but not 2006 ($F = 1.67$, d.f. $= 2$, $P = 0.14$). In the corresponding pairwise tests, interiors and small remnants were significantly different in 2002 ($P = 0.007$) and only marginally significant in 2007 ($P = 0.063$). All other pairwise tests were not significant. A SIMPER analysis (which identifies the variables with the greatest contribution to the patterns; Plymouth Marine Laboratory 2002) suggested that the underlying causes of these differences, for both years, were lower values of canopy height and woody debris in small remnants. In 2002 there were also some differences between these site types in the density of woody stems, with small remnants containing fewer large trees but more small trees 5–10 cm d.b.h. (see also Grimbacher et al. 2006).

One-way PERMANOVA comparing the change in habitat structure (post-cyclone values minus precyclone values) among site types (with eastings and northings as covariates) showed no significant effects of either site type or spatial position (for changes 2002–2006 site type $F = 0.67$, d.f. $= 2$, $P = 0.71$, position $F = 1.50$, d.f. $= 1$, $P = 0.17$; for changes 2002–2007 site type $F = 1.11$, d.f. $= 2$, $P = 0.36$, position $F = 1.27$, d.f. $= 1$, $P = 0.28$).

There was a significant degree of spatial autocorrelation in the index of overall structure among the edge and interior site pairs from the six large remnants in 2002 ($r = 0.82$, $P = 0.047$). After the cyclone this spatial autocorrelation was no longer present for either 2006 ($r = -0.00$, $P = 1.00$) or 2007 ($r = -0.27$, $P = 0.61$).

**DISCUSSION**

After the passage of Cyclone Larry there were significant changes to the structure of the 18 rainforest sites. Relative to other factors that influenced structure, the effect of the cyclone was by far the largest, although a few sites appeared surprisingly little affected. Post-cyclone measurements in 2006 and 2007 showed a reduced canopy height, canopy cover, stem density and increased cover of ground vegetation, relative to 2002. All these changes are consistent with cyclonic winds knocking down trees, removing branches and opening up the canopy. Similar impacts have been documented in studies of other sites affected by Cyclone Larry (Caterall et al. 2008; Kanowski et al. 2008; Pohlman et al. 2008) as well as in other parts of the Wet Tropics of Australia (Grove et al. 2000), and the world (Tanner et al. 1991; Bellingham et al. 1992; Imbert et al. 1996; Mabry et al. 1998; Franklin et al. 2004; Vandermeer & de la Cerda 2004; Ostertag et al. 2005).

Structural changes to rainforest sites brought about by Cyclone Larry were highly variable at local spatial scales, as indicated by the significantly lower variation among sites before the cyclone than after it, and also by the post-cyclone disappearance of the spatial autocorrelation between paired edge and interior sites 0.5–1.0 km apart. Spatial autocorrelation can result from spatially explicit ecological processes (such as dispersal and competition) or species’ responses to underlying environmental conditions (Wagner & Fortin 2005). The Atherton Tablelands is known for its strong climatic gradient running in a SE-NW direction, with the south-east being distinctly wetter and cooler (Nix 1991). This gradient has been identified as a major influence on the vegetation structure of this region (Tracey & Webb 1975), and thus is likely to be the primary cause of both the significant effect of spatial location in the landscape and the pre-cyclone spatial autocorrelation between the paired edge and interior sites. The autocorrelation may be expected to re-appear in future years as the rainforest structure recovers.

High patchiness of structural damage due to cyclones has also been reported by Pohlman et al. (2008) for cyclone Larry, by Grove et al. (2000) for rainforests in the Daintree region of north-eastern Australia, and by Bellingham et al. (1992) and Imbert et al. (1996) for hurricanes in the Caribbean. At spatial scales of less than 1 km, variation in wind speeds is the result of individual wind gusts from turbulent eddies, convective storm cells and tornadoes (Boose et al. 1994). Variation in the damage sustained by forests at this spatial scale can override underlying patterns caused by topography, vegetation type, distance from cyclone track, or other forms of disturbance such as logging (Boose et al. 1994; Everham & Brokaw 1996; Grove et al. 2000). Thus the heterogeneous damage to remnant rainforest patches observed in the present study may have affected the statistical detection of the underlying patterns related to site type and possibly distance from cyclone track.

The results of this study show that even sites very close (<30 m) to forest edges did not sustain more cyclone damage than interiors. This finding runs contrary to current thinking that edges should be more

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vulnerable than interiors to wind damage from cyclones (Laurance 1997; Laurence & Curran 2008). However, Caterall et al. (2008) found that sites 30–50 m from the edges of fragments 5–40 ha in area on the Atherton Tablelands were not more vulnerable to damage by cyclone Larry than sites 80–260 m from the edge of continuous forest, and Pohlman et al. (2008) also showed that distance to forest edge was not associated with degree of cyclone damage, for several different rainfall edge types. It appears that high wind velocities from severe tropical cyclones override the modest wind protection provided by surrounding forest, thereby removing the influence of edge proximity on wind damage (see also Caterall et al. 2008). This study has shown how cyclones introduce local structural heterogeneity into the landscape, at a scale of hundreds of metres, rather than causing predictable changes to fragmented forest.

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REFERENCES


