

**Hollow formation in the *Eucalyptus miniata* – *E. tetradonta*
open forests and savanna woodlands of tropical northern
Australia**

J.C.Z. Woinarski and J. Westaway

NT Department of Natural Resources Environment and The Arts
PO Box 496
Palmerston
Northern Territory, 0831
Australia

john.woinarski@nt.gov.au

**Final report to Land and Water Australia (Native Vegetation Program).
Project TRC-14.**

June 2008

Abstract

This study examines the abundance of hollows in the extensive *Eucalyptus miniata* – *E. tetradonta* dominated forests of northern Australia. Hollow occurrence was estimated for 1878 individual trees at 42 sites (mostly 0.4 ha) selected to representatively sample across broad environmental and disturbance gradients in the Northern Territory. Estimates of the abundance of hollows per tree were made from the ground, and these were shown to be adequately accurate using verification from a subset of 22 trees where hollows were definitively assessed either by climbing trees or felling them.

The mean density of hollows was 168 per ha (of which 100 were 0-5 cm size). The density of hollows increased strongly from lower rainfall sites to higher rainfall sites, consistent with increases across this rainfall gradient in tree size and forest stature (basal area). Hollow density was also affected by disturbance. There were more hollows at sites with less frequent fire. Regrowth forests 33 years after felling by Cyclone Tracy had very few hollows.

The mean number of hollows per individual tree was 1.94 (of which 1.14 were smaller than 5 cm). The number of hollows per tree was strongly related to tree size (dbh), but was also related to tree health (increasing with an increasing proportion of the tree being dead), tree species-group (highest for *E. miniata*, smooth bloodwoods and salmon gums, and least for *Acacia* spp. and other non-eucalypts), tree height, fire impact (more hollows in trees with less fire impact) and termite sign (increasing with termite sign). There was also a far weaker significant relationship with tree shape (more hollows in trees with proportionally shorter boles). From modeling, the tree size at which one hollow would be expected is 25.6 cm dbh for *E. tetradonta* and 19.4 cm for *E. miniata*; at which one hollow >5 cm would be expected is 38.5 cm dbh for *E. tetradonta* and 37.0 cm for *E. miniata*; at which one hollow >10 cm would be expected is 52.5 cm dbh for *E. tetradonta* and 52.1 cm for *E. miniata*; and at which one hollow > 20 cm would be expected is 64.7 cm dbh for *E. tetradonta* and 73.7 cm for *E. miniata*. Based on the frequency distribution of trees >20 cm measured in this study, these thresholds are exceeded in 61.1% (for all hollows), 19.3% (for hollows > 5cm), 3.3% (for hollows > 10 cm) and 0.5% (for hollows > 20 cm) of *E. tetradonta* stems, and for *E. miniata* by 100%, 25.7%, 3.6% and 0% (respectively) of stems.

In these northern Australian forests, variation in stand structure (and to a large extent, accordingly, the abundance of hollows) follows broad underlying environmental gradients, but the broad predictability of this patterning is substantially perturbed by disturbance history. The occurrence of cyclones is by far the most substantial of these disturbance agents, as a single major cyclone event can re-set the forest structure to scratch, and require at least 30 years of regrowth before hollows become available again. However, the aging of these forests (or the trees within them) is unsettled. Previous estimates of growth rates of about 0.7-1 cm dbh increment per year have been used to suggest that the dominant eucalypts in these forests never attain substantial age (i.e. almost always < 100 years old). However, these growth estimates were based at sites where the forest canopy (or all vegetation) had been removed, and are not consistent with more recent estimates based on growth rates in “undisturbed” forests. Growth rates in such forests are typically about 0.15-0.3 cm dbh, suggesting that trees would need to be 65-150 years old before forming any hollows, and 120-250 years old before forming hollows >10 cm.

Forest stand structure, and accordingly hollow abundance, is also affected by fire regimes. Based on results from this study, and previous information, hollow abundance in these forests will be reduced by frequent fire.

This study suggests that there may be some validity in applying old-growth criteria and categorisation to these forests. There are qualitative differences with forest age in the tree size distribution and abundance of hollows of varying sizes. Given differential dependence upon hollows of varying sizes by different fauna species, forests with more large trees (and hence more large hollows) will be expected to support a different fauna community to younger-aged forests. Further, large trees (e.g. > 50 cm dbh) and large hollows (>20 cm) are a relatively rare resource, and hence may merit more particular recognition and conservation protection.

Stand structure and hollow formation in the eucalypt forests of northern Australia contrast substantially with forest characteristics in temperate Australia. The tropical eucalypt forests typically comprise smaller trees (and total basal area), but hollow formation occurs in trees of smaller size. Despite their less substantial forest structure, the total density of hollow trees, and hollows, is greater in tropical eucalypt forests than is typical of forests in temperate Australia. These contrasts reflect or result from different disturbance regimes and the greater ecological role of termites in tropical eucalypt forests.

Introduction

Hollows are an important attribute of forests and woodlands for a large proportion of Australia's fauna (Gibbons and Lindenmayer 2002). This significance, and the recognised relationship between tree age and hollow formation and abundance, has led to the presence and abundance of hollows being a key component in the definition of "old-growth" forest (e.g. Burgman 1996), with the formation of hollows marking a critical threshold that allows for the occurrence of a distinctive set of fauna species and hence a shift in animal species composition. In reality, that threshold is not necessarily abrupt, because there is a gradation of tree ages at which different sized hollows may form, and different species of trees co-occurring in a forest may differ in their rates of hollow formation.

In the forests and woodlands of temperate Australia, fuelled largely by debate concerning commercial forestry, old-growth criteria are reasonably well-defined, and the abundance of hollows and the factors determining this abundance, have been reasonably well documented (e.g. Saunders 1979; Lindenmayer *et al.* 1991, 1993; Gibbons *et al.* 2000; Harper *et al.* 2004, 2005; Munks *et al.* 2007). There is far less information available for the forests and woodlands of tropical northern Australia, in part because these have been far less the focus of exploitation. The disturbance regimes (and hence hollow formation) in these forests contrast markedly with that of temperate Australia (Lacey and Whelan 1976; Bowman 1988). Influenced by the strongly seasonal climate, fire is commonplace in northern Australia, with about 30-50% of the forests of the monsoonal tropics of the Northern Territory burning every year (Russell-Smith *et al.* 2003a). Where these fires are severe, older hollow-bearing trees may be particularly likely to be destroyed (Williams *et al.* 1999). Further, destructive cyclones and other storm events (Williams and Douglas 1995) are frequent, particularly in high rainfall coastal areas, and these may fell all trees over broad swathes of land. In a landscape with low fertility soils (Cook 1994), a long annual dry season that severely constrains growth (Prior *et al.* 2004, 2006), and a regime of frequent disturbance, trees tend to be relatively young, short and of small diameter, and forests have little woody biomass (Bowman 1988).

To date, there have been few studies that have considered hollow availability in the tropical forests and savanna woodlands of northern Australia. Taylor *et al.* (2003) tallied the number and proportion of vertebrate species that were dependent upon or used hollows in forests of northern Australia, and noted that these were comparable to values in forests of southern Australia. The high incidence of hollows – and the association of these with the prevalence of termites – has been a well-remarked feature of these forests since some of the earliest forest resource assessments (e.g. Bateman 1955; Fox and Clarke 1972; Cameron 1985), although in the context of prospective exploitation of these forests, such hollow abundance ("defects") was considered unfortunate. Considering instead the availability of hollows as habitat for wildlife, Braithwaite *et al.* (1985) reported a high incidence of hollows across a range of tree species in Kakadu National Park (1.48 hollows per tree for *E. miniata* and 1.13 hollows per tree for *E. tetradonta*, based on samples of 422 *E. miniata* trees >10 cm dbh and 466 *E. tetradonta* trees > 10 cm dbh), with hollow abundance found to be significantly related to tree size (dbh). In a study in the Gulf region of the Northern Territory, Taylor and Chisholm (2005) reported an average of 1.65 hollows (comprising 0.73 small hollows (<5 cm), 0.73 medium hollows (5-10 cm) and 0.19 large hollows (>10 cm)) per tree for *E. miniata* (based on a sample of 75 trees > 10 cm dbh). They also demonstrated an increase in hollow abundance with tree size (dbh), and a significant difference between species in hollow abundance (with *E. miniata* intermediate between the larger hollow abundance in *E. camaldulensis* and the smaller hollow abundance in *Erythrophleum chlorostachys*). The studies of Braithwaite *et al.* (1985) and Taylor and Chisholm (2005) were snapshot estimates

of hollow prevalence: in contrast Werner and Prior (2007) examined the incidence of tree piping by termites and the subsequent growth rate and mortality patterns of piped and unpiped trees. They found that 66% of all sampled stems were piped, with this frequency significantly higher in eucalypts (including 82% of 165 sampled *E. tetradonta* stems and 97% of 102 sampled *E. miniata* stems) than non-eucalypts; and that piped stems had higher mortality and lower growth rates.

Here, we attempt a systematic assessment of the abundance of hollows in woodlands and forests dominated by either or both of the two (closely related) tree species Darwin Stringybark *Eucalyptus tetradonta* and Darwin Woollybutt *E. miniata*. These are the two characteristic tree species in forests and woodlands in northern Australia, and forest types dominated by either or both of these two species extend over 180,000 km² in the Northern Territory (Wilson *et al.* 1990) and 445,158 km² in northern Australia (calculated from Fox *et al.* 2001). This study addresses these specific questions:

- (1) what is the density of hollows in these forest types?
- (2) how does this density vary with environmental or disturbance factors?
- (3) what is the relationship between tree size and hollow abundance?
- (4) are there differences between tree species in the occurrence of hollows?; and
- (5) how does hollow availability in these forests differ from that in temperate eucalypt forests?

In northern Australia (as in all native forests in Australia), hollows provide a pivotal resource for fauna, with characteristics of hollows dictating suitability or different groups of species. In this study, we classified hollows as either small (1-5 cm minimum diameter), medium (5-10 cm), large (10-20 cm) or very large (>20 cm) and occurring either in the trunk or in a branch. Other dimensions of hollows, notably including depth and orientation, may also be critical factors in dictating suitability. In this region, typical vertebrate fauna using small hollows include arboreal gecko species (such as northern dtella *Gehyra australis*), small tree frogs (such as *Litoria rubella*), arboreal skinks (*Cryptoblepharus* spp.) and some small insectivorous bats; medium hollows by some small birds (such as striated pardalote *Pardalotus striatus*, gouldian finch *Erythrura gouldiae*), larger frogs (such as green tree-frog *Litoria caerulea*), small goannas (such as spotted tree monitor *Varanus scalaris*) and small mammals (including many insectivorous bats, fawn antechinus *Antechinus bellus* and sugar glider *Petaurus breviceps*); large hollows by many birds (including Australian owl-nightjar *Aegotheles cristatus*, northern rosella *Platycercus venustus*, red-winged parrot *Aprosmictus erythropterus*, rainbow lorikeet *Trichoglossus haematodus*, dollarbird *Eurystomus orientalis*) and mammals (including northern brush-tailed phascogale *Phascogale pirata*, brush-tailed rabbit-rat *Conilurus penicillatus* and northern quoll *Dasyurus hallucatus*) and very large hollows by some large-bodied bird species (e.g. radjah shelduck *Tadorna radjah*, red-tailed black-cockatoo *Calyptorhynchus banksii*, sulphur-crested cockatoo *Cacatua galerita*, blue-winged kookaburra *Dacelo leachii* and masked owl *Tyto novaehollandiae*) and some medium-sized mammals (common brushtail possum *Trichosurus vulpecula* and black-footed tree-rat *Mesembriomys gouldii*). Hollows may also provide the shelter requirements for many invertebrates, including native bees, a very significant cultural asset in northern Australia.

In the forests of *E. miniata*- *E. tetradonta*, hollows of specific dimensions are also a key resource for making didgeridoos, a traditional cultural artefact for which commercial trade now drives a far more substantial exploitation rate (Forner 1999). These forests are also now the main vegetation type exposed to broad-scale clearing, for agricultural development, forestry plantations and urban expansion (Woinarski 2004; Rankmore and Price 2004). Much

of this clearance focuses particularly on the forests of largest stature, but conservation management of these forests is hampered by the crude classification of these forest types, with no current recognition of old-growth nor consideration of the quality of the forests for wildlife habitat. The research described here aims to at least partly address that limitation.

Methods

Field procedures

We assessed hollow availability at a series of 42 sites supporting *Eucalyptus miniata*- *E. tetradonta* forests and woodlands across much of the range of this formation in monsoonal areas of the Northern Territory (Fig. 1). Study sites were selected to sample broadly across the rainfall, edaphic, disturbance and topographical range spanned by these woodlands: in some cases, sites in close proximity (minimum 1 km apart) were selected to represent contrasting environmental or management features. For each site, we recorded:

- latitude,
- longitude,
- soil texture (as either sand, sandy-loam, loam, clay-loam or clay),
- soil depth (as either <10 cm, 10-40 cm or >40cm),
- rock cover (estimated percentage cover),
- slope (°), and
- disturbance history, including:
 - fire – frequent (=burnt at least one year in three: coded as 1) or infrequent (code=0);
 - grazing - either grazed by livestock (code=1) or not (code=0); and
 - cyclone – either no discernible impact (code=0), regrowth following complete felling by Cyclone Tracy in December 1974 (code=2; Fig. 2), or recovery following impacts of Cyclones Monica (in April 2006) and/or Ingrid (in March 2005) (code=1), where at sampled sites, damage was more recent than for Tracy but less extreme, typically including felling of some trees and snapping of most others (Fig. 2).

We derived an estimate of mean annual rainfall per site from the location, using ANUCLIM (Houlder 2000).

At all but three sites, we sampled along four 50 m x 20 m belt transects, for a total sampled area of 0.4 ha. Three sites was sampled with different sampling effort (0.2, 0.57 and 0.6 ha), so all areal-based tallies are converted to numbers per hectare. For every tree >20 cm dbh in the sampled area, we recorded:

- species,
- dbh,
- canopy height,
- bole height (defined as the distance from the ground to the first branch that was at least 25% of the diameter of the trunk at the branching point),
- the number of hollows,
- the extent to which the trunk showed evidence of fire scarring [categorised as nil (=0), some (=1) or much (=2)],

- tree health [categorised as either few or no dead branches (=0); some or many dead branches (1), or entirely dead (2)], and
- the extent of termite activity at the tree base (as either nil (=0), signs of termite tracks on trunk (=1), or termite mound present at base of tree (=2)].

Trees with dbh smaller than 20 cm were not sampled, given their unlikelihood of containing hollows (Taylor and Chisholm 2005), and following precedents of previous hollow availability studies (e.g. Wormington *et al.* 2005). Note that, accordingly, our site assessments of stand basal area do not include a variable proportion of woody stems that are < 20 cm dbh.

For each sampled tree, the number of hollows present was estimated from ground inspection, using binoculars where appropriate.

At sites where fewer than 50 trees were sampled in the belt transects, additional trees were sampled outside transects to bring the tally per site to at least 50. These additional trees were not included in estimating tree and hollow density, but were used in regressions of hollow numbers against tree characteristics.

The reliability of our ground-based assessment of tree hollows was assessed by calibrating our estimates against actual counts for a random selection of 22 trees, of which 14 were climbed by arborists and eight were felled (Fig. 3), following the recommendation of Harper *et al.* (2004) “that efficient surveys of hollow occurrence could be undertaken by inexperienced surveyors with periodic climbing surveys to measure and correct for bias”.

Analysis

Analysis considered the abundance of hollows at both site level and the level of individual trees. At the site level, all strip transect data were first converted to values per hectare, given that three sites had sampling areas inconsistent with the otherwise typical 0.4 ha sampling area.

The following dependent variables were then considered: total number of hollows, total number of hollows >5cm diameter, number of trees with hollows, number of stems, basal area and median tree diameter. These were related to the set of environmental variables (rainfall, soil texture, soil depth, rock cover, fire history, grazing, cyclone impact) using generalised linear modelling. The site-based hollow availability (and basal area, median tree diameter and number of stems) variables were assumed to have a normal distribution, and an identity link function was used. Modelling was undertaken in Statistica, and used backwards stepwise deletion of non-significant variables until a minimum adequate model was obtained (Crawley 1993).

Where specified, the hollow availability models were re-run with the inclusion of the three forest structure variables (basal area, median tree diameter and number of stems) in addition to the site environmental variables.

At the level of individual trees, the hollow variables above were each related to the explanatory variables tree size (diameter and height), tree shape (bole height/total tree height), occurrence of termites, fire evidence, tree health and tree species-group (Table 1). Hollow abundance per tree was assumed to be poisson-distributed, and a logit link function was used.

Results

A total of 1878 trees were sampled. These included mostly *Eucalyptus tetradonta* (40% of all trees sampled) and *E. miniata* (34%) (Table 1).

The ground-based assessment of hollow numbers was highly correlated with proven numbers based on explicit inspection through climbing of trees and/or felling (Table 2). There was a slight tendency to over-estimate hollows from ground-based counts, with this trend being broadly consistent across hollow size classes and for branch and trunk hollows. Ground-based counts tended to over-estimate hollow abundance in trees with few hollows and under-estimate counts in trees with many hollows (i.e. for regressions of the form actual no. = a + bc, where c is the ground-based estimate, a was generally >0 and b was generally <1).

For the 22 trees considered in the calibration, a measure of the error in estimated count was derived as $(c-a)/(c+a)$, where c is the ground-based estimate and a is the actual count, and the index varies from -1 (if there were far more hollows actually present than estimated) to +1 (if there were far fewer hollows actually present than estimated from ground counts). This error index was significantly ($p < 0.05$) correlated with tree height ($r = 0.49$), indicating that ground-based counts were more likely to over-estimate actual hollow numbers when the trees were taller.

There was some disparity in the calibration for the eight trees that were felled (mean number of hollows from ground-based estimate = 4.50; mean number of hollows counted once felled = 4.88) compared with that derived from the 14 trees climbed (mean number of hollows from ground-based estimate = 6.29; mean number of hollows counted once felled = 5.29).

Variability in hollow density: site level.

Across sites, the mean density of hollows was 168/ha (of which 100/ha were <5cm diameter) and the number of trees with hollows was 63/ha (Table 3). These parameters varied by more than a magnitude between sites.

Generalised linear models relating tree size, forest structure and hollow abundance variables to site environmental variables are summarised in Tables 4 and 5.

The number of trees (>20 cm dbh) per ha was negatively related to grazing impact and was greatest in sites without cyclone impacts, although these relationships were not especially significant and the amount of deviance explained was low (Table 4). The density of trees of larger size (>30, >40, >50 and >60 cm dbh) was greater at sites with higher rainfall, less rock cover, less fire and less cyclone impact. The density of trees >30 cm dbh was higher at sites with deeper soils.

The median tree size (dbh) was highly influenced by cyclone impact (being least in the sites felled by cyclone Tracey), was less at rocky sites, less at sites with more fire impact, greater at high rainfall sites, and greater (although not so significantly) at sites with higher grazing impact. The model incorporating these terms explained 72% of the deviance (Table 4).

The total site basal area (m^2/ha of stems > 20 cm dbh) was significantly greater at high rainfall sites, sites with less rock, sites with less fire, and sites less affected by cyclone. The model incorporating these terms explained 67% of the deviance (Table 4).

The density of hollows increased very significantly at higher rainfall sites and was greatest at sites undisturbed by cyclone and with less fire impact (Table 5). A model incorporating these terms explained 64% of the deviance.

This model was improved (to explain 75% of the deviance) when forest structure variables were considered. In this case, the minimum adequate model dropped the term fire but included total basal area (as the most significant term) (Table 5).

The density of hollows >5cm diameter followed a similar model to that of total hollow density, being greatest at sites that had higher rainfall, were unaffected by cyclone and had less fire impact (Table 5). The model incorporating these terms explained 52% of the deviance. When forest structure variables were also considered, fire impact was no longer included as significant, but hollow density was shown to increase very significantly with total basal area and negatively (and less significantly) with total stem density. Inclusion of these forest structure variables improved the model's explanatory power to 67%.

The density of hollow trees increased very significantly with rainfall and was greater at sites unaffected by cyclone (Table 5). A model incorporating these terms explained 48% of the deviance. When forest structure variables were also considered, the number of hollow trees was found to also be highly positively related to the total density of trees, and model incorporating these terms explained a very high (83%) proportion of the deviance.

The most significant ($p < 0.01$) of these relationships are illustrated in Fig. 4. Fig. 5 illustrates the effect of cyclone impact on the strong underlying relationship between hollow abundance and rainfall.

Variability in hollow abundance: tree level

For the total set of all trees (>20 cm) sampled, the mean number of hollows per tree was 1.94 (s.e.=0.05, range 0-16), including 1.14 hollows < 5cm, 0.59 hollows 5-10 cm, 0.18 hollows 10-20 cm, and 0.04 hollows 20-30 cm. The mean number of hollows per tree (across all tree and hollow sizes) was 2.38 (s.e.=0.10, N=638) for *E. miniata* and 1.72 (s.e.=0.08, N=758) for *E. tetradonta*.

The total number of hollows per tree was most significantly related to tree size (diameter), but also strongly related to tree health (increasing with increased proportion of the tree being dead), tree species-group (highest for *E. miniata*, smooth bloodwoods and salmon gums, and least for *Acacia* spp. and other non-eucalypts), tree height, fire impact (more hollows in trees with less fire impact) and termite sign (increasing with termite sign) (Table 6). There was also a far weaker significant relationship with tree shape (more hollows in trees with proportionally shorter boles).

These relationships were broadly similar considering different size classes of hollows (Tables 6), although tree height and shape dropped out as significant terms in models for larger hollow sizes. Figure 6 presents observed relationships between hollow abundance and tree size (dbh) and species.

From modeling restricted to the relationship between hollow abundance and dbh, the dbh at which one hollow would be expected is 25.6 cm for *E. tetradonta* and 19.4 cm for *E. miniata*, at which one hollow > 5 cm would be expected is 38.5 cm for *E. tetradonta* and 37.0 cm for *E. miniata*, at which one hollow > 10 cm would be expected is 52.5 cm for *E. tetradonta* and 52.1 cm for *E. miniata*, at which one hollow > 20 cm would be expected is 64.7 cm for *E. tetradonta* and 73.7 cm for *E. miniata*. Based on the frequency distribution of dbhs of measured trees (>20 cm dbh only), these thresholds were met or exceeded for *E. tetradonta*

by 61.1% (for all hollows), 19.3% (for hollows > 5cm), 3.3% (for hollows > 10 cm) and 0.5% (for hollows > 20 cm) of stems, and for *E. miniata* by 100%, 25.7%, 3.6% and 0% (respectively) of stems.

Discussion

The verification of our ground-based assessments using actual counts derived from tree climbing and tree felling provided reassurance that our estimates were reasonable, with highly significant correlations between ground-based and actual counts. Overall, there was a weak tendency (10% difference) for us to over-estimate hollow numbers from ground counts, although this tendency was evident only when compared with counts derived from tree-climbing (where it is possible that for safety reasons the tree-climbers did not include hollows from more peripheral small branches). The extent of congruence between our ground-based estimates and actual counts was comparable to a similar study by Harper *et al.* (2004) that reported correlations of 0.57-0.83 between estimates from ground-based and climbing counts).

The study described here demonstrates a complex array of factors determining hollow availability in forests dominated by *E. miniata* and/or *E. tetradonta*. Broadly, tree size and stand basal area in this forest type increase along the rainfall gradient (as previously reported – Bowman and Connors 1996; Williams *et al.* 1996; Woinarski *et al.* 1999), with hollow abundance hence also increasing from lower to higher rainfall sites.

But this relatively ordered relationship may be substantially disrupted by some disturbance factors. By far the most acute and substantial of these is the impact of cyclones. To some extent this impact is counterbalancing the underlying response to rainfall of the linked set of tree size, stand basal area and hollow availability variables, with cyclones more likely to occur and/or be most destructive in coastal areas (that, in this region are also higher rainfall sites). But cyclone impact is both unpredictable and capricious in its timing and spatial distribution, and the consequences to forest stands (and thus hollow availability) of any cyclone vary widely depending upon its severity. In the set of sites examined here, present-day forest stand structure (and hence hollow availability) was imprinted far more by the destructive Cyclone Tracy of 1974 than by the less destructive cyclones of 2005 and 2006. Thirty-three years after Cyclone Tracy felled almost all trees in areas sampled by a set of sites here, the natural regrowth forest has far smaller trees, far smaller stand basal area and hence far fewer hollow trees and tree hollows than would be expected for a forest in this rainfall zone (Fig. 5). In contrast, at a different set of sites sampled here, the far more recent Cyclones Monica and Ingrid were less destructive (Fig. 5), and hence had far less impact on stand structure and hollow availability. Nonetheless, their impact is still discernible (Fig. 2), and may become more so over the next few years with the collapse of currently standing stags. Further, hollowed trees may be unrepresentatively likely to be felled by cyclones (Stocker 1976). Indeed, there may be a general tendency for forest communities to be affected by cyclone impacts well after the cyclone's brief episode, as subsequent fires may be exceptionally intense because of the unusually high fuel loads attributable to fallen limbs and trees (Bowman and Panton 1994).

Thirty-three years after Cyclone Tracy, the regrowth forests now provide substantially fewer hollows than would be expected for "mature" forests based on the annual rainfall of these sites. As with eucalypt trees elsewhere, *Eucalyptus miniata* and *E. tetradonta* take many decades to be large enough for hollow formation. Just how quickly do they grow, and how big (or old) do they have to be before hollows (or hollows of particular size) are formed? There are only limited and somewhat divergent data available to answer these questions.

Partly fuelled by interest in the forestry potential of these species, Mucha (1979) measured dbh for 19 eucalypt stems regenerating after clearing either 4, 8 or 23-26 years previously. For eight individual *E. miniata* the mean annual increment was 1.06 cm (range 0.54-2.55; s.e. =0.23) and for 11 individual *E. tetradonta* the mean annual increment was 0.96 cm (range 0.55-1.9, s.e.=0.15) cm. Mucha (1979) then extrapolated these results to conclude that trees in general in these forests were short-lived, setting or reflecting an orthodoxy:

“The eucalypts of this region thus probably rarely reach the age of 100 years, while in the southeast of Australia some species, for example, *E. regnans*, have been recorded to live for over 300 years.”

Without noting any disparity, Mucha (1979) also made repeated measurements over a 2-year period of nine 20-year old tagged *E. tetradonta* trees, and reported average annual girth increment of 1.28 cm (i.e. annual dbh increment of 0.39 cm).

Mucha's results are broadly consistent with the data reported here for post-Tracy sites, where the forest stand structure is now dominated by trees with diameter < 24 cm dbh, i.e. with average annual dbh increments of up to 0.72 cm. Woinarski *et al.* (2005) reported on growth in *Eucalyptus miniata* and *E. tetradonta* in post-mining rehabilitation at Gove, north-eastern Arnhem Land. They reported the three largest stems for each of *E. miniata* and *E. tetradonta* at two 30 year post-mining sites to be 18-29 cm dbh for *E. miniata* and 25-28 cm for *E. tetradonta* (i.e. average annual growth rates of 0.6-0.97 cm for *E. miniata* and 0.83-0.93 cm for *E. tetradonta*), and at 20 years post-mining to be 14-26 for *E. tetradonta* (i.e. average annual growth rates of 0.7-1.3 cm). Crase *et al.* (2007) calculated growth rates for a set of tagged trees at these rehabilitation post-mining sites between 2005 and 2006 and reported average annual growth rates of 0.98 cm dbh for *E. miniata* (based on 81 individual stems) and 0.87 for *E. tetradonta* (based on 152 individual stems). Assuming relatively constant 1 cm dbh increments irrespective of tree size (as reported in Crase *et al.* 2007, and Prior *et al.* 2004), this suggests that small hollows are unlikely to form in trees of these two species until the trees are 25-30 years old, medium-sized hollows are unlikely to form until the trees are 35-40 years old, large hollows unlikely to form until the trees are 50-55 years old and very large hollows unlikely to form until the trees are 60-75 years old.

But all of the above annual tree growth rates are based on stems in regrowth at sites in which the overstorey (or all vegetation) has been removed. Growth rates of eucalypts in undisturbed forest sites are appreciably less (presumably because of competition: Fensham and Bowman 1992). For example, Prior *et al.* (2004) measured dbh at six small and six large tagged *E. tetradonta* trees over a two year period at a site near Darwin, and calculated annual dbh increments of only 0.09 cm. In a more complex study (at Kapalga, in Kakadu National Park) that included an examination of the influence of fire regimes on growth rates of a far larger number of tagged trees in “mature” forest over a four year period, Prior *et al.* (2006) demonstrated substantial differences in growth rates associated with fire regime, but recorded overall mean annual dbh increments of 0.23 cm for adult *E. miniata* and 0.15 for adult *E. tetradonta*. In a previous study in the same general area, Werner (1986) measured tagged trees and calculated mean annual dbh increments of 0.30 for *E. miniata* (from 113 trees) and 0.15 for *E. tetradonta* (from 65 trees). The far lower annual growth rates for trees in “mature” forests than in regrowth suggests that Mucha's (1979) assessment of tree age in forest stands are substantially underestimates. Werner (1986) extrapolated from the growth rates she reported to provide estimates of the age of larger *E. miniata* and *E. tetradonta* trees in these forests as “not older than 150-180”, or up to 400 years. Accepting a value of about 0.15-0.3 cm dbh annual increment from the set of studies of growth rates in mature forests, hollow formation is unlikely to occur in *E. miniata* or *E. tetradonta* trees until they are 65-150 years (for small hollows), 120-250 years (for medium hollows), 170-350 years (for large hollows) and 220-500 years (for very large hollows). These ages are clearly substantially

greater than those suggested in the previous paragraph based on growth rates from regrowth sites.

The tropical eucalypt forests described here are distinctive in being exposed also to two other disturbance factors, termite activity and fire, operating in regimes that are distinctly different to temperate eucalypt forests. The high incidence of termites (particularly tree-piping termites *Coptotermes* spp: Andersen *et al.* 2005) is a pivotal ecological feature of these tropical forests and savanna woodlands (Braithwaite *et al.* 1988), and a direct cause of the high incidence of hollow formation in trees (particularly eucalypts) in these forests.

Forests of *E. miniata* and *E. tetradonta* are exposed to frequent fire (in the Top End of the Northern Territory, about 30-50% of the forest extent is burnt each year: Russell-Smith *et al.* 2003a). Fire generally will affect hollow formation directly and indirectly (through its influence on growth rates), and specific fires or fire regime will have different effects. Prior *et al.* (2006) reported higher growth rates for these two tree species in forests under a regime of no fire, with next highest growth rates in forests with a regime of fires in the early dry season, with least growth in forests under a regime of regular late dry season fires (see Table 7). These results corroborate similar conclusions from previous studies (e.g. Mucha 1979; Werner 1986; Prior *et al.* 2004), and are consistent with results reported here, and suggest a higher abundance of hollows in forests that are infrequently burnt. Regimes of frequent fires, and particularly of intense (late dry season fires) also increase stem mortality and reduce stand basal area (Williams *et al.* 1999, 2003). While fires may also be involved in hollow formation, the evidence is stronger that fires (particularly late dry season fires) are more likely to cause mortality in large hollow-bearing trees (Lonsdale and Braithwaite 1991; Williams *et al.* 1999). Hence, hollows are likely to be far more abundant in forests that are unburnt or infrequently burnt. This conclusion may be tempered should fire exclusion lead to state change in these forests to increasing importance of rainforest-associated trees and consequential reduction in the importance of eucalypts (Woinarski *et al.* 2004), but such an outcome at a landscape scale is beyond the plausible bounds of current fire management (Russell-Smith *et al.* 2003b).

These tropical forests are mostly co-dominated by two closely related tree species, *E. miniata* and *E. tetradonta*. The results reported here (e.g. Fig. 6) suggest that hollow formation follows a largely similar pattern for these two species, with but minor differences (e.g. Table 6 shows that a *E. miniata* tree of any given size is likely to have marginally more hollows than a tree of *E. tetradonta* of that size). Our results also suggest comparably high rates of hollow formation for other eucalypt species in these forests (Table 6), with this rate showing some variation between species-groups but typically being appreciably higher than for co-existing non-eucalypts. These results are broadly similar to those reported by Werner and Prior (2007), Braithwaite *et al.* (1985) and by Taylor and Chisholm (2005). For example, the mean number of hollows reported per *E. miniata* tree in our study (2.38) was comparable to those reported for this species by Braithwaite *et al.* (1985) (1.48 hollows per tree) and Taylor and Chisholm (2005) (1.65 hollows per tree): our higher rate is due to our consideration only of trees >20 cm dbh whereas both previous studies included trees >10 cm in their assessments.

To what extent does this account of hollow occurrence in these forests provide perspective on the applicability and/or circumscription of “old-growth” characterisation? In part, the patterning of hollow formation clearly follows an age-related stepped function, where hollows in these trees are not evident until the trees are of sufficient size (and age). While small hollows may form when trees are 20-25 cm dbh (and hence between 25-30 years old in regrowth situations and 65-100 years old in “undisturbed” sites), large hollows require appreciably longer time frames. These hollows provide resources that are of substantial ecological or conservation significance that are simply unavailable in trees (or forests) of younger age. This qualitative difference is consistent with the concept of old-growth, and it

would be feasible to craft quantitative qualifying criteria, such as the occurrence of >5 trees of dbh >50 cm per ha. Given that such trees (or forests) are likely to provide large or very large hollows (obligatorily required for a range of forest vertebrate species), this simple qualification criterion is likely to also be associated with an indicative faunal species composition.

There are two interpretational considerations with such a simple and straightforward ascription. Firstly – perhaps more so than with defined old-growth forests elsewhere – this is a highly dynamic system, and the spatial distribution of old-growth will change substantially following the erratic pathways of frequent cyclones. Secondly, the size distribution of forests stands (and hence hollow availability) is a function not only of forest age but also of the location of the forest relative to broad environmental gradients (particularly position along the rainfall gradient). A 40 year old tree (or forest) is likely to have larger size (and hence more hollows) at a high rainfall site than at a site with lower rainfall. Accordingly if an old-growth definition is based on tree size, it will take longer for a forest at a low rainfall site than a high rainfall site to reach that definitional threshold.

These tropical eucalypt forests differ notably from temperate eucalypt forests in forest dynamics and hollow availability (Table 8). Notwithstanding the generally smaller stature of their trees, the tropical eucalypt forests typically contain appreciably more hollows. This is largely due to the far higher incidence (and impact) of termites. Although growth-rates and aging of trees in these forests remains unresolved, hollows in the tropical eucalypt forests may also form at appreciably younger ages, and the lifespan of the dominant eucalypts (and hence forest stands) is likely to be somewhat shorter in these tropical forests (albeit this disparity is probably nowhere near as marked as that conjectured by Mucha (1979)). As noted previously by Bowman (1988), part of this contrast is due to the markedly different disturbance regime of these forests. Whereas in temperate forests, stand structure is largely dictated by time since very occasional catastrophic fire events, in tropical forests fire is frequent and the stand structure may be far more dictated by infrequent but catastrophic cyclone.

This study corroborates previous studies (Braithwaite *et al.* 1985; Taylor and Chisholm 2005; Werner and Prior 2007) that have reported hollows to be abundant in these tropical eucalypt forests. In many forests of temperate Australia, hollow availability is a factor limiting the abundance and distribution of hollow-dependent fauna. It is not clear whether the greater abundance of hollows in these tropical forests eases this limitation. Indeed, the only study that has focused on this question (Pittman 2003) found substantial interspecific competition between black-footed tree-rats and common brushtail possums for hollows, and reported that black-footed tree-rats were forced to use sub-optimal denning sites (foliage of *Pandanus spiralis*) at sites with higher possum density, because there were insufficient large hollows available. Other studies of these species (Kerle 1985; Rankmore 2006) and other hollow-dependent mammals (such as brush-tailed rabbit-rat *Conilurus penicillatus*: e.g. Firth *et al.* 2006) have also found an association with forests with abundant larger trees, presumably because these contain hollows of sufficient size or abundance. Such association and interspecific interactions suggests that hollows in these tropical eucalypt forests should be viewed as a critical resource for fauna, and that sites with abundant large hollows and large trees form an important resource for conservation.

Acknowledgements

For assistance with sampling we thank Riikka Hokkanen and Tida Nou.

For statistical advice, we thank Tony Griffiths. For assistance with climbing and felling trees, we are grateful to Barry Scott and the George Brown Darwin Botanical Gardens staff. We thank Matthew Fegan for preparing Figure 1.

For advice about forest structure and or hollows we thank Garry Cook, Dick Williams, Pat Werner and Caroline Lehmann.

This study was supported by Land and Water Australia (Native Vegetation Program), and we thank Mick Quirk there for his support and interest.

For other assistance with this project we thank Janely Seah, Annie Palmer, Blair Grace, Brydie Hill, Gordon Duff, Jason Alexander and David Garnett.

References

- Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J., and Woinarski, J.C.Z. (2005). Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* **30**, 155-167.
- Andersen, A.N., Jacklyn, P., Dawes-Gromadzki, T., and Morris, I. (2005). *Termites of northern Australia*. (Barker Souvenirs, Alice Springs.)
- Bateman, W. (1955). *Forestry in the Northern Territory*. Leaflet no. 72. (Forestry and Timber Bureau, Canberra.)
- Bowman, D.M.J.S. (1988). Stability amid turmoil?: towards an ecology of north Australian eucalypt forests. *Proceedings of the Ecological Society of Australia* **15**, 149-158.
- Bowman, D.M.J.S., and Connors, G.T. (1996). Does low temperature cause the dominance of *Acacia* on the central Australian mountains? Evidence from a latitudinal gradient from 11° to 26° South in the Northern Territory, Australia. *Journal of Biogeography* **23**, 245-256.
- Bowman, D.M.J.S., and Panton, W.J. (1994). Fire and cyclone damage to woody vegetation on the north coast of the Northern Territory, Australia. *Australian Geographer* **25**, 32-35.
- Braithwaite, R.W., Parker, B.S., Wood, J.T., and Estbergs, J.A. (1985). The distribution and abundance of termite-induced tree hollows in tropical forests of northern Australia. In *Kakadu Fauna Survey final report* (ed. R.W. Braithwaite.) pp. 651-729. (CSIRO, Darwin.)
- Braithwaite, R.W., Miller, L., and Wood, J.T. (1988). The structure of termite communities in the Australian tropics. *Australian Journal of Ecology* **13**, 375-391.

- Burgman, M.A. (1996). Characterisation and delineation of the eucalypt old-growth forest estate in Australia: a review. *Forest Ecology and Management* **83**, 149-161.
- Cameron, D.M. (1985). Forest crops. In *Agro-research for the semi-arid tropics: northwest Australia*. (ed. R.C. Muchow.) pp. 165-178. (University of Queensland Press, St. Lucia.)
- Cook, G.D. (1994). The fate of nutrients during fires in tropical savanna. *Australian Journal of Ecology* **19**, 359-365.
- Cook, G.D., Taylor, R.J., Williams, R.J., and Banks, J.C.G. (2005). Sustainable harvest rates of ironwood, *Erythrophleum cholorostachys*, in the Northern Territory, Australia. *Australian Journal of Botany* **53**, 821-826.
- Cruse, B., Woinarski, J., and Brennan, K. (2007). Assessment of vegetation in regenerating and unmined woodland sites within the Alcan mining lease, 2006. Report to Matrix+ (Department of Natural Resources, Environment and The Arts, Darwin.)
- Crawley, M.J. (1993). *GLIM for ecologists*. (Blackwell, Cambridge.)
- Eyre, T.J. (2005). Hollow-bearing trees in large glider habitat in south-east Queensland, Australia: abundance, spatial distribution and management. *Pacific Conservation Biology* **11**, 23-37.
- Fensham, R.J., and Bowman, D.M.J.S. (1992). Stand structure and the influence of overwood on regeneration in tropical eucalypt forest on Melville Island. *Australian Journal of Botany* **40**, 335-352.
- Firth, R.S.C., Woinarski, J.C.Z., and Noske, R.A. (2006). Home range and den characteristics of the brush-tailed rabbit-rat *Conilurus penicillatus* in the monsoonal tropics of the Northern Territory, Australia. *Wildlife Research* **33**, 397-408.
- Fornier, J. (1999). Harvesting of *Eucalyptus phoenicea* for didgeridoo production: the use of remote sensing and GIS to map the distribution of a natural, cultural and economic resource B.Sc. (Hons.) thesis, Northern Territory University, Darwin.
- Fox, I.D., Neldner, V.J., Wilson, G.W., Bannink, P.J., Wilson, B.A., Brocklehurst, P.S., Clark, M.J., Dickinson, K.J.M., Beard, J.S., Hopkins, A.J.M., Beeston, G.R., Harvey, J.M., Thompson, E.J., Ryan, T.S., Thompson, S.L., Butler, D.W., Cartan, H., Addicott, E.P., Bailey, L.P., Cumming, R.J., Johnson, D.C., Schmeider, M., Stephens, K.M. and Bean, A.R. (2001). *The vegetation of the Australian tropical savannas*. (Environment Protection Agency: Brisbane.)
- Fox, R.E., and Clark, N.B. (1972). The incidence of termites in eucalypts of the Darwin area. *Australian Forest Research* **5**, 29-36.
- Gibbons, P., and Lindenmayer, D.B. (2002). *Tree hollows and wildlife conservation in Australia*. (CSIRO, Melbourne.)
- Gibbons, P., Lindenmayer, D.B., Barry, S.C., and Tanton, M.T. (2000). Hollow formation in eucalypts from temperate forests in southeastern Australia. *Pacific Conservation Biology* **6**, 218-228.

- Harper, M.J., McCarthy, M.A., van der Ree, R., and Fox, J.C. (2004). Overcoming bias in ground-based surveys of hollow-bearing trees using double-sampling. *Forest Ecology and Management* **190**, 291-300.
- Harper, M.J., McCarthy, M.A., and van der Ree, R. (2005). The abundance of hollow-bearing trees in urban dry sclerophyll forest and the effect of wind on hollow development. *Biological Conservation* **122**, 181-192.
- Houlder, D.J. (2000). ANUCLIM (Version 5.1). (Centre for Resource and Environmental Studies, Australian National University, Canberra.)
- Kerle, J.A. (1985). Habitat preference and diet of the northern brushtail possum *Trichosurus vulpecula* in the Alligator Rivers region, N.T. *Proceedings of the Ecological Society of Australia* **13**, 161-176.
- Lacey, C.J., and Whelan, P.I. (1976). Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Australian Forestry* **39**, 131-139.
- Lindenmayer, D.B., Cunningham, R.B., Nix, H.A., Tanton, M.T., and Smith, A.P. (1991). Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. *Australian Journal of Ecology* **16**, 91-98.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Tanton, M.T., and Nix, H.A. (1993). The abundance and development of cavities in *Eucalyptus* trees – a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management* **60**, 77-104.
- Lonsdale, W.M., and Braithwaite, R.W. (1991). Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* **16**, 363-374.
- Mucha, S.B. (1979). Estimation of tree ages from growth rings of eucalypts in northern Australia. *Australian Forestry* **42**, 13-16.
- Munks, S., Wapstra, M., Corkrey, R., Otley, H., Miller, G., and Walker, B. (2007). The occurrence of potential tree hollows in the dry eucalypt forests of south-eastern Tasmania, Australia. *Pacific Conservation Biology* **34**, 22-36.
- Pittman, G.W. (2003). Occurrence and use of tree hollows by mammals in fragmented and continuous savanna woodlands in northern Australia. B.Sc. (Hons.) thesis. Northern Territory University, Darwin.
- Prior, L.D., Eamus, D., and Bowman, D.M.J.S. (2004). Tree growth rates in north Australian savanna habitats: seasonal patterns and correlations with leaf attributes. *Australian Journal of Botany* **52**, 303-314.
- Prior, L.D., Brook, B.W., Williams, R.J., Werner, P.A., Bradshaw, C.J.A., and Bowman, D.M.J.S. (2006). Environmental and allometric drivers of tree growth rates in a north Australian savanna. *Forest Ecology and Management* **234**, 164-180.
- Rankmore, B. (2006). *Impacts of habitat fragmentation on the vertebrate fauna of the tropical savannas of northern Australia; with special reference to medium-sized mammals* PhD Thesis. (Charles Darwin University, Darwin.)

- Rankmore, B.R., and Price, O.F. (2004). Effects of habitat fragmentation on the vertebrate fauna of tropical woodlands, Northern Territory. In *Conservation of Australia's Forest Fauna* (second edition) (ed. D. Lunney). pp. 3452-473. (Royal Zoological Society of New South Wales, Sydney.)
- Russell-Smith, J., Yates, C., Edwards, A., Allan, G.E., Cook, G.D., Cooke, P., Craig, R., Heath, B., and Smith, R. (2003a). Contemporary fire regimes of northern Australia, 1997-2001: change since Aboriginal occupancy, challenges for sustainable management. *International Journal of Wildland Fire* **12**, 283-297.
- Russell-Smith, J., Whitehead, P.J., Cook, G.D., and Hoare, J.L. (2003b). Response of *Eucalyptus*-dominated savanna to frequent fires: lessons from Munmarlary 1973-1996. *Ecological Monographs* **73**, 349-375.
- Saunders, D.A. (1979). The availability of tree hollows for use as nest sites by white-tailed black cockatoos. *Australian Wildlife Research* **6**, 205-216.
- Stocker, G.C. (1976). *Report on cyclone damage to natural vegetation in the Darwin area after Cyclone Tracy, 25 December 1974*. (Australian Government Publishing Service, Canberra.)
- Taylor, R.J., and Chisholm, R.A. (2005). The occurrence of hollows in eucalypts and Ironwood *Erythrophleum cholorostachys* in the Gulf region of the Northern Territory and its implications for timber harvesting. *Pacific Conservation Biology* **11**, 57-63.
- Taylor, R., Woinarski, J. and Chatto, R. (2003). Hollow use by vertebrates in the Top End of the Northern Territory. *Australian Zoologist* **32**, 462-476.
- Tidemann, S.C., Boyden, J., Elvish, R., Elvish, J., and O'Gorman, B. (1992). Comparison of the breeding sites and habitat of two hole-nesting estrildid finches, one endangered, in northern Australia. *Journal of Tropical Ecology* **8**, 373-388.
- Werner, P.A. (1986). *Population dynamics and productivity of selected forest trees in Kakadu National Park*. Report to Australian National Parks and Wildlife service (CSIRO, Darwin.)
- Werner, P.A., and Prior, L.D. (2007). Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia. *Journal of Tropical Ecology* **23**, 611-622.
- Williams, R.J., and Douglas, M. (1995). Windthrow in a tropical savanna in Kakadu National Park, north Australia. *Journal of Tropical Ecology* **11**, 547-558.
- Williams, R.J., Duff, G.A., Bowman, D.M.J.S., and Cook, G.D. (1996). Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory. *Journal of Biogeography* **23**, 747-756.
- Williams, R.J., Cook, G.D., Gill, A.M., and Moore, P.H.R. (1999). Fire regimes, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50-59.
- Williams, R.J., Muller, W.J., Wahren, C.H., Setterfield, S.A., and Cusack, J. (2003). Vegetation. In *Fire in Tropical Savannas: the Kapalga experiment*. (eds A.N. Andersen, G.D. Cook, and R.J. Williams.) pp. 79-106. (Springer, New York.)

- Wilson, B.A., Brocklehurst, P.S., Clark, M.J. and Dickinson, K.J.M. (1990) *Vegetation survey of the Northern Territory, Australia*. Technical report no. 49. (Conservation Commission of the Northern Territory, Darwin.)
- Woinarski, J.C.Z. (2004). The forest fauna of the Northern Territory: knowledge, conservation and management. In *Conservation of Australia's Forest Fauna* (second edition) (ed. D. Lunney). pp. 36-55. (Royal Zoological Society of New South Wales, Sydney.)
- Woinarski, J.C.Z., Fisher, A., and Milne, D. (1999). Distribution patterns of vertebrates in relation to an extensive rainfall gradient and soil variation in the tropical savannas of the Northern Territory, Australia. *Journal of Tropical Ecology* 15, 381-398.
- Woinarski, J.C.Z., Risler, J., and Kean, L. (2004). The response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. *Austral Ecology* 29, 156-176.
- Woinarski, J., Risler, J., and Brennan, K. (2005). Alcan Gove vegetation rehabilitation. Report to Matrix+ (Department of Natural Resources, Environment and The Arts, Darwin.)
- Wormington, K.R., Lamb, D., McCallum, H.I., and Moloney, D.J. (2005). The status of hollow-bearing trees required for the conservation of arboreal marsupials in the dry sclerophyll forests of south-east Queensland, Australia. *Pacific Conservation Biology* 11, 38-49.

Table 1. The number of individual trees sampled, and grouping used for related species.

species-groups	no. of trees sampled	species included
<i>Eucalyptus tetradonta</i>	758	
<i>E. miniata</i>	638	
salmon gums	6	<i>E. tintinnans</i> , <i>E. alba</i> , <i>E. bigalerita</i>
<i>Corymbia porrecta</i>	22	
<i>C. polycarpa</i>	10	
smooth-barked bloodwoods	98	<i>Corymbia nesophila</i> , <i>C. dichromophloia</i> , <i>C. foelscheana</i> , <i>C. polysciadia</i> , <i>C. bleeseri</i> , <i>C. dunlopiana</i> , <i>C. latifolia</i> , <i>C. confertiflora</i>
rough-barked bloodwoods	17	<i>C. ferruginea</i> , <i>C. setosa</i>
<i>Erythrophleum chlorostachys</i>	132	
<i>Acacia</i> spp.	16	<i>A. auriculiformis</i> , <i>A. lamprocarpa</i>
other non-eucalypt species	31	<i>Alstonia</i> , <i>Brachychiton</i> , <i>Buchanania</i> , <i>Ficus</i> , <i>Gardenia</i> , <i>Gronophyllum</i> , <i>Lophostemon</i> , <i>Owenia</i> , <i>Petalostigma</i> , <i>Syzygium</i> , <i>Terminalia</i> , <i>Xanthostemon</i> spp.
dead trees	150	

Table 2. Calibration of ground-based sampling (“count”, “c”) with actual values derived from climbing and/or felling. Significance levels: ns = not significant, * p<0.05, ** p<0.01; *** p<0.001.

hollow variable	mean (count)	mean (actual)	r (count vs actual)	regression
all hollows	5.64	5.14	0.54 **	1.38 + 0.67c
all branch hollows	3.32	3.05	0.68 ***	0.81 + 0.67c
all trunk hollows	2.32	2.09	0.73 ***	0.42 + 0.72c
all hollows < 5 cm	2.55	2.45	0.49 *	1.10 + 0.53c
all hollows 5-10 cm	1.77	1.41	0.23 ns	1.00 + 0.23c
all hollows 10-20 cm	1.27	1.09	0.63 **	0.26 + 0.65c
all hollows >20 cm	0.05	0.18	0.46 *	0.14 + 0.86c

Table 3. Summary of site parameters.

variable	mean	s.e.	range
trees (stems>20cm)/ha	95.2	4.9	41.7 - 172.5
trees (stems>30cm)/ha	39.8	3.9	2.5 – 110
trees (stems>40cm)/ha	14.3	2.3	0 – 70
trees (stems>50cm)/ha	3.8	0.9	0 -30
trees (stems>60cm)/ha	0.9	0.3	0 - 10
basal area (m ² /ha)	7.4	0.6	2.2 - 20.2
median diameter (cm)	28.6	0.8	21.5 – 45
no. hollow trees/ha	62.6	4.6	7.5 – 122.5
no. hollows/ha	167.8	16.1	15 – 412.5
no. hollows >5cm diameter/ha	67.6	7.3	5 - 185

Table 4. Summary of generalised linear models relating tree characteristics with site-level environmental variables.

(a) Number of tree stems >20 cm per hectare.

term	estimate	Wald	p	% deviance explained (df)
intercept	94.5	309.0	<0.0001	17.9 (3)
grazing	-35.0	7.5	0.006	
cyclone (0)	14.8	5.0	0.025	
cyclone (1)	-4.1	0.3	0.58	

(b) Number of tree stems >30 cm per hectare.

term	estimate	Wald	p	% deviance explained (df)
intercept	5.4	0.23	0.63	60.6 (4)
soil depth	17.8	22.6	<0.0001	
fire	-23.8	16.1	0.00006	
cyclone (0)	9.6	7.5	0.0061	
cyclone (1)	18.9	22.1	<0.0001	

(c) Number of tree stems >40 cm per hectare.

term	estimate	Wald	p	% deviance explained (df)
intercept	0.247	0	0.98	66.2 (5)
rainfall	0.020	8.3	0.0040	
rock	-0.360	25.2	<0.0001	
fire	-16.90	23.6	<0.0001	
cyclone (0)	8.7	14.9	0.00011	
cyclone (1)	7.5	11.0	0.00091	

(d) Number of tree stems >50 cm per hectare.

term	estimate	Wald	p	% deviance explained (df)
intercept	-4.56	0.86	0.35	58.3 (5)
rainfall	0.0098	9.4	0.002	
rock	-0.115	12.5	0.0004	
fire	-6.51	17.1	0.00004	
cyclone (0)	3.46	11.5	0.0007	
cyclone (1)	2.93	8.2	0.004	

(e) Number of tree stems >60 cm per hectare.

term	estimate	Wald	p	% deviance explained (df)
intercept	0.85	0.64	0.43	47.6 (5)
soil texture	0.93	4.6	0.031	
rock	-0.055	10.4	0.0013	
fire	-2.08	11.45	0.0007	
cyclone (0)	0.49	2.16	0.14	
cyclone (1)	1.09	7.88	0.005	

(f) Median tree diameter.

term	estimate	Wald	p	% deviance explained (df)
intercept	17.5	12.0	0.0005	71.6 (6)
rainfall	0.00985	8.8	0.003	
rock cover	-0.115	23.9	<0.0001	
fire	-3.80	11.6	0.0007	
grazing	4.7	6.0	0.014	
cyclone (0)	2.4	11.0	0.0009	
cyclone (1)	5.3	53.6	<0.0001	

(g) basal area (m²/ha)

term	estimate	Wald	p	% deviance explained (df)
intercept	0.13	0.003	0.96	67.0 (5)
rainfall	0.0069	16.9	<0.0001	
rock cover	-0.090	28.3	<0.0001	
fire	-2.79	11.5	0.0007	
cyclone (0)	2.72	26.1	<0.0001	
cyclone (1)	1.93	13.0	0.0003	

Table 5. Summary of generalised linear models relating hollow abundance with site-level environmental variables.

(a) no. of hollows/ha

term	estimate	Wald	p	% deviance explained (df)
intercept	-201.0	6.8	0.0094	64.4 (4)
rainfall	0.288	33.4	<0.0001	
fire	-84.6	12.0	0.0053	
cyclone (0)	105.8	43.4	<0.0001	
cyclone (1)	24.5	2.4	0.12	

(b) no. of hollows/ha (including no. stems/ha, median tree diameter and basal area as candidate variables in model).

term	estimate	Wald	p	% deviance explained (df)
intercept	-267.5	20.8	<0.0001	74.5 (4)
rainfall	0.219	23.4	<0.0001	
basal area	15.6	33.9	<0.0001	
cyclone (0)	65.3	19.1	<0.0001	
cyclone (1)	0.7	0.003	0.96	

(c) no. of hollows >5 cm /ha.

term	estimate	Wald	p	% deviance explained (df)
intercept	-64.7	2.50	0.11	51.7 (4)
rainfall	0.107	16.5	<0.0001	
fire	-40.48	9.8	0.0017	
cyclone (0)	44.8	27.91	<0.0001	
cyclone (1)	6.1	0.52	0.47	

(d) no. of hollows >5 cm /ha. (including no. stems/ha, median tree diameter and basal area as candidate variables in model)

term	estimate	Wald	p	% deviance explained (df)
intercept	-80.59	6.8	0.0091	67.4 (5)
rainfall	0.077	11.0	0.0009	
stems/ha	-0.46	5.4	0.021	
basal area	10.66	30.37	<0.0001	
cyclone (0)	26.94	12.3	0.0005	
cyclone (1)	-10.78	2.1	0.14	

(e) no. of hollow trees /ha.

term	estimate	Wald	p	% deviance explained (df)
intercept	-65.0	7.7	0.0057	48.1 (3)
rainfall	0.086	27.6	<0.0001	
cyclone (0)	27.3	24.8	<0.0001	
cyclone (1)	6.6	1.5	0.22	

(f) no. of hollow trees /ha. (including no. stems/ha, median tree diameter and basal area as candidate variables in model)

term	estimate	Wald	p	% deviance explained (df)
intercept	-69.9	26.4	<0.0001	82.5 (5)
rainfall	0.051	24.4	<0.0001	
stems/ha	0.60	84.4	<0.0001	
cyclone (0)	15.7	20.9	<0.0001	
cyclone (1)	8.8	7.7	0.0055	

Table 6. Summary of generalised linear models for the number of hollows in individual trees. For the term “species-group”, factors are compared with the species *E. tetradonta*.

(a) all hollows

term	factor	estimate	Wald	p	% deviance explained (df)
intercept		-1.53	255.5	<0.0001	38.4 (16)
dbh		0.047	823.5	<0.0001	
tree height		0.028	35.3	<0.0001	
tree shape		-0.002	4.9	0.026	
fire impact		-0.204	35.5	<0.0001	
tree health		0.366	108.1	<0.0001	
termite sign		0.133	38.5	<0.0001	
tree species-group			126.4	<0.0001	
	miniata	0.36	31.4	<0.0001	
	dead	-0.04	0.2	0.65	
	Erythrophleum	-0.05	0.3	0.56	
	smooth bloodwoods	0.27	9.0	0.003	
	Acacia	-1.23	10.8	0.001	
	porrecta	0.27	2.6	0.10	
	polycarpa	0.23	1.0	0.32	
	ferruginea	0.13	0.44	0.51	
	other non-eucalypts	-0.47	4.44	0.035	
	salmon gums	0.55	8.0	0.005	

(b) hollows >5 cm

term	factor	estimate	Wald	p	% deviance explained (df)
intercept		-3.27	410.9	<0.0001	39.8 (15)
dbh		0.065	853.6	<0.0001	
tree shape		0.005	10.8	0.001	
fire impact		-0.314	35.4	<0.0001	
tree health		0.495	92.7	<0.0001	
termite sign		0.204	36.8	<0.0001	
tree species-group			55.3	<0.0001	
	miniata	0.505	14.6	<0.0001	
	dead	0.047	0.09	0.77	
	Erythrophleum	-0.018	0.01	0.92	
	smooth bloodwoods	0.244	1.90	0.17	
	Acacia	-1.63	3.19	0.07	
	porrecta	0.388	1.78	0.18	
	polycarpa	0.420	1.33	0.25	
	ferruginea	-0.497	1.12	0.29	
	other non-eucalypts	-0.961	3.19	0.07	
	salmon gums	1.202	23.4	<0.0001	

(c) hollows >10 cm

term	factor	estimate	Wald	p	% deviance explained (df)
intercept		-10.9	801.3	<0.0001	42.6 (10)
dbh		0.085	395.9	<0.0001	
fire impact		-0.47	22.3	<0.0001	
tree health		0.66	46.5	<0.0001	
termite sign		0.36	28.0	<0.0001	
tree species-group					
	miniata	5.99	318.2	<0.0001	
	dead	5.73	221.1	<0.0001	
	Erythrophleum	-3.96	43.7	<0.0001	
	smooth bloodwoods	5.77	178.8	<0.0001	
	Acacia	-11.32	26.6	<0.0001	
	porrecta	-11.71			
	polycarpa	6.12	60.9	<0.0001	
	ferruginea	-8.89			
	other non-eucalypts	-8.40			
	salmon gums	6.93			

(d) hollows >20 cm

term	factor	estimate	Wald	p	% deviance explained (df)
intercept		-15.1	435.4	<0.0001	46.2 (9)
dbh		0.098	82.9	<0.0001	
fire impact		-0.63	6.8	0.009	
tree health		1.13	21.5	<0.0001	
termite sign		0.57	8.6	0.003	
tree species-group					
	miniata	7.1	172.5	<0.0001	
	dead	7.2	119.6	<0.0001	
	Erythrophleum	-12.5	18.8	<0.0001	
	smooth bloodwoods	6.6	35.1	<0.0001	
	Acacia	-11.2			
	porrecta	-7.5			
	polycarpa	9.5	110.6	<0.0001	
	ferruginea	-8.0			
	other non-eucalypts	-7.1			
	salmon gums	9.2			

Table 7. Mean annual growth rates reported by Prior *et al.* (2006). Values shown are means, with s.e. and N in brackets.

species	size	annual dbh increment				overall mean
		early fires	late fires	no fires	extreme fire	
<i>E. miniata</i>	sapling	0.14 (0.09, 70)	0.07 (0.06, 203)	0.31 (0.04, 237)	-1.15 (0.31, 14)	0.25
	adult	0.37 (0.04, 294)	0.10 (0.03, 359)	0.24 (0.02, 741)	0.05 (0.12, 44)	0.23
<i>E. tetradonta</i>	sapling	0.02 (0.09, 63)	-0.42 (0.07, 128)	0.12 (0.05, 142)	-2.20 (0.20, 2)	-0.12
	adult	0.38 (0.05, 147)	-0.12 (0.04, 258)	0.18 (0.01, 1152)	0.40 (0.10, 2)	0.15

Table 8. Comparison between results reported here and analogous studies in Australian forests elsewhere.

study	region	stand basal area (m ² /ha)	maximum size of sampled tree (cm dbh)	no. hollow trees/ ha	proportion of trees with hollows		no. hollows / ha
					at 30 cm dbh	at 50 cm dbh	
this study		2.2 – 20 (for stems >20 cm dbh only)	65	8 – 122 (mean 63) [for all hollows]	0.78 [for all hollows] 0.39 [for hollows >5 cm]	0.93 [for all hollows] 0.87 [for hollows >5 cm]	15 – 413 (mean 168) [for all hollows] 5 – 185 (mean 68) [for hollows > 5 cm]
Gibbons <i>et al.</i> (2000)	mountain forests, SE Australia	20 - 120 (live eucalypts)	300+	10 - 30	0 - 0.15	0 - 0.2	
Munks <i>et al.</i> (2007)	dry eucalypt forests, Tasmania			14 - 33			24 – 55 [for hollows >3 cm]
Wormington <i>et al.</i> (2005)	dry sclerophyll forest, SE Qld	8 - 30	100+	1.8 - 20			
Eyre <i>et al.</i> (2005)	dry sclerophyll forest, SE Qld		80+	1 – 19 (mean 5.9) [for hollows >10 cm]			
Harper <i>et al.</i> (2005)	dry sclerophyll forest, urban SE Australia		100+	0 -21 (mean 5.8) [for hollows >5 cm]		0.1 – 0.3	
Gibbons & Lindenmayer (2003)	range of studies in temperate forests			13-27			
	range of studies in temperate woodlands			7-17			

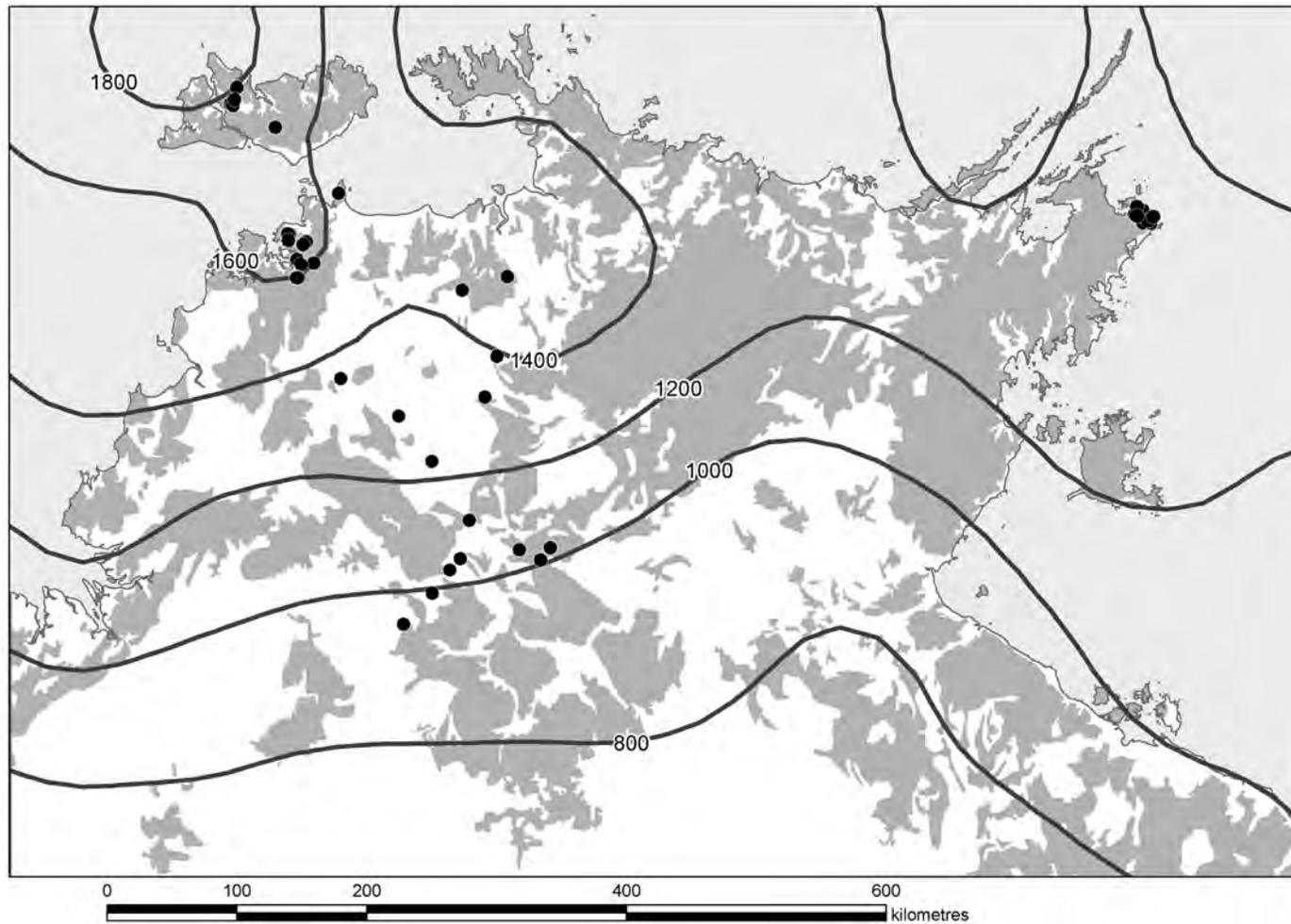


Figure 1. Location of sampling sites, and of forests dominated by *Eucalyptus miniata* and/or *E. tetradonta* (shaded).



(a)



(b)



(c)

Figure 2. Examples of structure in forests dominated by *Eucalyptus miniata* and/or *E. tetradonta*: (a) tall forests typical of higher rainfall areas; (b) forests showing some partial damage from recent cyclone (Cyclone Ingrid), (c) forest regrowth 33 years after complete felling in Cyclone Tracy.



Figure 3. Example of calibration of ground-based hollow assessment with direct count by arborists.

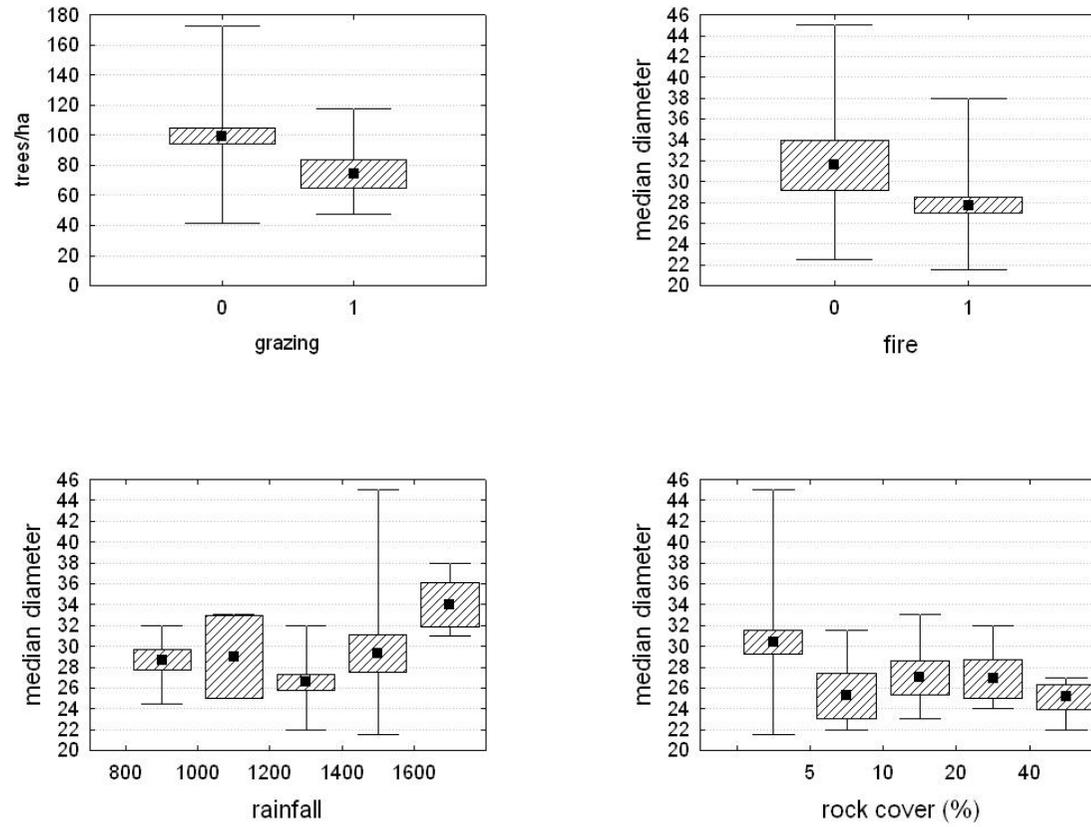


Figure 4 (a). Significant relationships between tree size, forest structure and hollow abundance variables with site environmental variables

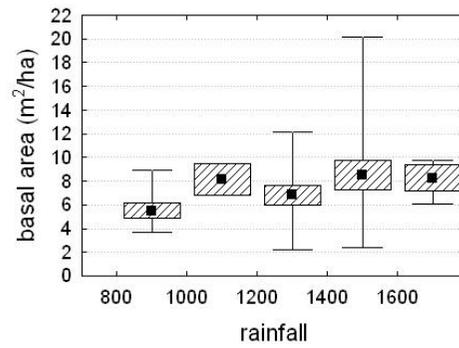
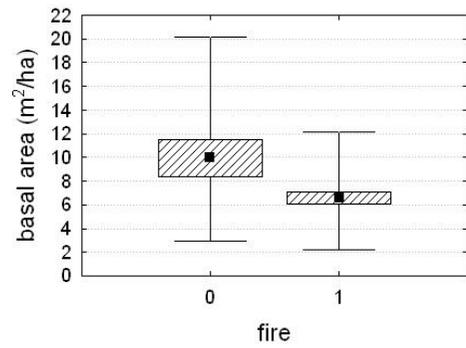
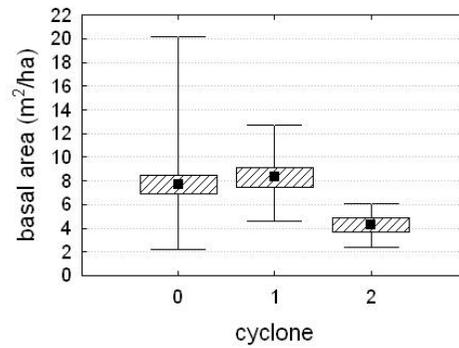
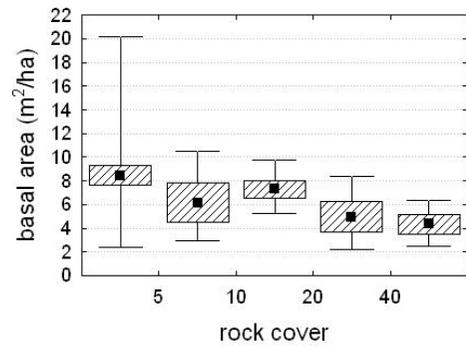


Figure 4 (b). Significant relationships between tree size, forest structure and hollow abundance variables with site environmental variables

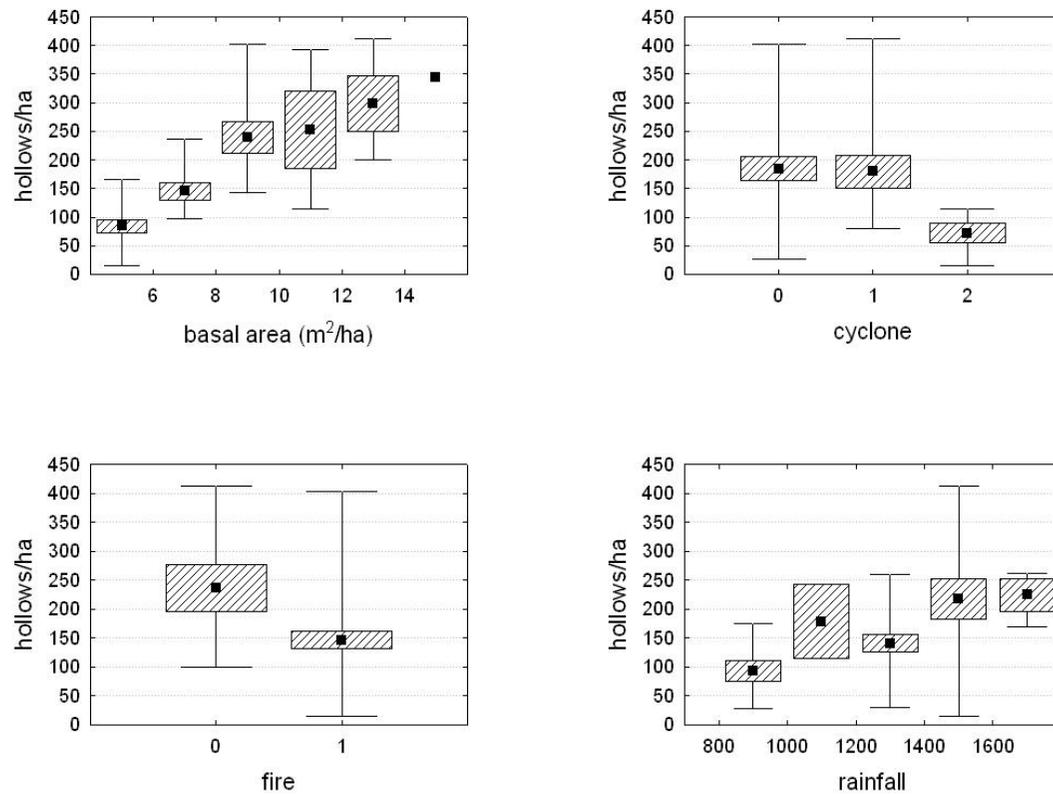


Figure 4 (c). Significant relationships between tree size, forest structure and hollow abundance variables with site environmental variables

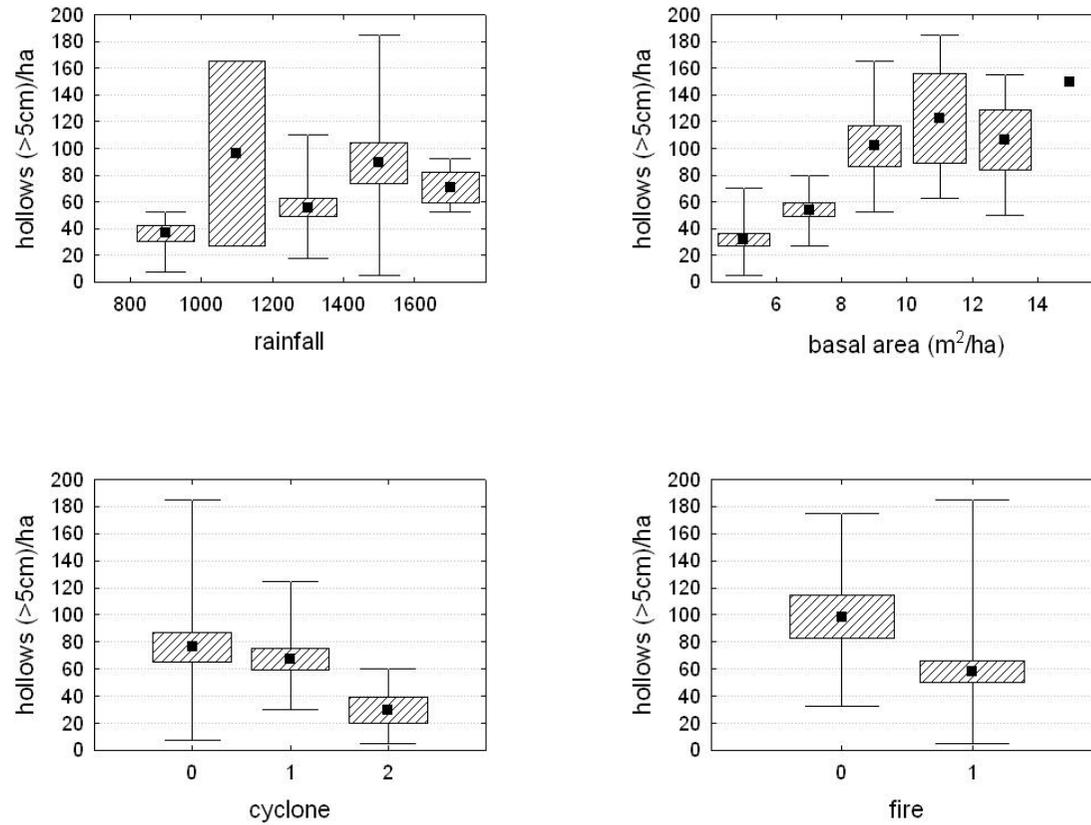


Figure 4 (d). Significant relationships between tree size, forest structure and hollow abundance variables with site environmental variables

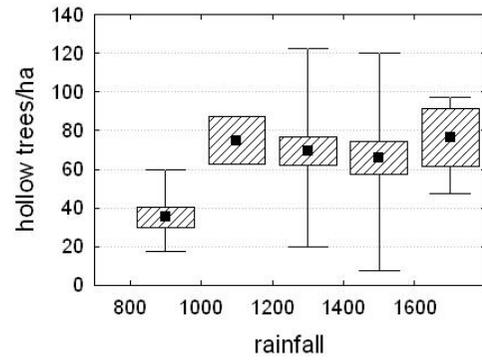
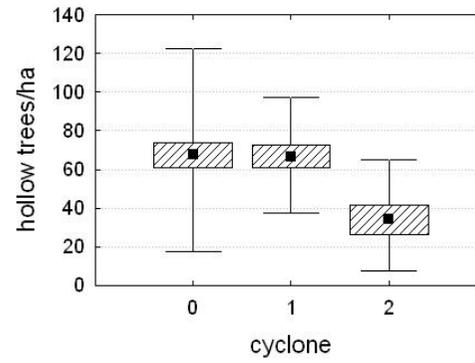
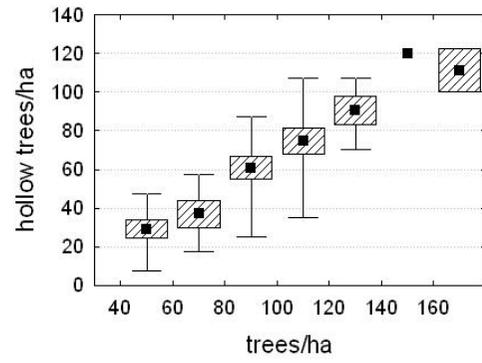


Figure 4 (e). Significant relationships between tree size, forest structure and hollow abundance variables with site environmental variables

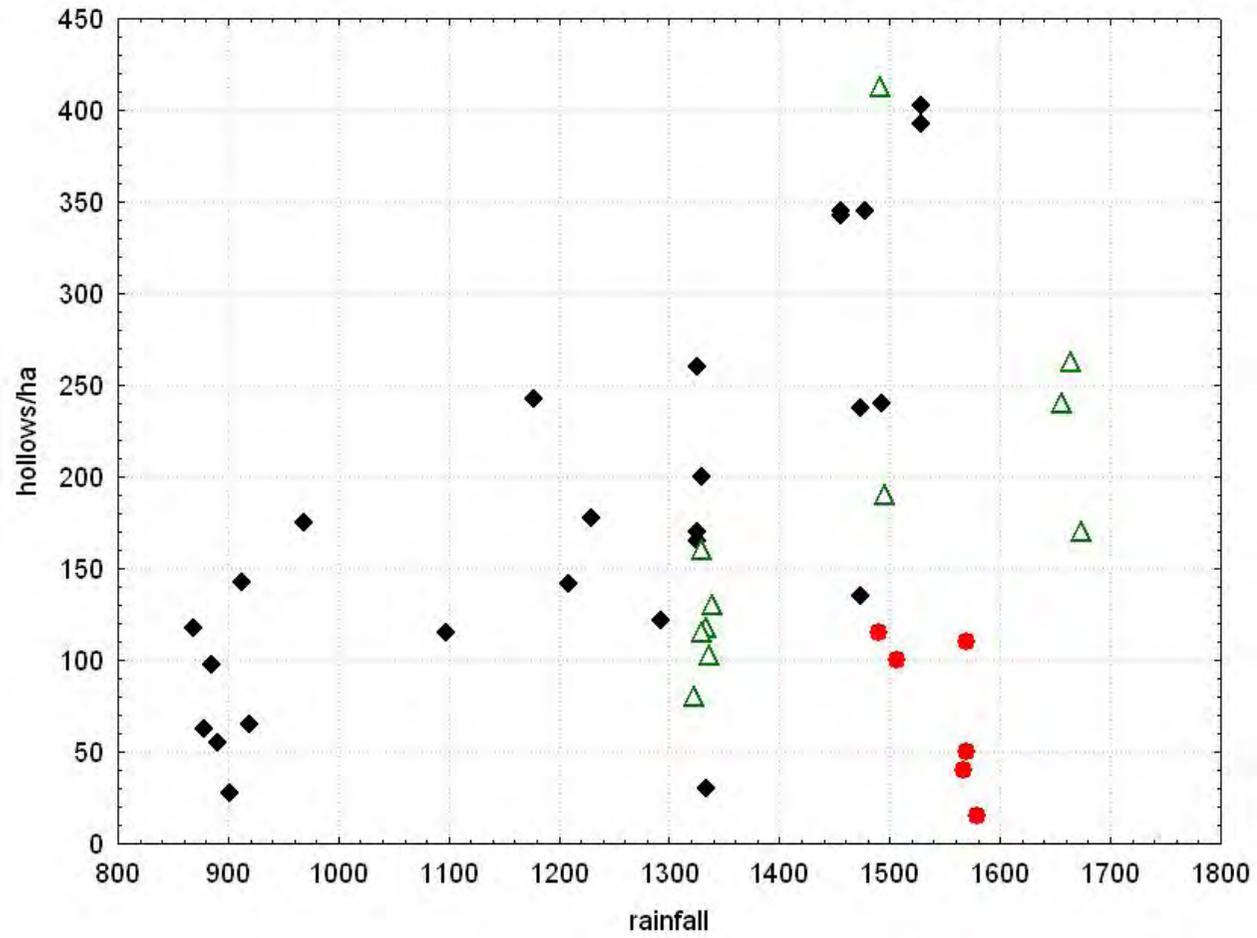


Figure 5. Relationship between hollow abundance and average annual rainfall, with cyclone impact indicated (filled black diamond = no impact; filled red circle=33 year regrowth after Cyclone Tracy; open green triangle=partial impact of more recent Cyclone Ingrid and/or Monica).

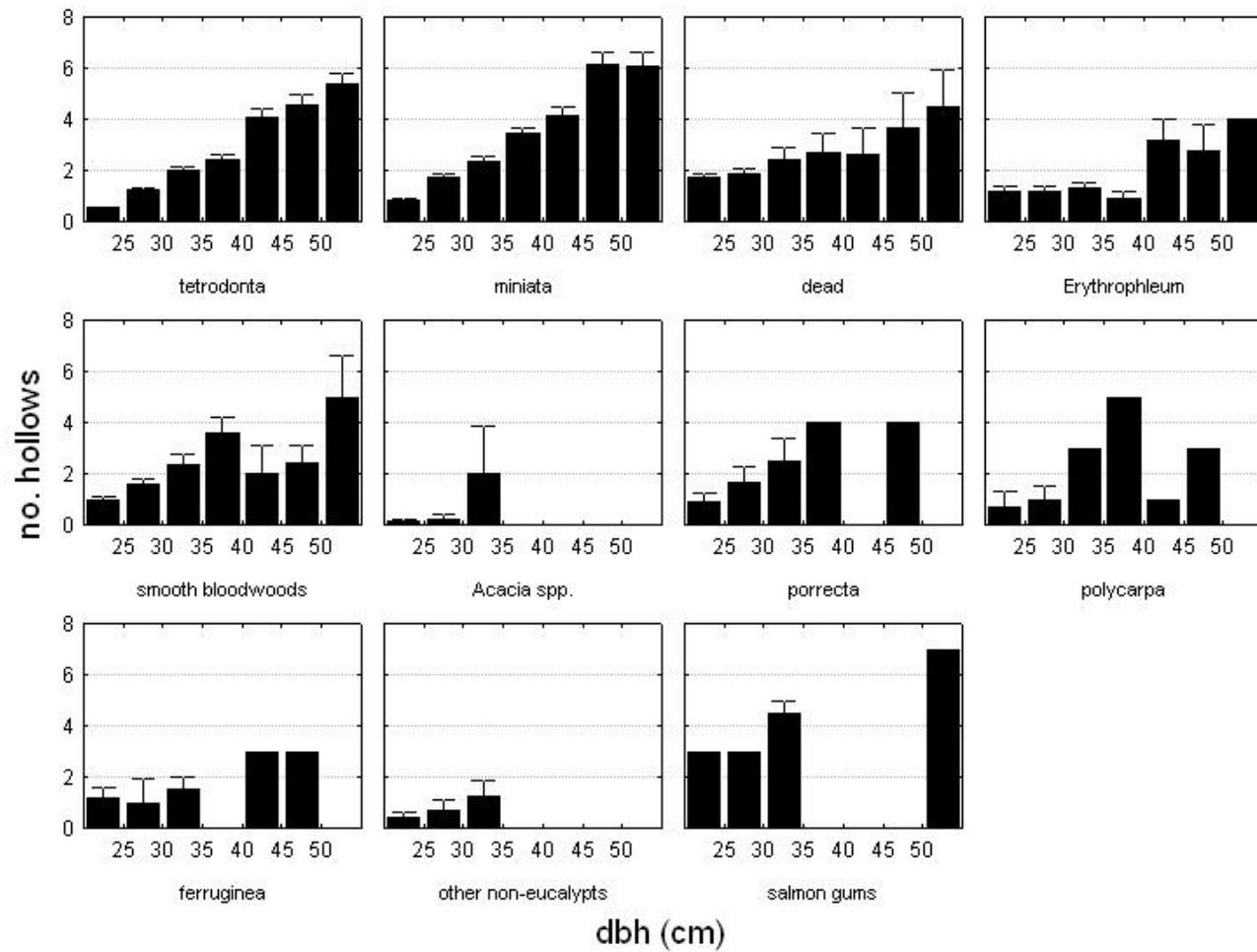


Figure 6 (a). Relationships between hollow abundance (all sizes) and tree size and species.

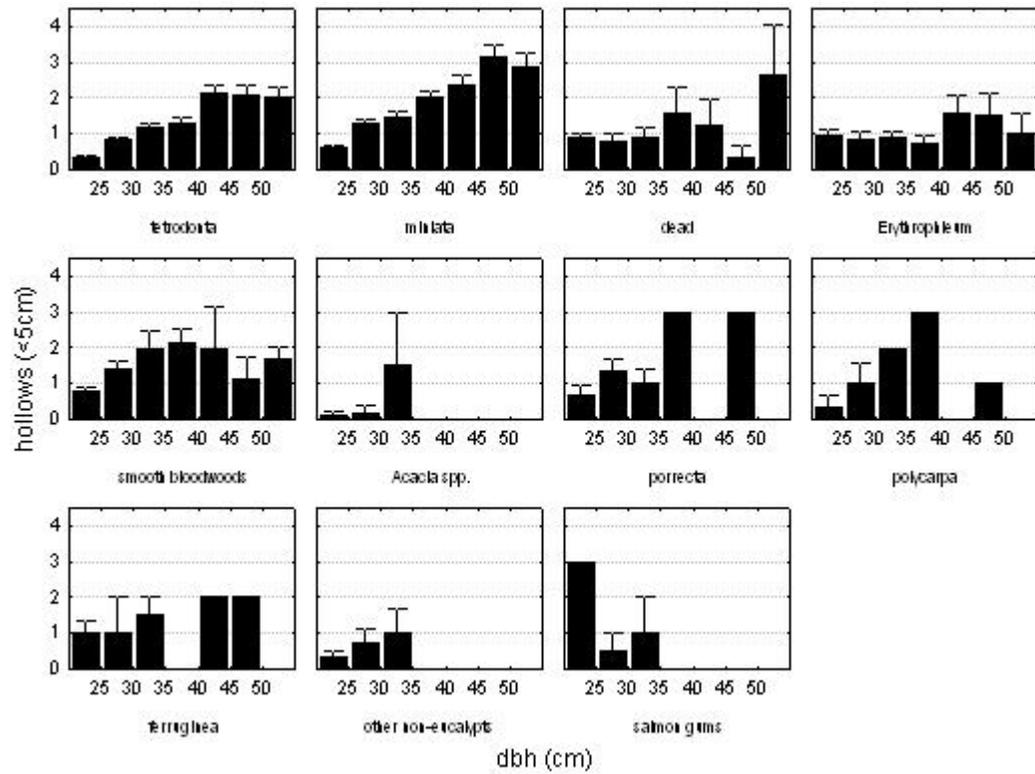


Figure 6 (b). Relationships between hollow abundance ($< 5\text{cm}</math>) and tree size and species.$

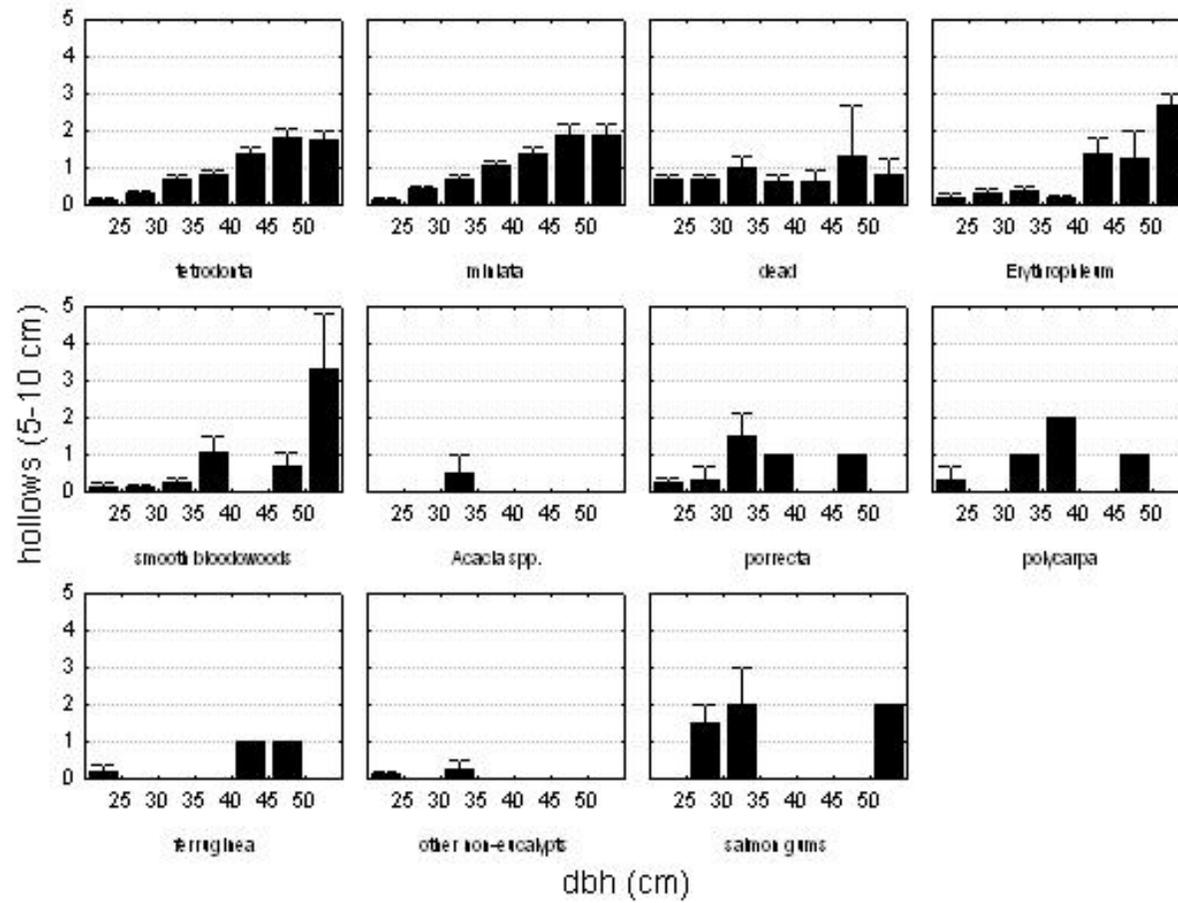


Figure 6 (c). Relationships between hollow abundance (5-10 cm) and tree size and species.

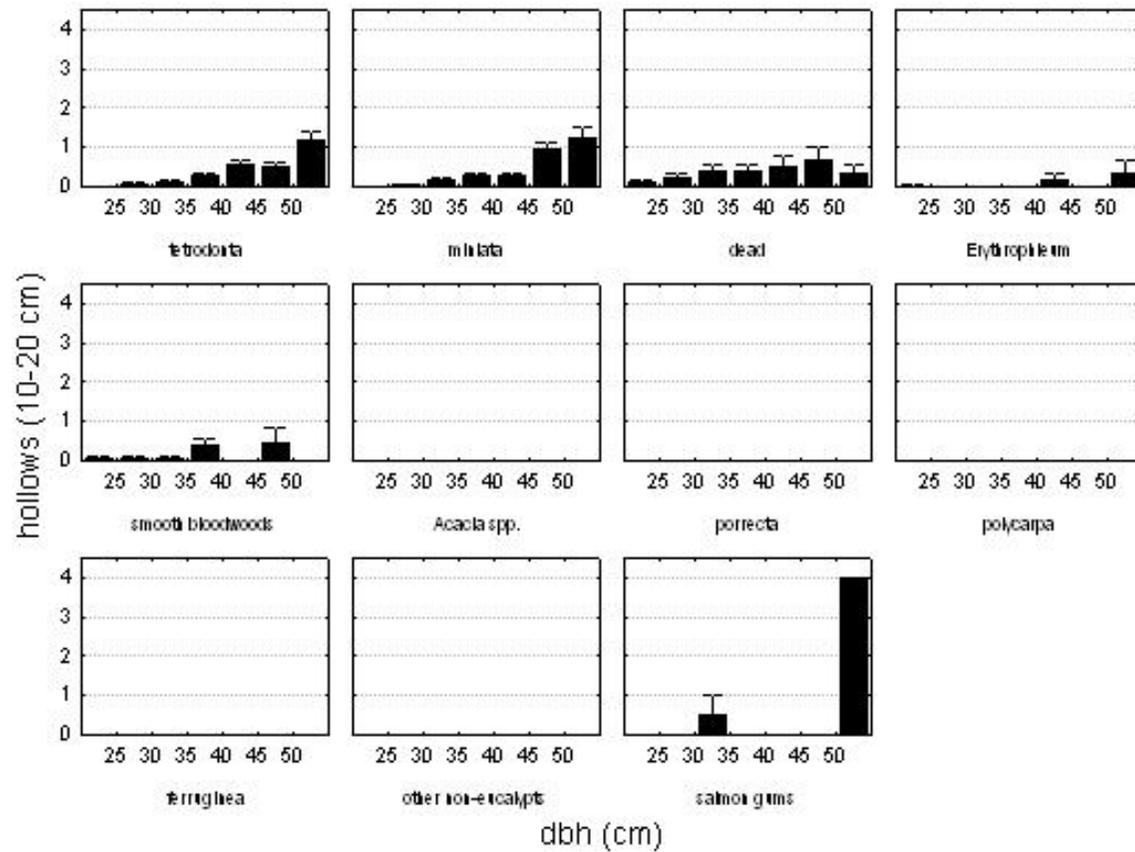


Figure 6 (d). Relationships between hollow abundance (10-20 cm) and tree size and species.

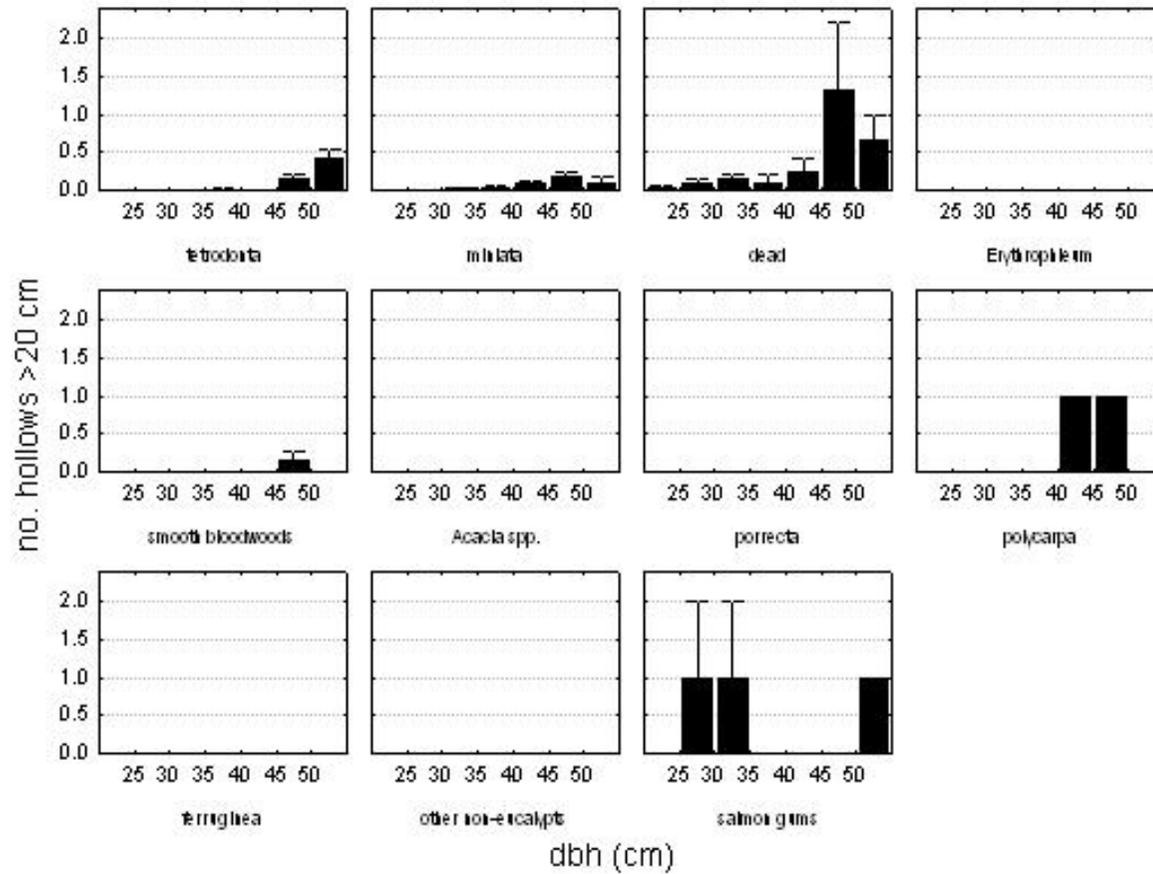


Figure 6 (e). Relationships between hollow abundance (>20 cm) and tree size and species.

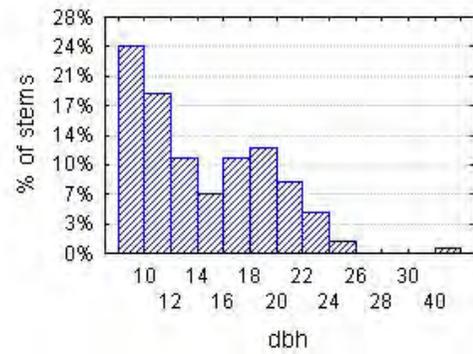
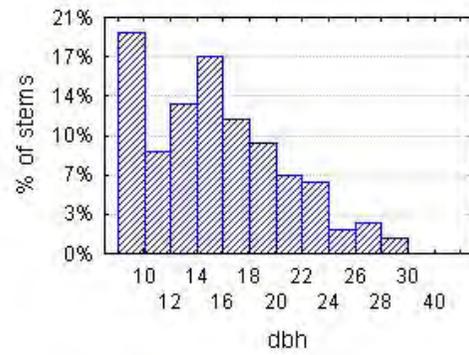
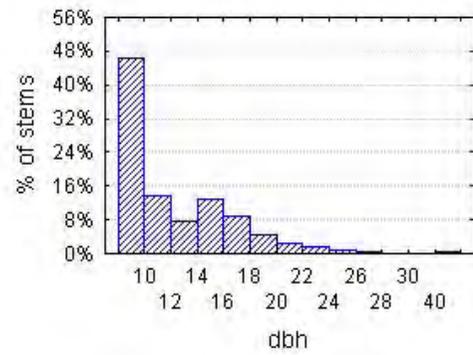


Figure 7. Frequency distribution of eucalypt stem sizes (dbh) at three sites of regrowth eucalypt forest 33 years after Cyclone Tracy.