Cyclones, fire, and termites: the drivers of tree hollow abundance in northern Australia’s mesic tropical savanna

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Tree hollows are a vital wildlife feature, whose abundance and availability has declined in many regions due to broad-scale vegetation clearance, timber-harvesting, and disturbance such as fire. In the temperate forests and woodlands of eastern and southern Australia, the loss of large, old trees and associated tree hollows has severely impacted populations of hollow-dependent fauna. In the tropical savannas of northern Australia, many hollow-dependent mammals are in decline, and habitat simplification and resultant hollow limitation have been suggested as potential contributors to these declines. Hence, we sought to quantify the abundance of hollows, and identify the key drivers of this abundance in northern Australian savannas. We modelled the environmental and ecological correlates of hollow abundance across an extensive area of eucalypt savanna in Australia’s Northern Territory. We found that hollow abundance was significantly related to tree characteristics (size, species) and broad environmental gradients (annual rainfall, soil depth). Key disturbances – cyclones, fire, and termites – substantially disrupted these relationships and led to high variation in hollow abundance, even at a local scale. Hollow abundance across the study area was high by both Australian and global standards (hollows > 5 cm entrance diameter: 88 ha\(^{-1}\), hollows > 10 cm: 23 ha\(^{-1}\)) and greatest in high rainfall areas (associated with the abundance of large eucalypts). Many arboreal mammal species in northern Australia have now contracted to higher rainfall parts of their former range (where hollows are at highest density); however such higher rainfall areas are also more likely to be affected by stochastic cyclonic events that can severely reduce the abundance of hollows. Hollow abundance was also affected by recent fire history and, in many areas, the current regime of frequent, high intensity fires will lead to marked reduction in this resource.

**Key words**

Tree cavities; hollow-bearing trees; eucalypt woodland; disturbance ecology; arboreal fauna
1. Introduction

Tree hollows are a critical resource for many animal species across the globe (e.g. Blakely et al. 2008, Lindenmayer and Wood 2010, Ouellet-Lapointe et al. 2012, Altamirano et al. 2017). As such, tree hollows form part of the fundamental habitat requirements of hollow-using species and a reduction in hollow abundance has been linked to a reduction in the abundance, survival, and breeding success of many hollow-dependent species (e.g. Du Plessis 1995, Sedgeley 2001, Robles et al. 2011, Bonaparte and Cockle 2017, Lindenmayer et al. 2017).

In Australia, many vertebrate and invertebrate species rely on tree hollows (Taylor et al. 2003, Goldingay 2009, 2012). The co-evolution of Australia’s eucalypts (family: Myrtaceae) and its diverse fauna has created the opportunity for many hollow-using species to co-exist in the forests and woodlands across the continent (Woinarski et al. 1997), and even in the absence of avian excavators such as woodpeckers, hollows are often abundant in many Australian forests and woodlands (Gibbons and Lindenmayer 2002, Remm and Lõhmus 2011). This is primarily due to eucalypt propensity for hollow formation by microbial decay of heartwood, especially after mechanical disturbance, e.g. wind, water, fire, termites (Gibbons and Lindenmayer 2002, Harper et al. 2005, Taylor and Chisholm 2005, Adkins 2006).

Many studies have documented the abundance of hollows in temperate Australia, and the factors influencing this abundance, with hollow availability found to be reduced by broad-scale vegetation clearance, timber-harvesting, livestock grazing, soil structural decline, and fire (Yates and Hobbs 1998, Lindenmayer et al. 2012). In at least some habitats and regions in temperate Australia, hollow availability is limiting for hollow-dependent species, and many of these species are consequently declining and are now threatened (Lindenmayer et al. 1997, Webb and Shine 1997, Ford et al. 2001, Gibbons et al. 2002, Lindenmayer et al. 2011, Manning et al. 2013).
In contrast, little is known about hollow availability and the factors that influence it in woodlands of the tropical savannas of northern Australia, whose environmental and disturbance factors show some distinct differences to that of temperate Australia (Bowman 1988). For example, less than 2% of the savanna woodlands in the region considered here have been cleared (Woinarski 2004), substantially less than for Australian forests and woodlands generally (Bradshaw 2012). Furthermore, in the north Australian savannas, timber-harvesting has been limited and focused almost exclusively on two tree species, Callitris intratropica and Erythrophleum chlorostachys, both favoured for timber because they are relatively termite-resistant (Hanssen and Wigston 1989, Woinarski and Dawson 2004). However, the savanna woodlands of northern Australia are now subject to increasing intensification of land use and marked changes in fire regime (Woinarski et al. 2007): such changes may be expected to increasingly influence hollow availability and hence habitat suitability for many hollow-dependent species.

Of the nine mammal species that have declined markedly in northern Australia since its European settlement, six are arboreal (including semi-arboreal and scansorial) and are facultative or obligate hollow users (Fitzsimons et al. 2010). For most of this set of species, the decline occurred earlier (and most severely) in lower rainfall areas (McKenzie 1981, Woinarski et al. 2011, Start et al. 2012, Ziembicki et al. 2015). Despite this recognised decline of hollow-dependent species, there have been very few studies of hollow abundance and the extent to which animals are reliant on hollows in the tropical savannas of northern Australia. Braithwaite et al. (1985) and Taylor and Chisholm (2005) conducted snapshot estimates of hollow prevalence in Kakadu National Park and the Gulf region of the Northern Territory, respectively. Both reported an increase in hollow abundance with tree size (estimated by diameter at breast height, DBH) and significant differences in hollow abundance among tree species, but neither of these localised studies investigated the
environmental predictors of hollow abundance. Some more recent studies of single bird or mammal species have demonstrated or inferred that hollows may be limiting, and such limitation may constrain breeding success or abundance of threatened hollow-dependent species in Australian savanna (Kurucz 2000, Pittman 2003, Firth et al. 2010, Brazill-Boast et al. 2011, Hohnen et al. 2015). However, an explicit link between potential hollow limitation and arboreal fauna declines at a landscape scale has not been established. This study does not directly address this issue: rather, we establish a foundation towards future studies on it by describing hollow abundance at a landscape and site scale and the factors (including management issues) that affect such abundance.

As in other savannas globally, the vegetation structure and floristic composition of Australia’s tropical savannas is controlled by a highly seasonal wet–dry climate and frequent fires (Sankaran et al. 2005, Staver et al. 2011, Lehmann et al. 2014) Furthermore, a distinct combination of factors are operating in this tropical, mesic savanna including high monsoonal summer rainfall, low soil fertility, low human population density, and disturbance such as cyclones and very frequent fires (Bowman 1988, Woinarski et al. 2007). Across the area sampled in this study, the fire regime is approximately bi- or triennial in frequency with around two-thirds of burnt area occurring in the late dry season, when fires are of highest intensity and impact (Edwards et al. 2018). Arboreal termites are also abundant in these woodlands, resulting in a high incidence of piping and hence hollow formation in eucalypt species (Taylor and Chisholm 2005, Werner and Prior 2007).

Therefore, in the first study of its kind in Australian tropical savanna, we (i) assess variability in stand structure and hollow abundance across an extensive rainfall gradient in the tropical mesic savannas of northern Australia, and across a set of sites exposed to variable disturbance regimes; (ii) investigate the factors related to the abundance of hollows and of hollow size composition at a landscape scale and at the scale of the individual tree; (iii)
compare characteristics of hollow abundance in these environments with those in temperate
forests and woodlands, and (iv) consider how the observed abundance of hollows in this
environment, and the factors that affect that abundance, may affect hollow-dependent fauna
and its management.

2. Methods

2.1 Field procedures

Tree hollow abundance was assessed for 1809 trees on 43 sites in eucalypt woodlands in the
monsoonal tropics of the Northern Territory (Fig. 1). All sample sites were in woodlands
dominated or co-dominated by the tree species *Eucalyptus miniata* and *E. tetrodonta*.
Woodlands dominated by either or both of these species are the most extensive and
characteristic woodland types in northern Australia, comprising ca. 180,000 km² of
continuous, intact savanna in the Northern Territory (Woinarski 2004) and ca. 445,000 km²
across northern Australia (Fox et al. 2001). Sites were selected to sample broadly across the
rainfall, edaphic, disturbance and topographic range spanned by these woodlands, and every
site was situated in a relatively homogenous environment. Typical of the region, no sites
sampled had been subject to timber-harvesting, and no cut stumps indicative of previous
timber-harvesting were observed in our sampling.

At 39 of the 43 sites, we established four belt transects (50 x 20 m, i.e. 0.4 ha) and all
trees with a diameter at breast height (DBH) greater than 20 cm were counted and identified
to species or species-group (in some cases several taxonomically similar tree species were
indistinguishable in the field due to an absence of reproductive material at the time of
sampling). Due to site constraints, the total area sampled at four of the 43 sites differed from
the standard 0.4 ha (i.e. 0.2 ha at two sites, 0.57 ha and 0.6 ha at one site respectively). This
methodological variation is accounted for in the models, with all per site abundance variables
evaluated per hectare. Trees smaller than 20 cm DBH were excluded given they were likely to contain hollows (Kurucz 2000, Taylor and Chisholm 2005), with this exclusion consistent with precedents of previous hollow availability studies (Wormington et al. 2005).

Hollows were counted from the ground (using binoculars where required) for each tree within the transects at a site. The presence of a hollow was defined as any entrance that may have depth exceeding the minimum entrance diameter. Every hollow present was categorised into one of four size classes, based on minimum entrance diameter: small (< 5 cm); medium (5 - 10 cm); large (10 - 20 cm); very large (> 20 cm). At sites where fewer than 50 trees occurred in the four belt transects, additional trees were sampled randomly outside the transects where possible, to bring the tally to a minimum of 50 trees per site. These additional trees were included in the tree-level, but not the site-level, analysis. The range of tree characteristics and environmental variables recorded for each tree and site is detailed in Appendix A, with these variables shown in many studies elsewhere to be useful predictors of hollow abundance (Munks et al. 2007, Koch et al. 2008, Fox et al. 2009, Lindenmayer et al. 2016, 2017).

The reliability of our ground-based hollow counts was assessed by comparing estimates against actual counts for a random selection of 22 trees, of which 14 were climbed by arborists and eight were felled. A hollow was confirmed if hollow depth exceeded minimum entrance diameter. There was a weak tendency (10% difference) to over-estimate hollow numbers from ground counts, although this tendency was evident only when compared with counts derived from tree-climbing (where for safety reasons the tree-climbers did not include hollows from more peripheral small branches). The ground-based assessments of total hollows per tree were strongly correlated with actual counts (r = 0.75, p < 0.001).

2.2 Statistical analysis
Analysis considered hollow counts at site-level and the level of an individual tree. All models were run using R version 3.4.3 (R Core Team 2017). The density of total hollows (and also density of hollows in the four size classes) was modelled against all possible combinations of predictor variables (Appendix A) using generalised linear models (GLM) at site-level and generalised linear mixed models (GLMM) with site as a random effect at tree-level (R package lme4: Bates et al. (2015), R package glmmADMB: Fournier et al. (2012)). Poisson models were fitted first, but where overdispersion was evident, negative binomial distributions were considered, followed by zero-inflated models (Zuur et al. 2012). Model validation was conducted by evaluation of Pearson residuals plotted against fitted values as well as included and excluded covariates to check for homogeneity, independence and model fit (Zuur et al. 2012). To assess whether Poisson or negative binomial models predicted enough zeros, 10,000 datasets were simulated from the models and the percentage of zeros calculated for each simulated dataset. If the observed versus simulated percentage of zeros was similar, the model was accepted.

Due to collinearity between bole height (height of first branch) and tree height, and between bole height and bole:trunk ratio (ratio of bole height to total tree height), bole height was dropped from tree-level models. Tree height and bole:trunk ratio were retained (little collinearity). Grazing was strongly correlated with rainfall, rock cover with soil texture and depth, and stand density/stand basal area with soil depth and cyclone impact. Therefore grazing, rock cover, stand density and stand basal area were dropped from site-level models, however information on their relationships with hollow density is presented in Appendix B. We allowed the effect of continuous variables to be non-linear by introducing a quadratic term into models. All continuous variables were standardised by dividing by two times the standard deviation (Gelman 2008).
An information-theoretic approach to model selection was used to identify the best models according to Akaike Information Criterion (AIC) (R package MuMIn: Barton (2016)). These best models were used for visualisation of variable effects (R package visreg: Breheny and Burchett (2016)). Log-transformed total area sampled per site was incorporated as an offset variable in site-level models and its inclusion fixed in all models during model-averaging. Relationships are presented for highly influential predictors of total hollows per tree or per site, but where additional predictors were important or relationships differed from that of total hollows, figures were presented for hollow size classes.

3. Results

Across all sites sampled, we found a mean hollow density of 207 (± 22.1 SE) ha⁻¹, of which 88 (± 11.6) ha⁻¹ were > 5 cm in diameter and 23 (± 4.8) ha⁻¹ were > 10 cm (Table 1). These values varied by more than an order of magnitude between sites (total hollows: 15 – 735 ha⁻¹, Table 1). The mean density of hollow-bearing trees was 73 (± 5.8) ha⁻¹, and this too varied substantially among sites (range: 8 – 200, Table 1). Hollows occurred in 67% of all trees sampled. Trees > 50 cm DBH comprised only a very small proportion (4%) of all trees, with mean density of 5.3 (± 1.2) ha⁻¹ (range 0 – 40 ha⁻¹). The densities of such large trees were highest on high rainfall sites (>1300 mm mean annual rainfall), with a mean density (ha⁻¹) of 8 (± 1.4) trees > 50 cm DBH and 23 (± 3.2) trees > 40 cm DBH on high rainfall sites compared with 2 (± 0.4) trees > 50cm DBH and 15 (± 1.9) trees > 40 cm DBH on lower rainfall sites. Woody stand basal area averaged 9.0 (± 0.6) m².ha⁻¹ (range 2.2 – 32.2 m².ha⁻¹) across all sites (Table 1). There was a strong relationship between stand basal area and total hollow density, with rainfall and cyclone impact the strongest predictors of stand basal area and stand density (Appendix B).
At a per tree level, hollow abundance increased continuously with tree size (Table 2, Fig. 2a). Although only 17% of all trees sampled were large (> 40 cm DBH), 95% of these were hollow-bearing (Fig. 3a) and these trees contributed disproportionately (39%) to the total number of hollows counted (Fig. 3b). Most hollows were classed as small (< 5 cm) or medium (5-10 cm) and were dispersed across tree sizes (Fig. 3c, d), but only 10% of all hollows in the landscape were large (8% 10-20 cm, 2% > 20 cm, Fig. 3e, f). These large hollows were most commonly (80%) associated with large (> 40 cm DBH) eucalypts (68%) or stags (entirely dead trees; 12%).

Eucalypts (family: Myrtaceae, i.e. *Eucalyptus* and *Corymbia* spp.) contained the most hollows per tree (Fig. 2b, Appendix C). *Eucalyptus miniata* and *E. tetrodonta* were the dominant tree species in the vegetation type sampled, and hence most common species sampled: they contained a mean 2.3 (± 0.1) and 1.7 (± 0.1) hollows per tree respectively. These two eucalypts also had the highest frequency of larger (> 10 cm) hollows (Appendix C). From modelling, the minimum DBH at which one hollow >10 cm would be expected in *E. miniata* is 38 cm and *E. tetrodonta* is 39 cm; and a very large hollow (> 20 cm) at 45 and 47 cm DBH respectively. Large *E. miniata* trees (> 40 cm DBH) contained a mean of 5.1 (± 0.3) hollows per tree (17% were > 10 cm in diameter). Large *E. tetrodonta* contained a mean of 4.4 (± 0.2) hollows per tree (18% were > 10 cm in diameter). Large trees of other species supported relatively fewer hollows; 2.9 (± 0.2) hollows per tree (9% were >10 cm in diameter).

Total hollow abundance per tree was greatest for the tallest trees; for trees with a canopy height approximately double that of bole height; and for trees with many dead branches or entirely dead trees (Table 2, Fig. 2c-e). Where tree canopies were damaged by cyclones there were fewer small hollows per tree, but more very large (> 20 cm) hollows per
tree (Table 2, Fig. 2f, g). Where tree trunks had more extensive fire scarring (indicative of recent or more severe fires) there were fewer medium hollows per tree (Table 2, Fig. 2h).

Increased termite activity on a tree was strongly associated with greater hollow (> 5cm) abundance (Table 2, Fig. 2i).

3.2 Site-level

At a site level, the density of hollows was greatest in high rainfall areas (Fig. 4a), and mean annual rainfall was an important predictor across all hollow size classes (Table 2). Very large hollows (> 20 cm) were more abundant at sites with deeper soils (Fig. 4b).

The disturbance factors most strongly affecting hollow abundance were cyclone impact and fire history (Table 2, Fig. 4c-e). There were fewer medium hollows at sites exposed to more frequent fire, and relatively few large hollows at sites with a higher incidence of late dry season fire (Table 2, Fig. 4d, e). Hollow abundance was relatively low at cyclone-impacted sites, and cyclone impact was an important predictor of a decreasing abundance of smaller-sized (< 10 cm) hollows (Table 2, Fig. 4c). Cyclone impact had a strong effect on the underlying relationship between hollow abundance and rainfall, and at sites sampled after 33 years of regrowth following a severe cyclone the abundance of hollows remained low (Fig. 5). Hollow density at high rainfall (>1300 mm) sites was reduced from a mean of 236 (± 2.6) hollows ha⁻¹ at sites unaffected by cyclones to 179 (± 2.2) hollows ha⁻¹ with moderate cyclone impact, and 71 (± 1.0) hollows ha⁻¹ on severely impacted sites.

4. Discussion

Cyclones, fire, and termites – the primary disturbance drivers affecting vegetation structure in northern Australian tropical savannas – substantially perturbed the predictability of relationships between tree hollow abundance and broad underlying environmental gradients.
In this tropical savanna environment, stand basal area was greatest and hence large trees and tree hollows were generally more abundant at high rainfall (> 1300 mm) sites and sites with deeper soils (> 10 cm), consistent with studies identifying the dominant effects of rainfall and soil properties on tree basal area in Australian savanna (Williams et al. 1996, Lehmann et al. 2014, Murphy et al. 2015). An individual tree was most likely to contain numerous hollows if it was a large (> 40 cm DBH, > 15 m height) eucalypt. Large eucalypts contributed disproportionately to total hollow abundance across all hollow size classes and particularly to the abundance of large hollows. Therefore it is the abundance of eucalypts and their size distribution which is the proximate controller of hollow abundance. At a landscape scale, this is evident in a strong correlation between stand density (and stand basal area) and hollow density. However, rainfall and cyclone impact were the ultimate drivers of both stand density/basal area and total hollow density. The underlying relationship of hollow abundance with the landscape-scale factors of rainfall and soil depth, as well as tree size and species, was markedly disrupted by disturbance factors (cyclone impact, frequent fires, termite activity).

Cyclone effects vary with intensity (Bowman and Panton 1994, Cook and Goyens 2008, Hutley et al. 2013), and impacts on hollow abundance are complex due to variable reduction in basal area, as well as snapping of trunks and large branches which may create large hollows and/or cause the loss of small hollows. Small hollows may decrease after cyclones due to the loss of branches (where small hollows mainly form), but the base of the lost branch could create sites for large hollows to form.

There were relatively few small and medium hollows at sites exposed to frequent fire. We considered fire history over an eight year span prior to sampling, therefore we cannot infer the longer-term influence of fire regimes on large tree recruitment dynamics, however other studies have shown that frequent and/or intense fires cause suppressed recruitment and
increased mortality of large trees (Liedloff and Smith 2010, Bond et al. 2012, Murphy et al. 2015). Reduced densities of small and medium hollows could be associated with the loss of small trees and branches over the short-term (Murphy et al. 2010). Our data showed that increased frequency of late dry season fire (i.e. higher intensity fires) was associated with lower density of large hollows, suggestive of the direct loss of large trees with high intensity fires, consistent with the findings of Williams et al. (1999) and Edwards et al. (2018). The incidence of fire scars on a tree (indicative of an intense fire in the recent past) was associated with fewer large hollows, again suggesting that high-intensity fires reduce the number of large hollows.

High termite activity generally resulted in more hollows per tree, highlighting the importance of the contribution of termites to hollow formation, especially in eucalypts (Werner and Prior 2007). Termites are abundant in these tropical savanna environments, and most trees in northern Australian savannas have hollow cores or pipes due to termite activity, with this frequency significantly higher for eucalypts (82% of E. tetrodonta, 97% of E. miniata) than non-eucalypts (27%) (Werner and Prior 2007). The termite species most commonly responsible is Coptotermes acinaciformis and is most likely to enter a tree from underground or aboveground points of mechanical or fire injury (Andersen et al. 2005). In Australian tropical savanna, microbial decay is accelerated by moisture and termite intrusion (Cheesman et al. 2017).

The three main disturbance events considered here may also have strong interactive and/or additive effects. For example, Murphy and Legge (2007) found two tropical cyclones caused a direct increase in the abundance of very large hollows required for nesting palm cockatoos (Probosciger aterrimus) on Cape York Peninsula, Queensland. However, in the years after the cyclones, wind damage, fire, and severe decay caused the eventual marked decline in the abundance of nesting trees at a landscape level. Indeed, fires after cyclones...
may be exceptionally intense due to unusually high fuel loads attributable to fallen limbs and
trees (Bowman and Panton 1994) and increases in fire frequency may occur due to increased
grass biomass in areas where cyclones have reduced the canopy cover (Hutley et al. 2013).
There may also be interactive impacts of fire and termites on hollow formation and longevity
in northern Australian savannas, and in other savannas globally, as fire may access the
internal structure of the tree at termite mound entrances and cause external openings to
extend, ultimately compromising the structural integrity of the tree and increasing the
likelihood of tree mortality (Williams et al. 1999, Cook et al. 2005, Werner et al. 2008, Prior

In Australian tropical woodlands, trees are generally smaller than those of the forests
of temperate Australia (Ball et al. 2011). Despite this, we found that the mesic tropical
savannas of Australia’s Northern Territory support greater densities of hollows than those in
many temperate eucalypt woodlands and forests populated by trees of much larger stature,
and densities of larger hollows may approach similar levels to that of long unburnt, unlogged,
intact forests in particular temperate regions (Table 1). This is most likely because tropical
woodlands may typically support a higher density of hollow-bearing trees (current study 73
ha$^{-1}$) than temperate forests or woodlands (e.g. 7 – 17 ha$^{-1}$ over a range of studies in
temperate woodlands (Gibbons and Lindenmayer 2002)). In turn, this higher density of
hollow-bearing trees in the tropical woodlands is because termite prevalence causes hollow
formation to occur in much smaller trees than those of temperate eucalypt forests (Table 1)
(Braithwaite et al. 1985, Taylor and Chisholm 2005, Rayner et al. 2014, Cheesman et al.

As is typical with studies of hollow abundance (Braithwaite et al. 1985, Bennett et al.
et al. 2011, Goldingay 2012, Rayner et al. 2014, Treby and Castley 2015), we found that most
hollows in this system are small, and that large and very large hollows are much rarer. In
many temperate eucalypt forests, small hollows are unsuitable for most vertebrates (Gibbons
et al. 2002), however many small reptile and frog species in the region of our study are
hollow-dependent (Taylor et al. 2003), so it is likely that many small hollows are used by
vertebrates. However, most birds and mammals, including many declining species, in this
region require large or very large hollows (Kurucz 2000), so the abundance of these may be a
critical conservation resource. Taylor et al. (2003) estimated that there are more species of
hollow-using mammal and reptile species in northern Australian savannas than in woodlands
in temperate southern Australia, and some studies indicate tree hollows may be a limiting
resource in northern Australian savannas for at least some species that have specialised
hollow requirements (Kurucz 2000, Pittman 2003, Firth et al. 2010, Brazill-Boast et al. 2011,
Hohnen et al. 2015). However, far less information on habitat quality and the link to fauna
occupancy is available for Australia’s tropical north than for the temperate south where tree
hollow limitation has been linked to hollow suitability, e.g. only 5% of potential hollows
were suitable for wildlife in a sample of mature trees in Tasmania (Stojanovic et al. 2014).
Indeed, a key question now is whether the seeming abundance of hollows in northern
Australian tropical savannas meets the requirements of the suite of hollow-using species
occurring there, or whether these species may be limited by the availability of suitable (large)
hollows across the landscape.

Many hollow-dependent mammal species across northern Australia have contracted to
higher rainfall parts of their ranges (Woinarski et al. 2014), where large trees (and hollows)
are most abundant. However, there is insufficient information currently available to assess
whether this may be a causal relationship or reflect the influence of other factors, e.g. other
resources may also be at higher abundance in higher rainfall areas. Experimental studies,
such as the assessment of mammal survival and density at paired sites with and without provision of artificial hollows, may be required to consider whether hollows are limiting in this environment, and hence whether there is a need to attempt to manage those controllable factors influencing hollow availability (most notably fire). The coastline of northern Australia is likely to experience frequent disturbance by storms and tropical cyclones during the monsoonal wet season and has a significantly higher risk of cyclones than inland regions more than 100 km from the coast (Cook and Goyens 2008). There is thus a relatively high likelihood for severe disturbance to reduce hollow abundance in these areas, placing hollow-dependent fauna at particular risk to potential impacts of hollow limitation and raising further concerns over the threats to the declining mammal populations in these coastal zones.

5. Conclusion

Large hollow-bearing trees are keystone habitat structures in northern Australia's mesic tropical savannas, as they are in other savannas globally (Remm and Lõhmus 2011, Shannon et al. 2011, Lindenmayer et al. 2014, Pringle et al. 2015). Hollows are abundant in this system, especially in eucalypts and in higher rainfall areas. However, further research is required to establish whether hollow availability may be adequate to retain hollow-dependent fauna species, particularly a set of threatened and declining mammals. Management can affect hollow availability, with a particular priority to reduce the frequency of high-intensity (i.e. late dry season) fires (Russell-Smith et al. 2013), especially in high rainfall coastal zones where the risk of marked reduction in hollows due to synergistic effects of disturbance factors following cyclones is greatest.

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References


with uncertainty and ignorance in northern Australia. Pages 83-115 in J. W. Handmer,

Woinarski, J. C. Z., S. Legge, J. A. Fitzsimons, B. J. Traill, A. A. Burbidge, A. Fisher, R. S.
C. Firth, I. J. Gordon, A. D. Griffiths, C. N. Johnson, N. L. McKenzie, C. Palmer, I.
disappearing mammal fauna of northern Australia: context, cause, and response.

Woinarski, J. C. Z., L. McMillan, and B. Traill. 2007. The Nature of Northern Australia :
Natural values, ecological processes and future prospects. ANU E Press, Canberra.

Pages 303-341 in J. E. Williams and J. C. Z. Woinarski, editors. Eucalypt ecology:
individuals to ecosystems. Cambridge University Press, Cambridge.

Wormington, K. R., D. Lamb, H. I. McCallum, and D. J. Moloney. 2005. The status of
hollow-bearing trees required for the conservation of arboreal marsupials in the dry
diderophyll forests of south-east Queensland, Australia. Pacific Conservation Biology
11:38-49.

processes threatening their persistence and techniques for restoration. Australian

Ritchie, T. B. Reardon, I. J. Radford, N. Preece, J. Perry, B. P. Murphy, H. McGregor,
S. Legge, L. Leahy, M. J. Lawes, J. Kanowski, C. N. Johnson, A. James, A. D.
Griffiths, G. Gillespie, A. Frank, A. Fisher, and A. A. Burbidge. 2015. Stemming the
tide: progress towards resolving the causes of decline and implementing management
responses for the disappearing mammal fauna of northern Australia. Therya 6:169-
225.

mixed models with R. Highland Statistics Limited Newburgh.
Table 1. Comparison between current study and analogous studies in Australian forests and woodlands elsewhere, highlighting the greater propensity for smaller trees to be hollow-bearing in tropical mesic savanna resulting in greater hollow and hollow-bearing tree densities than that of temperate woodlands but similar densities to intact, long-unburnt forests in temperate regions. Note that many of the included studies measured abundance of hollows with varying minimum diameter, and some of the Table parameters were not assessed in some studies (indicated as N/A).

<table>
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<tr>
<th>Study</th>
<th>Region</th>
<th>Hollows ha⁻¹ (mean range)</th>
<th>Hollow-bearing trees ha⁻¹ (mean range)</th>
<th>Proportion of trees with hollows at 30 cm DBH</th>
<th>Proportion of trees with hollows at 50 cm DBH</th>
<th>Stand basal area (m²·ha⁻¹) (mean range)</th>
<th>Max DBH (cm)</th>
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<tr>
<td>Current study</td>
<td>Tropical savanna, Northern Territory</td>
<td>88 (5–395) for hollows &gt;5cm; 207 (15–735) for all hollows</td>
<td>42 (5–155) for hollows &gt;5cm; 73 (8–200) for all hollows</td>
<td>0.56 for hollows &gt;5cm; 0.72 for all hollows</td>
<td>0.89 for hollows &gt;5cm; 0.97 for all hollows</td>
<td>9.0 (2.2–32.2) for stems &gt;20cm DBH</td>
<td>65</td>
</tr>
<tr>
<td>Ball et al. (2011)</td>
<td>Tropical eucalypt woodland, central Queensland coast (remnant woodland)</td>
<td>13 (2–36) for hollows &gt;4cm</td>
<td>40 (11–92) for hollows &gt;4cm</td>
<td>0.63 for hollows &gt;4cm</td>
<td>0.90 for hollows &gt;4cm</td>
<td>N/A</td>
<td>94</td>
</tr>
<tr>
<td>Eyre (2005)</td>
<td>Dry sclerophyll forest, SE Queensland</td>
<td>~ 20 for hollows &gt;10cm</td>
<td>5.9 (1–19) for hollows &gt;10cm</td>
<td>0–0.06 for hollows &gt;10cm</td>
<td>0.02–0.5 for hollows &gt;10cm</td>
<td>N/A</td>
<td>80+</td>
</tr>
<tr>
<td>Wormington et al. (2005)</td>
<td>Dry sclerophyll forest, SE Queensland</td>
<td>N/A</td>
<td>1.8–20 for hollows &gt;2cm and stems &gt;20cm DBH</td>
<td>0 for hollows &gt;2cm and stems &gt;20cm DBH</td>
<td>0 for hollows &gt;2cm and stems &gt;20cm DBH</td>
<td>8–30 for stems &gt;10cm DBH</td>
<td>100+</td>
</tr>
<tr>
<td>Eyre et al. (2010)</td>
<td>Dry sclerophyll forest, SE Queensland</td>
<td>N/A</td>
<td>4 (0–23) for hollows &gt;10cm and live stems &gt;20cm DBH</td>
<td>0.01–0.03 for hollows &gt;10cm and live stems &gt;20cm DBH</td>
<td>0.05–0.18 for hollows &gt;10cm and live stems &gt;20cm DBH</td>
<td>N/A</td>
<td>185</td>
</tr>
<tr>
<td>Harper et al. (2005)</td>
<td>Dry sclerophyll forest, urban SE Australia</td>
<td>N/A</td>
<td>5.8 (0–21) for hollows &gt;5 cm</td>
<td>N/A</td>
<td>0.1–0.3 for hollows &gt;5 cm</td>
<td>N/A</td>
<td>100+</td>
</tr>
<tr>
<td>Treby and Castley (2015)</td>
<td>Wet sclerophyll forest, urban SE Queensland</td>
<td>88 (1–165) for hollows &gt;10cm</td>
<td>37.5 (1–86) for hollows &gt;10cm</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>80+</td>
</tr>
<tr>
<td>McLean et al. (2015)</td>
<td>Wet sclerophyll forest, New South Wales</td>
<td>80–140 intact forest; 30–50 logged forest (for hollows &gt;2cm)</td>
<td>40–50 intact forest; 10–20 logged forest (for hollows &gt;2cm)</td>
<td>N/A</td>
<td>N/A</td>
<td>24–29 intact forest; 10–20 logged forest (for stems &gt;15cm DBH)</td>
<td>N/A</td>
</tr>
<tr>
<td>McLean et al. (2015)</td>
<td>Dry sclerophyll forest, New South Wales</td>
<td>90–130 intact forest; 50–90 logged forest (for hollows &gt;2cm)</td>
<td>30–50 intact forest; 10–30 logged forest (for hollows &gt;2cm)</td>
<td>N/A</td>
<td>N/A</td>
<td>18–28 intact forest; 16–18 logged forest (for stems &gt;15cm DBH)</td>
<td>N/A</td>
</tr>
<tr>
<td>Rayner et al. (2014)</td>
<td>Dry sclerophyll woodlands, central W New South Wales</td>
<td>82 for hollows &gt;1cm</td>
<td>17 for hollows &gt;1cm</td>
<td>0.02–0.35 for hollows &gt;1cm, four common eucalypts</td>
<td>0.3–0.75 for hollows &gt;1cm, four common eucalypts</td>
<td>N/A</td>
<td>200+</td>
</tr>
<tr>
<td>Croft et al. (2016)</td>
<td>Open eucalypt forests and woodlands, SE New South Wales</td>
<td>61 frequently burnt; 110 long unburnt (for all hollows)</td>
<td>29 long unburnt (for all hollows)</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Gibbons et al. (2016)</td>
<td>Mountain forests, SE</td>
<td>N/A</td>
<td>22 (10 – 30) intact</td>
<td>0–0.15</td>
<td>0–0.2</td>
<td>20–120</td>
<td>300+</td>
</tr>
<tr>
<td>(2000)</td>
<td>Australia</td>
<td>forest (for hollows &gt;2cm)</td>
<td>for hollows &gt;2cm</td>
<td>for hollows &gt;2cm</td>
<td>for live eucalypts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------------</td>
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<td>-----------------</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Whitford (2002)</td>
<td>Wet sclerophyll forests (Jarrah), SW Western Australia</td>
<td>25–30 for hollows &gt;2cm</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>180+</td>
<td></td>
</tr>
<tr>
<td>Munks et al. (2007)</td>
<td>Dry eucalypt forests, Tasmania</td>
<td>24–55 for hollows &gt;3cm</td>
<td>14–33 for hollows &gt;3cm</td>
<td>0 for hollows &gt;3cm</td>
<td>0 for hollows &gt;3cm</td>
<td>N/A</td>
<td>150+</td>
</tr>
<tr>
<td>Gibbons and Lindenmayer (2002)</td>
<td>Range of studies in temperate forests</td>
<td>N/A</td>
<td>13–27</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td>Gibbons and Lindenmayer (2002)</td>
<td>Range of studies in temperate woodlands</td>
<td>N/A</td>
<td>7–17</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td></td>
</tr>
</tbody>
</table>
### Table 2. Model selection results based on Akaike Information Criterion (AIC) to test the effects of predictor variables on hollow abundance at tree- and site-level. Relative variable importance ($w_v$) is the sum of Akaike weights (Akaike weight is the probability that model $i$ is the best model) for all models containing a given predictor variable. Highly influential variables have $w_v \geq 0.73$ (equivalent to an AIC difference of 2) and are indicated in bold. All continuous variables (DBH, tree height, BT ratio, rainfall, soil depth) also include a quadratic term which allowed their effect to be non-linear in all models (for definitions of variables see Appendix A). $R^2$ is the conditional goodness-of-fit pseudo-$R^2$ (not supported for zero-inflated model classes) of the best model which included only highly influential variables (Nakagawa and Schielzeth 2013).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model distribution</th>
<th>$w_v$</th>
<th>DBH</th>
<th>Tree height</th>
<th>BT ratio</th>
<th>Tree health</th>
<th>Species group</th>
<th>Cyclone</th>
<th>Fire scar</th>
<th>Termite</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tree-level analysis</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total hollows</td>
<td>Poisson</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.94</td>
<td>0.25</td>
<td>1.00</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>Small (&lt;5cm)</td>
<td>Poisson</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.05</td>
<td>0.59</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>Medium (5-10cm)</td>
<td>Poisson</td>
<td>1.00</td>
<td>0.98</td>
<td>0.59</td>
<td>1.00</td>
<td>0.98</td>
<td>0.24</td>
<td>0.87</td>
<td>1.00</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>Large (10-20cm)</td>
<td>Zero-inflated negative binomial</td>
<td>1.00</td>
<td>0.28</td>
<td>0.94</td>
<td>1.00</td>
<td>1.00</td>
<td>0.49</td>
<td>0.55</td>
<td>0.76</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td>Very large (&gt;20cm)</td>
<td>Zero-inflated negative binomial</td>
<td>1.00</td>
<td>0.30</td>
<td>0.30</td>
<td>1.00</td>
<td>0.36</td>
<td>1.00</td>
<td>0.73</td>
<td>0.95</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td><strong>Site-level analysis</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total hollows</td>
<td>Negative binomial</td>
<td>1.00</td>
<td>0.27</td>
<td>0.01</td>
<td>0.35</td>
<td>0.96</td>
<td>0.35</td>
<td>0.25</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (&lt;5cm)</td>
<td>Negative binomial</td>
<td>1.00</td>
<td>0.24</td>
<td>0.01</td>
<td>0.27</td>
<td>0.99</td>
<td>0.25</td>
<td>0.20</td>
<td>0.34</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medium (5-10cm)</td>
<td>Negative binomial</td>
<td>1.00</td>
<td>0.15</td>
<td>0.01</td>
<td>0.49</td>
<td>1.00</td>
<td>0.73</td>
<td>0.21</td>
<td>0.41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large (10-20cm)</td>
<td>Negative binomial</td>
<td>0.40</td>
<td>0.47</td>
<td>0.01</td>
<td>0.27</td>
<td>0.11</td>
<td>0.25</td>
<td>0.82</td>
<td>0.19</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Very large (&gt;20cm)</td>
<td>Negative binomial</td>
<td>0.31</td>
<td>0.80</td>
<td>0.20</td>
<td>0.23</td>
<td>0.05</td>
<td>0.19</td>
<td>0.30</td>
<td>0.16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Location of sample sites within eucalypt-dominated savanna (grey shading) across the Northern Territory, Australia (above ca. 800mm mean annual rainfall). The contour lines represent mean annual rainfall isohyets.
Figure 2. Relationships between change (Δ) in number of hollows per tree and key tree-level predictors: (a) diameter at breast height (DBH), (b) species group, (c) tree height, (d) tree shape, (e) tree health, (f–g) cyclone damage to canopy, (h) evidence of trunk fire scar and (i) termite activity. Relationships are displayed as contrast plots of fixed effects and show mean hollow number (continuous variables) or first category (categorical variables) as a reference point for change. Relationships are shown for highly influential predictors of total hollows per tree, and for other hollow size classes where additional predictors were important or relationships differed from that of total hollows (see...
The black line is model fit and the grey band represents 95% confidence interval. Codes for categorical variables: Species group (E.min = *Eucalyptus miniata*, E.tet = *E.tetrodonta*, RBB = Rough/thick-barked bloodwoods, SBB = Scaly/thin-barked bloodwoods, Eryth = *Erythrophleum chlorostachys*, Acacia = *Acacia* spp., Non-euc = Non-eucalypt spp.); Tree health (Nil/few = no/few dead branches, Some/many = some/many dead branches, Entirely = entirely dead), Cyclone damage to canopy (No = no cyclone damage to canopy, Yes = canopy damage due to cyclone); Evidence of trunk fire scar (Nil = no evidence of trunk fire scar, Some = superficial/minimal trunk fire scar; Much = extensive/cambial trunk fire scarring); Termite activity (Nil = No sign of termite activity, Tracks = termite tracks on trunk, Mound = termite mound at base of tree). See Appendix A for variable definitions.
Figure 3. The link between tree-level and site-level tree hollow density shown by the relationship between tree size (DBH categories 20–30cm, 30–40cm, 40–50cm and > 50cm) and (a) proportion (%) of hollow-bearing trees sampled; (b) total hollows (of different size classes) sampled; and the mean (±SE) proportion of: (c) total hollows, and hollow sizes (d) > 5cm, (e) > 10cm and (f) > 20cm across all sites.
Figure 4. Relationships between number of hollows per hectare (ha⁻¹) and key site-level predictors: (a) mean annual rainfall, (b) soil depth, (c) cyclone impact, (d) fire frequency, and (e) frequency of late dry season fire. Relationships are shown for the highly influential predictors of total hollow density (i.e. mean annual rainfall, cyclone impact), and for other hollow size classes where additional predictors were important (see Table 3). The black line is model fit while holding all other variables at a fixed...
median level (continuous variables) and most common category (categorical variables), and the grey band represents 95% confidence interval. See Appendix A for variable definitions.
Figure 5. (a) Relationship between hollow density per hectare (ha\(^{-1}\)) and mean annual rainfall, with sites categorised by cyclone impact (circle = no impact; triangle = partial impact of more recent Cyclone Ingrid and/or Monica; square = 33 year regrowth after Cyclone Tracy). Examples of savanna structure: (b) woodlands typical of higher rainfall areas; (c) woodlands showing damage after a recent cyclone (Cyclone Ingrid), (d) woodland regrowth 33 years after complete felling in Cyclone Tracy. Photos: J.C.Z. Woinarski.
**Appendix A.** Tree- and site-level variables used in modelling. Italics indicate name used in reporting of modelling results. All continuous variables were centred and standardised by dividing by two times the standard deviation (Gelman 2008). Sample size is given for all classes of categorical variables and median value (and range (in brackets)) for continuous variables.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coding</th>
<th>Comment</th>
<th>Sample median (and range) or total sample size per category</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tree-level analysis</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter at breast height (DBH)</td>
<td>Continuous, standardised</td>
<td>Diameter (cm) of main stem measured at 1.3m from the ground</td>
<td>28 (20-65)</td>
</tr>
<tr>
<td>Tree height</td>
<td>Continuous, standardised</td>
<td>Total tree canopy height (m)</td>
<td>15 (2-32)</td>
</tr>
<tr>
<td>Bole height</td>
<td>Continuous, standardised</td>
<td>Height (m) from the ground to the first branch that was at least 25% of the diameter of the trunk at the branching point</td>
<td>8 (1-25)</td>
</tr>
<tr>
<td>Bole:trunk (BT ratio)</td>
<td>Continuous, standardised</td>
<td>Assessment of tree shape given by the ratio of bole height to canopy height</td>
<td>0.53 (0.1-1.0)</td>
</tr>
<tr>
<td><strong>Species group</strong></td>
<td>Categorical</td>
<td>Species included in Rough/thick-barked bloodwoods (RBB) = (includes half-barked) C.confertiflora, C.dunlopiana, C.ferruginea, C.nesophila, C.polycarpa, C.polycadi, C.porrecta, C.setosa; Scaly/thin-barked bloodwoods (SBB) = C.blesseri, C.thromphloia, C.foelscheana, C.latifolia; Acacia spp. = Acacia auriculiformis, A.lamprocarpa; Other non-eucalypt spp. = Alstonia, Brachychiton, Buchanania, Ficus, Gardenia, Lophostemon, Owenia, Petalostigma, Syzygium, Terminalia, Xanthostemon spp.</td>
<td>E.miniata 657, E.tetrodonta 822, Erythrophleum chlorostachys 133, RBB 106, SBB 43, Acacia spp. 18, Other non-eucalypt spp. 30</td>
</tr>
<tr>
<td>Fire scar</td>
<td>Categorical</td>
<td>The extent to which the trunk showed evidence of fire scarring depending on height of fire scar and depth of scarring Note: Fire scar height on the trunk and depth of tissue damage can indicate whether a tree has experienced an intense fire in the recent past, with greater height and depth indicative of greater intensity fire</td>
<td>Nil 391, Some 1305, Much 113</td>
</tr>
<tr>
<td>Tree health</td>
<td>Categorical</td>
<td>The extent of tree mortality</td>
<td>No/few 1064, Some/many 576, Entirely dead 169</td>
</tr>
<tr>
<td>Termite sign</td>
<td>Categorical</td>
<td>The extent of termite activity on the tree</td>
<td>Nil 852, Tracks 534, Mound 423</td>
</tr>
<tr>
<td>Cyclone damage to canopy</td>
<td>Categorical (No, Yes)</td>
<td>The presence or absence of cyclone damage to canopy</td>
<td>No 1665, Yes 144</td>
</tr>
</tbody>
</table>
### Site-level analysis

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Description</th>
<th>Estimate/Mean (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean annual rainfall</strong></td>
<td>Continuous, standardised</td>
<td>Estimate of mean annual rainfall (mm) per site from lat/long location sourced from ANUCLIM (Houlder et al. 2000)</td>
<td>1333 (868-1674)</td>
</tr>
<tr>
<td><strong>Fire frequency</strong></td>
<td>Continuous, standardised</td>
<td>Number of years burned out of 8 (prior to survey), based on 8-year satellite-derived (Moderate Resolution Imaging Spectroradiometer, MODIS) fire history (North Australian Fire Information, <a href="http://www.firenorth.org.au">www.firenorth.org.au</a>)</td>
<td>0.5 (0-1.0)</td>
</tr>
<tr>
<td><strong>Late dry season fire frequency</strong></td>
<td>Continuous, standardised</td>
<td>Number of years burned in late dry season (i.e. July – October) out of 8 (prior to survey), based on 8-year satellite-derived (Moderate Resolution Imaging Spectroradiometer, MODIS) fire history (North Australian Fire Information, <a href="http://www.firenorth.org.au">www.firenorth.org.au</a>)</td>
<td>0.125 (0-0.5)</td>
</tr>
<tr>
<td><strong>Cyclone impact</strong></td>
<td>Categorical (No discernible impact, Moderate, Severe)</td>
<td>Categorised as severe when sampled sites showed regrowth following complete felling by Cyclone Tracy in December 1974; and moderate when sampled sites showed recovery following impacts of Cyclones Monica (in April 2006) and/or Ingrid (in March 2005) where damage was more recent than for Tracy but less extreme, typically including felling of some trees and snapping of most others</td>
<td>None 26, Moderate 11, Severe 6</td>
</tr>
<tr>
<td><strong>Slope</strong></td>
<td>Continuous, standardised</td>
<td>Estimate of slope (degrees)</td>
<td>1 (0-15)</td>
</tr>
<tr>
<td><strong>Soil depth</strong></td>
<td>Categorical (0-10cm, 10-40cm, &gt;40cm)</td>
<td>Measure of soil depth (cm), average from three sample points per site</td>
<td>0-10cm 4, 10-40cm 10, &gt;40cm 29</td>
</tr>
<tr>
<td><strong>Soil texture</strong></td>
<td>Categorical (sand, sandy-loam, loam, clay-loam)</td>
<td>Field or hand-texturing estimate of soil texture (McDonald et al. 1998), average from three sample points per site</td>
<td>Sand 8, Sandy-loam 23, Loam 10, Clay-loam 2</td>
</tr>
<tr>
<td><strong>Rock cover</strong></td>
<td>Continuous, standardised</td>
<td>Estimate of percentage (%) rock cover on the land surface, average from three sample points per site</td>
<td>2 (0-75)</td>
</tr>
<tr>
<td><strong>Livestock grazing</strong></td>
<td>Categorical (Grazed by livestock, Not grazed by livestock)</td>
<td>Presence or absence of evidence of livestock grazing, based on tenure (i.e. pastoral property or not).</td>
<td>Grazed 7, Not grazed 36</td>
</tr>
<tr>
<td><strong>Stand density index</strong></td>
<td>Continuous, standardised</td>
<td>Calculated from number of trees (per ha) and mean tree DBH (cm) on each site, after Reineke (1933), i.e. Stand density index = trees/ha * (mean DBH/25.4) (^{1.605})</td>
<td>114.9 (14.3-310.5)</td>
</tr>
<tr>
<td><strong>Stand basal area</strong></td>
<td>Continuous, standardised</td>
<td>Total basal area of all trees on a site calculated from DBH (m(^2).ha(^{-1}))</td>
<td>9.0 (2.2-32.2)</td>
</tr>
</tbody>
</table>
Appendix B. Relationship between total hollow density per site and (a) stand density index (calculated from number of trees and average stand DBH, see Appendix A), (b) stand basal area, and (e) presence of livestock grazing on a site, and relationship between (f) rainfall and grazing. Modelled relationships between stand density and the most important predictors of stand density (c) rainfall and (d) cyclone impact, derived from model-averaged gamma GLM. In figures (a) – (d) black circles are data points, the black line is model fit, and the grey band represents 95% confidence interval. In figure (e) and (f) median (thick, line), upper and lower quartiles (box), minimum and maximum values (whiskers) and outliers (black circles) are shown. Stand basal area or stand density index may be a valuable field measure as a coarse proxy for direct counts of total hollow density (Pearson’s correlation $r = 0.63$), but this relationship is weaker for large hollows $> 10$ cm diameter ($r = 0.42$). Note that grazing was highly correlated with rainfall ($p < 0.001$) and therefore this relationship may actually be a response to the confounding relationship of
grazing with rainfall. Grazing was quantified as the presence of livestock, but neither stocking rate, nor some quantification of grazing pressure, was available during survey.
Appendix C. Relationship between total hollow abundance per tree against tree size (DBH), conditional on species or species group. Solid black circles are data points, solid lines are the fitted model mean, and the shaded area around the line represents 95% confidence intervals of the predicted mean. The number of trees sampled (n) and the frequency of occurrence (FO) of all trees sampled with large or very large hollows (> 10cm) for each species or species group. Species groups: Rough/thick-barked bloodwoods = (includes half-barked) *C.confertiflora*, *C.dunlopiana*, *C.ferruginea*, *C.nesophila*, *C.polycarpa*, *C.polysciadia*, *C.porrecta*, *C.setosa*; Scaly/thin-barked bloodwoods = *C.bleeseri*, *C.dichromophloia*, *C.foelscheana*, *C.latifolia*; Other non-eucalypt spp. = *Acacia*, *Alstonia*, *Brachychiton*, *Buchanania*, *Ficus*, *Gardenia*, *Lophostemon*, *Owenia*, *Petalostigma*, *Syzygium*, *Terminalia*, *Xanthostemon* spp.