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Impacts of cyclone Larry on arboreal folivorous marsupials endemic to upland rainforests of the Atherton Tableland, Australia.

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Running title: Cyclone impacts on arboreal folivores

Abstract

Intense cyclones might be expected to adversely affect populations of arboreal mammals, either directly or as a consequence of the destruction of food resources and other key habitat elements. However, such impacts have rarely been quantified. The present study examined the response of five species of arboreal folivorous marsupials to severe cyclone Larry at nine sites in upland rainforests of the Atherton Tableland, north-east Australia. Sites were originally surveyed for folivores in 1995-7, and then resurveyed in 2006, six to eight months after cyclone Larry had traversed the region. All sites showed evidence of structural damage to vegetation, but overall damage levels (assessed in terms of canopy cover, damage to trees, basal area of dead trees and volume of woody debris) decreased from east to west across the study region. The detectability of rainforest possums increased after the cyclone. For the most commonly observed species, the proportion of individuals observed >5 m from survey transects was correlated with the amount of structural damage to vegetation. To avoid confounding changes in detectability with changes in abundance, only observations close (<5 m) to transects were used to estimate folivore abundance before and after the cyclone. On this basis, there were no significant differences between pre- and post-cyclone abundance estimates for any folivore species. Further, changes in folivore abundance after the cyclone were not correlated with damage to vegetation across sites. Cyclone Larry does not appear to have caused a catastrophic loss of key habitat resources for marsupial folivores at the sites surveyed. The high degree of folivory practiced by marsupial folivores may help make them resilient to cyclone impacts. These conclusions are more robust for three commonly observed folivore species (*Hemibelideus lemuroides*, *Pseudochirulus herbertensis* and *Trichosurus* *vulpecula johnstonii*) than for two less frequently encountered species (*Pseudochirops archeri* and *Dendrolagus lumholtzi*).

Key words: arboreal mammal, hurricane, possum, tree-kangaroo, resilience.

Introduction

Five species of arboreal leaf-eating marsupials inhabit rainforests of the Atherton Tableland, north-east Australia, including three species of ringtail possums (*Hemibelideus lemuroides*, *Pseudochirops archeri* and *Pseudochirulus herbertensis*: Pseudocheiridae), a subspecies of the common brushtail possum (*Trichosurus vulpecula johnstonii*: Phalangeridae) and Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*: Macropodidae) (Winter 1997). The arboreal folivores are an important component of the mammalian biodiversity of the Wet Tropics (Williams *et al.* 1996), have high levels of community recognition (Kanowski *et al.* 2001a), and support a growing ecotourism industry (WTMA 2000).

The effects of cyclones on vertebrates have rarely been quantified (Tanner *et al.* 1991). However, the limited evidence available suggests that cyclones may have significant negative impacts on populations of arboreal folivores. The only comprehensive account is that of Pavelka *et al.* (2003), who found that populations of *Alouatta pigra* (black howler monkey), a folivore/ frugivore, were reduced by 40% following an intense hurricane which completely stripped foliage from a riverine forest in Belize. Some animals were injured during the storm, while surviving individuals were forced to forage on fallen leaves and fruit for several weeks, until the remaining trees began to flush new foliage. Wright (1999) provided a similar anecdotal account of populations of folivorous/ frugivorous lemurs declining by 50% at a site completely defoliated by an intense cyclone in Madagascar.

As a guild, arboreal folivores might be expected to be particularly vulnerable to the impacts of an intense cyclone, for several reasons. First, cyclones can cause extensive defoliation of trees, the impact persisting for several weeks until damaged trees begin to resprout (Webb 1958; Tanner *et al.* 1991). Arboreal folivores would be expected to be very sensitive to the loss of their food resource, because the constraints of arboreality limit their capacity to lay down stores of body fat to help them survive lean periods (Janzen 1978). Second, large trees are particularly susceptible to cyclone damage (Dittus 1985; Brokaw & Walker 1991). Rainforest possums preferentially den in large trees (Kanowski 2004), and the destruction of den trees might kill possums directly, or increase their exposure to predation if individuals were unable to locate alternative den sites. Third, damage to forest structure wrought by a cyclone (e.g., reduction of canopy cover, loss of limbs, snapped or uprooted trees) might be expected to increase the energetic costs of foraging, locomotion and thermoregulation (Laurance & Laurance 1996), which if extreme could affect the survival of folivores in damaged forests.

In the present paper, we quantify the impacts of cyclone Larry on the abundance of arboreal folivorous marsupials in upland rainforests of the Atherton Tableland, north-east Australia. The intensity of the cyclone, combined with the speed at which it traversed the Wet Tropics region, meant that significant damage was caused to upland rainforest sites known to support relatively abundant populations of the arboreal folivores. We compared the abundance of folivores at sites before and after the cyclone, and examined whether changes in folivore abundance were related to the extent of cyclone damage at study sites.

Methods

The study was conducted in upland rainforests of the Atherton Tableland (Fig. 1: 17^{o}30 S, 145^{o}30 E). The study takes advantage of systematic pre-cyclone surveys of the abundance of arboreal folivores at 40 sites in the region (Kanowski *et al.* 2001b). Although these baseline surveys were conducted in 1995-97, a decade prior to the cyclone, the abundance of arboreal folivores appears to be quite stable at sites in intact rainforests in the region (Laurance & Laurance 1996; J. Winter & J. Kanowski, unpublished data, 1973 - 2005).

For the present study, sites were selected on the following criteria: (i) they supported a high abundance of folivores in pre-cyclone surveys; (ii) they were exposed to moderate or severe levels of cyclone damage (assessed as per Unwin *et al.* 1988); and (iii) they were accessible after the cyclone. The first criterion essentially restricted the study to sites above 750 m elevation, the second to sites south of the township of Atherton, while the third reduced the number of potential survey sites to 10. Of these, nine sites were surveyed. The selected sites were located at 760-1180 m above sea level. Seven sites were on nutrient-rich basaltic soils, supporting complex notophyll vine forests, and two on relatively nutrient-poor soils derived from acid igneous rocks, supporting simple notophyll vine forests (Tracey 1982). All sites were within large areas (> 1000 ha) of forest to avoid any confounding effects that forest fragmentation may have on folivore abundance (Pahl *et al.* 1988; Laurance 1990). Adjacent sites were separated by >1 km. All but one site were located on or near ridge tops.

<insert Fig. 1 here>

Surveys of arboreal folivores

Arboreal folivores were surveyed using the methods described in Kanowski *et al.* (2001b). Briefly, surveys were conducted at night, from the period of complete darkness to midnight, using a 30 W spotlight to detect folivores. Surveys were conducted on foot along narrow roads or tracks within the forest (seven sites) or along the forest edge (two sites). Transects were 0.55 to 1.10 km long. Individuals considered to be juveniles (according to size and/ or colouration) were recorded separately from adults. For each observation, the perpendicular distance from the edge of the vegetation along the transect to the folivore was estimated (‘detection distance’).

Baseline surveys were conducted between March 1995 and August 1997, and post-cyclone surveys from September to November 2006 (i.e., six to eight months after cyclone Larry). Four surveys were conducted at each site during each period. This level of effort is sufficient to estimate the abundance of the more commonly encountered folivore species (*H. lemuroides*, *P. herbertensis* and *T. v. johnstonii*) with enough precision to detect major changes in abundance between sites or time periods (Laurance & Laurance 1996; Kanowski *et al.* 2001b). One to three sites were surveyed each night, and survey effort was dispersed across sites over time. Baseline surveys were conducted by one observer (JK); while post-cyclone surveys were split between two observers (JK and JW), each of whom conducted two complete rounds of surveys.

Survey of cyclone damage to vegetation structure

A range of vegetation structural attributes was measured to assess the extent of cyclone damage on two 50 x 10 m plots per site using a standard methodology (Kanowski & Catterall 2007). Attributes included canopy cover, the abundance of trees by diameter class (2.5 – 10 cm, 10 – 20 cm, 20 – 50 cm, >50 cm), damage to trees by diameter class, the basal area of live trees, the basal area of dead trees ('stags'), and the volume of woody debris (>2.5 cm diameter). Canopy cover was determined from digital photographs of the canopy at six points per site, by overlaying a 10 x 10 grid on photographs and counting intersections with vegetation (Kanowski & Catterall 2007). Canopy cover was also estimated visually at six points per site, to enable comparisons with pre-cyclone cover estimates made by the same observer at sites elsewhere in the study region (Kanowski *et al.* 2003). Damage to trees was assessed on a three point scale: 1 = defoliation and terminal branches broken; 2 = major branches broken, 3 = trunk snapped or pushed over. Trees in the last two categories were considered to have experienced 'severe' damage. Vegetation structure was assessed between September and November 2006.

<insert Table 1 here>

Analyses

Preliminary analyses showed that most measures of cyclone damage to vegetation were highly intercorrelated. Consequently, the dataset was reduced to fewer dimensions using principal components analysis (Quinn & Keogh 2002). The first principal component was used as a measure of overall cyclone damage.

So that estimates of folivore abundance were not confounded with changes in the detectability of folivores resulting from cyclone damage to vegetation structure, abundance estimates were restricted to observations made within a defined distance from the transect, within which detectability was uniformly high in both survey periods (i.e., a ‘strip transect’ approach: Kavanagh 1984; Buckland *et al.* 1993; Struhsaker 1997). The width of the strip transect was determined by examining histograms of detection distances for each survey period (Fig. 2), and selecting a threshold distance within which a high proportion of observations were made in both time periods. Folivore abundance was defined as the average number of individuals observed within the strip transect across surveys conducted at each site, standardised to individuals per ha to account for the different transect lengths. Juveniles were excluded from abundance estimates, in part because post-cyclone surveys were restricted to a single season, whereas pre-cyclone surveys were conducted at all months of the year.

<insert Fig. 2 here>

The impacts of cyclone Larry on folivore abundance were analysed by comparison of pre- and post-cyclone abundance data at the nine sites surveyed, using two approaches. First, we tested the hypothesis that the cyclone had affected overall folivore abundance at the study sites, using paired t-tests to compare abundance before and after the cyclone at the nine sites surveyed. Second, we tested the hypothesis that cyclone impacts on folivore abundance were related to the extent of damage to vegetation structure at study sites, by examining correlations between changes in folivore abundance following the cyclone and the overall measure of cyclone damage to vegetatation at each site. To improve normality, abundance data were ln(x + 1) transformed prior to these analyses.

The impact of the cyclone on the detectability of folivores was assessed by comparing the number of folivores detected outside the strip transect before and after the cyclone, using two approaches: (i) using paired t-tests to compare the number of folivores detected outside the strip transect in the two survey periods (based on ln(x+1) transformed counts); and (ii) by examining correlations between damage measures and the proportion of observations made outside the strip transect at each site after the cyclone.

Because the pre-cyclone surveys were conducted by one observer (JK), and post-cyclone surveys by two (JK, JW), observer bias could potentially confound comparison of pre- and post-cyclone abundance estimates. Such bias could result from differences between observers in the number of folivores each observed; and/ or from differences in their estimates of detection distances, particularly whether observations were considered to be within the strip transect. Paired t-tests were used to compare abundance estimates made by the two observers who conducted post-cyclone surveys at each of the nine study sites. Data were ln(x + 1) transformed prior to analysis. To test for observer bias in estimating detection distances, chi-square tests were used to examine whether the total number of observations made of each species within or outside the strip transect by each of the two observers were independent.

Results

Cyclone damage to sites

All sites displayed evidence of cyclone damage, but damage levels were highest in the two most easterly sites, where 48-51% of trees 10-20 cm diameter, 61-67% of trees 20-50 cm diameter, and 75-100% of trees >50 cm diameter had been severely damaged by the cyclone. Across all sites, average damage levels for these size classes were 21%, 32% and 31%, respectively (Table 1).

The various measures of cyclone damage to vegetation structure were reduced to two principal components (Table 2). The first (explaining 65% of the variance in the dataset) contrasted sites which had a high proportion of severely damaged trees in all size classes, large volumes of woody debris and a relatively high basal area of dead trees, with sites retaining a relatively intact canopy. The second component contrasted sites with a large basal area of live trees with other sites. The first factor was used as an overall measure of cyclone damage in subsequent analyses. Overall levels of cyclone damage declined from east to west across the study area (r = 0.83; d.f. = 7; P = 0.006).

<insert Table 2 here>

Impacts of cyclone on folivore abundance

In total, 1079 observations of folivores were made in the study, of which 72 were juveniles. Observations of adults, on which abundance estimates were based, comprised 389 observations made in surveys conducted prior to the cyclone and 618 after the cyclone. In both surveys, *H. lemuroides* was by far the most commonly observed folivore species (58% and 69% of records in pre-and post-cyclone surveys, respectively), followed by *P. herbertensis* (16% and 14%), *T. v. johnstonii* (13% and 11%), *P. archeri* (7% and 5%) and *D. lumholtzi* (5% and 1%). Juveniles of all species were observed in both survey periods, with the exception of *D. lumholtzi* (no juveniles observed in post-cyclone surveys).

<insert Fig. 3 here>

<insert Fig. 4 here>

The great majority of observations of all folivore species were made within 5 m of the edge of transects, in both pre- and post-cyclone surveys (Fig. 2). Consequently, 5 m was chosen as the width of the strip transect: i.e., only observations of folivores within 5 m of the transect were included in abundance estimates.

Overall, there were no significant differences between pre- and post-cyclone abundance estimates for any folivore species (Fig. 3). Further, changes in the abundance of folivores following the cyclone were not correlated with the extent of cyclone damage at each site (results for correlations of damage with changes in abundance for: *H. lemuroides*, $r = 0.56$, $P = 0.12$; *P. herbertensis*, $r = 0.03$, $P = 0.93$; *P. archeri*, $r = 0.31$, $P = 0.42$; *T. v. johnstonii*, $r = -0.04$, $P = 0.93$; *D. lumholtzi*, $r = 0.44$, $P = 0.23$). These results were not confounded by observer bias. The two observers who conducted post-cyclone surveys recorded similar numbers of folivores at the study sites (Fig. 4). The proportion of observations made within the strip transect also did not differ significantly between the two observers (chi-squared tests, d.f. = 1, $P > 0.5$ for all species).

The detectability of the rainforest possums increased following the cyclone. More observations were made >5 m from the transect after than before the cyclone for *H. lemuroides*, *P. herbertensis*, *P. archeri* and *T. v. johnstonii* (paired t-tests, d.f. = 8, P = 0.001, 0.044, 0.010 and 0.031 for each species, respectively). The proportion of observations made >5 m from the transect increased from 18% of total observations, before the cyclone, to 48% of observations following the cyclone for *H. lemuroides*; from 19% to 43% for *P. herbertensis*; from 8% to 46% for *P. archeri*; and from 11% to 32% for *T. v. johnstonii* (Fig. 2). The increase in detectability was significantly correlated with levels of cyclone damage at study sites for *H. lemuroides* (r = 0.93, d.f. = 7, $P < 0.001$), but not for other species ($P > 0.35$ for all species).

Discussion

Given the intensity of cyclone Larry and the evident damage to vegetation, it was thought that some folivores might have been killed directly by the cyclone, and that survivors would have been exposed to a scarcity of food and an increased risk of predation in the following weeks, when trees were defoliated and folivores presumably forced to forage on or close to the ground. By the time of the surveys, six to eight months following the cyclone, any adverse impacts of the cyclone on folivore populations should still have been evident, because marsupial folivores have a relatively low rate of increase. For example, tree-kangaroos and most of the possum species only produce a single young a year (Winter & Atherton 1984; Goudberg 1990; Flannery *et al.* 1996). In any case, young produced after the cyclone would have been distinguishable from adults on the basis of size, and abundance estimates were derived from observations of adults only.

Contrary to predictions, there was no evidence that populations of any folivore species were adversely affected by the cyclone. The study design (nine sites, before-and-after surveys, four repeat spotlight surveys in each sampling period) should have been sufficient to detect major impacts of the cyclone on populations of the more common arboreal folivore species (*H. lemuroides*, *P. herbertensis* and *T. v. johnstonii*). We cannot confidently assess cyclone impacts on the less commonly observed species (*P. archeri* and *D. lumholtzi*). Very few individuals and no juveniles of *D. lumholtzi* were observed after the cyclone, however, the species was recorded at the two most heavily damaged sites.

There are no previous studies of cyclone impacts on folivorous marsupials with which to compare these results, but studies of the impacts of logging and clearing on the folivores also suggest they may be rather resilient to disturbance. For example, Newell (1999) found that many individuals of *D. lumholtzi* survived for some time after the clearing of remnant rainforest at a site on the Atherton Tableland. Surviving animals largely stayed within their former home ranges, foraging on vines, regrowth and any remaining trees amongst the fallen timber, although over time, some individuals were killed by dogs. Laurance and Laurance (1996) found the abundances of four of the five species of folivorous marsupials on the Atherton Tableland were not affected by selective logging (based on the response to logging at a single site compared with two control sites). The authors attributed the resilience of these species to their dietary preferences for plant species favoured by disturbance and their flexible denning requirements. The remaining species, *H. lemuroides*, was reported to decline in abundance in response to logging. This may reflect qualitative differences in the impacts of logging and cyclones on the resources required by *H. lemuroides* (e.g., the tree species targeted by logging included several important in the diet of *H. lemuroides*: Goudberg 1990), but it is difficult to draw robust generalisations from a study of impacts on a single site.

The apparent resilience of arboreal marsupials to cyclone Larry contrasts with reports of significant impacts of intense cyclones on populations of folivorous primates (Wright 1999; Pavelka *et al.* 2003). The reasons for this apparent difference can only be speculated upon. One possibility is that cyclone damage to sites surveyed in the present study was less intense, or more patchy, than the damage to the primate study sites. Even though cyclone Larry caused unusually high levels of damage to upland forests on the Atherton Tableland, there was a general reduction in damage with distance from the coast. Even the most damaged sites surveyed in this study were less severely affected by the cyclone than lowland forests further to the east, where most trees were severely damaged and the loss of canopy was nearly complete (Bureau of Meteorology 2007). Consequently, arboreal folivores at the upland forest sites surveyed in this study may not have suffered a catastrophic loss of their food resources, dens or other key habitat attributes as a result of cyclone Larry.

Another possibility is that arboreal folivorous marsupials may be better able to cope with cyclonic disturbances than primates. Most primates are at least partly frugivorous (Primack & Corlett 2005) and, in the absence of hunting, the susceptibility of primates to disturbance generally increases with their dependence on fruit (Johns & Skorupa 1987). Foliage is an abundant resource in disturbed forest, once damaged trees have begun to resprout; whereas the availability of fruit can be severely reduced for many months following an intense disturbance. Further, although canopy trees are often defoliated for several weeks following a cyclone, green foliage may persist on understorey trees and shrubs, on partially uprooted trees or even on the forest floor if conditions are cool and wet, such as those that prevailed after cyclone Larry. Following the initial period of scarcity, the abundance of young foliage sprouting from damaged trees should provide a high-quality food resource (Pavelka & Behlie 2005), which in turn should promote high reproductive and survival rates amongst folivores (Martin 1985; Norton 1987). Indeed, many young and juvenile possums were observed in post-cyclone surveys, indicating that adults surviving the cyclone were in good condition in subsequent months.

While folivorous marsupials appeared resilient to the impacts of cyclone Larry at the sites surveyed, there are likely to be cases where cyclones exert profound negative effects on folivore populations. These include the occurrence of so-called ‘dry cyclones’, where cyclones are followed by hot, dry weather (Webb 1958; Unwin *et al.* 1988). Such conditions are likely to greatly reduce the availability of green foliage in cyclone damaged sites, and would also increase thermoregulatory demands on folivores, apparently a key determinant of habitat quality for arboreal marsupials in north-east Australia (Kanowski 2004). Cyclones may also have a greater impact on folivore populations in small remnant forests than in the extensive forest tracts surveyed in the present study. In remnant forests, alterations to microclimate wrought by cyclone damage may be more pronounced than in extensive forests, due to the influence of the surrounding cleared landscape. Predation from domestic animals is also likely to be more intense in remnants, with negative consequences for folivores (Laurance 1990; Newell 1999). For these reasons, it would be useful to study the response of folivores to future cyclones, particularly in the circumstances discussed above. Where possible, such studies should attempt to track the short-term impacts of cyclones on the availability of green foliage, as this is presumably critical for the persistence of folivore populations in damaged sites. Behavioural studies of folivores at cyclone damaged sites (e.g., Pavelka *et al.* 2003) would also increase our understanding of the factors favouring the persistence of folivore populations following intense disturbance.

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Table 1. Vegetation structural attributes at nine sites in upland rainforest on the Atherton Tableland, north-east Australia, following cyclone Larry.

Structural attribute	Minimum	Mean	Maximum
Canopy cover[†] (%)	71	82	90
Basal area live trees (m^2 ha^{-1})	37	54	69
Basal area dead trees (m^2 ha^{-1})	0	5	13
Trees 2.5-10 cm d.b.h.[‡] (% severely damaged)	0	6	15
Trees 10-20 cm d.b.h. (% severely damaged)	4	21	50
Trees 20-50 cm d.b.h. (% severely damaged)	0	32	67
Trees >50 cm d.b.h. (% severely damaged)	0	31	100
Woody debris (>2.5 cm diameter) m^3 ha^{-1}	16	70	146

[†] Canopy cover values reported here are derived from photographs (see text). Visual estimates of canopy cover at the study sites ranged from 47-85%, compared with values of 93-97% for intact upland rainforest sites (Kanowski *et al.* 2003).

[‡] diameter at 1.3 m.

Table 2. Correlation of vegetation structural attributes with their derived principal components.

Structural attribute	Component 1 (65% of variance)	Component 2 (17% of variance)
Canopy cover (%)	**-0.89**	0.30
Basal area live trees (m^2 ha^{-1})	0.26	**0.92**
Basal area dead trees (m^2 ha^{-1})	**0.90**	-0.17
Trees 2.5-10 cm d.b.h. (% severely damaged)	**0.92**	0.23
Trees 10-20 cm d.b.h. (% severely damaged)	**0.93**	-0.12
Trees 20-50 cm d.b.h. (% severely damaged)	**0.89**	-0.37
Trees >50 cm d.b.h. (% severely damaged)	**0.79**	0.47
Woody debris (>2.5 cm diameter) m^3 ha^{-1}	**0.67**	0.06

Attributes most strongly correlated with each component are highlighted in bold font.

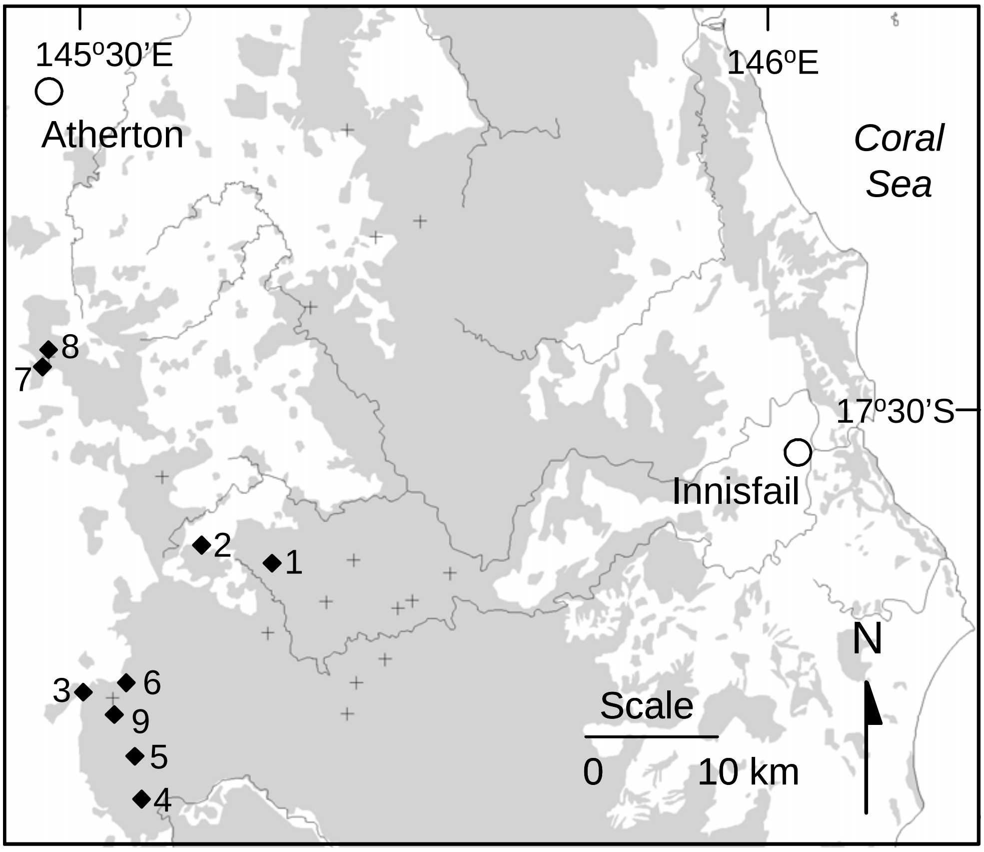

Fig. 1. Map of study sites on the Atherton Tableland, north Queensland. Diamonds = sites surveyed in present study, numbered according to the rank order of overall cyclone damage (1 = most damaged, 9 = least). Crosses = sites surveyed pre-cyclone, but not resurveyed in present study. Dark grey = rainforest. Cyclone Larry crossed the coast near Innisfail and moved west across the region (Bureau of Meteorology 2007).

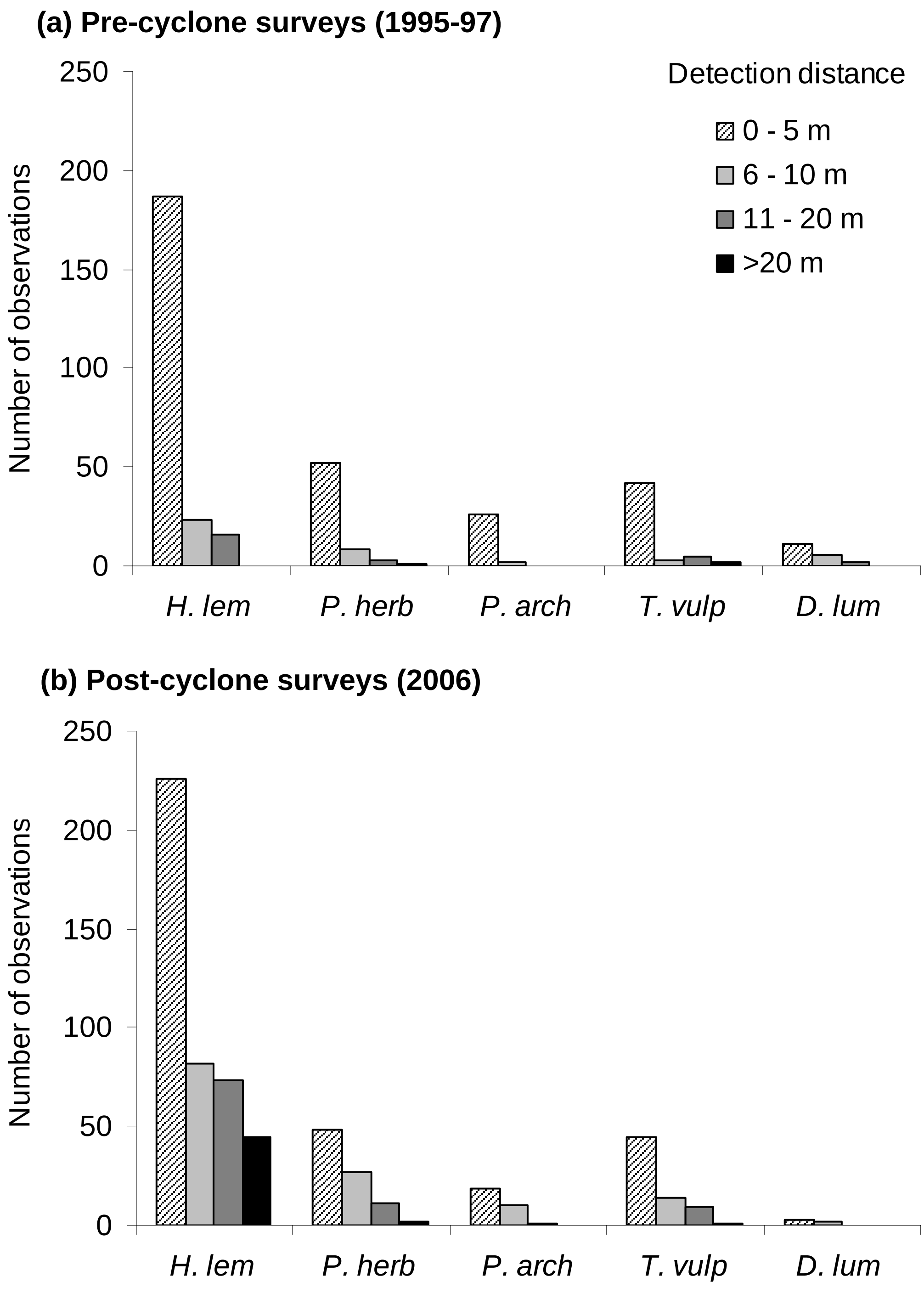

Fig. 2. Number of observations of arboreal folivores at different distances from the edge of transect during surveys of nine sites conducted (a) before, and (b) after cyclone Larry. *H. lem = Hemibelideus lemuroides, P. herb = Pseudochirulus herbertensis*; *P. arch = Pseudochirops archeri*; *T. vulp = Trichosurus vulpecula johnstonii*; *D. lum = Dendrolagus lumholtzi*.

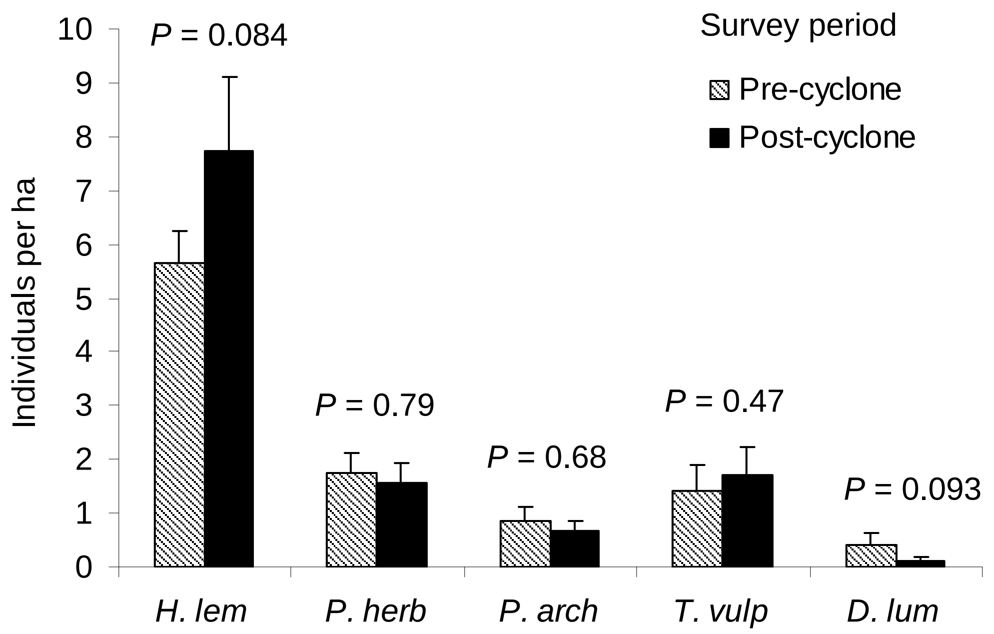

Fig. 3. Mean (SE) abundance of arboreal folivores at nine sites on the Atherton Tableland before and after cyclone Larry. Only observations within 5 m of the transect are included in abundance estimates. *P* values show results of paired t-tests (d.f. = 8) comparing pre-and post-cyclone abundance of each folivore species, based on ln(x + 1) transformed data. Species abbreviations as per Fig. 2.

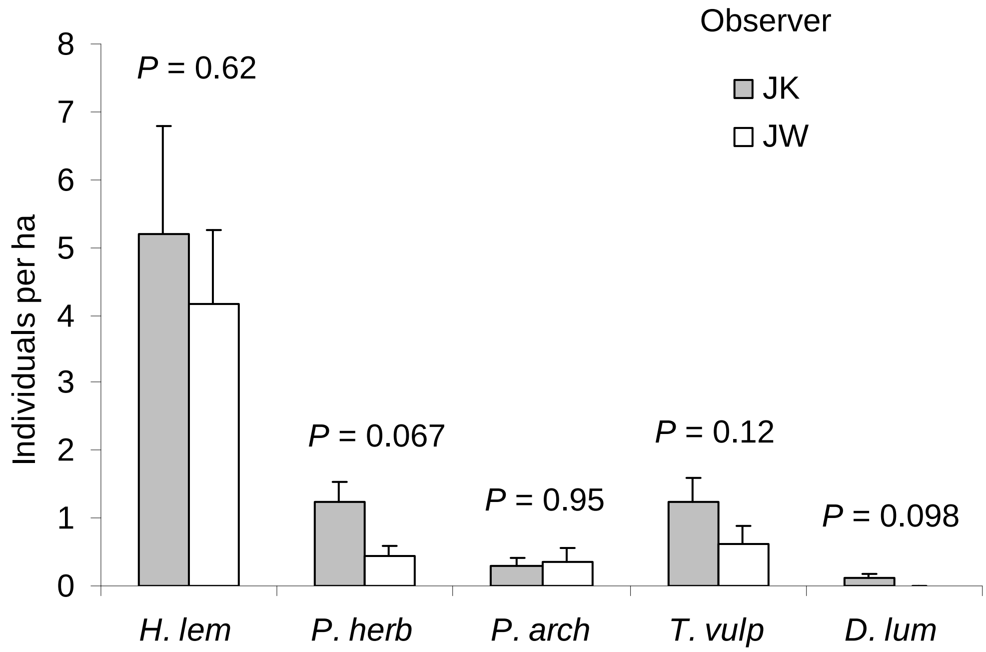

Fig. 4. Comparison of mean (SE) abundance estimates of arboreal folivores according to two observers (JK, JW), each of whom conducted two surveys of nine sites on the Atherton Tableland after cyclone Larry. Only observations within 5 m of the transect are included in abundance estimates. *P* values show results of paired t-tests (d.f. = 8) for each folivore species, based on ln(x + 1) transformed data. Species abbreviations as per Fig. 2.