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1	Cyclones, fire, and termites: the drivers of tree hollow abundance
2	in northern Australia's mesic tropical savanna
3	
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#### 20 Abstract

21 Tree hollows are a vital wildlife feature, whose abundance and availability has declined in 22 many regions due to broad-scale vegetation clearance, timber-harvesting, and disturbance 23 such as fire. In the temperate forests and woodlands of eastern and southern Australia, the 24 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-25 26 dependent mammals are in decline, and habitat simplification and resultant hollow limitation 27 have been suggested as potential contributors to these declines. Hence, we sought to quantify 28 the abundance of hollows, and identify the key drivers of this abundance in northern 29 Australian savannas. We modelled the environmental and ecological correlates of hollow 30 abundance across an extensive area of eucalypt savanna in Australia's Northern Territory. 31 We found that hollow abundance was significantly related to tree characteristics (size, 32 species) and broad environmental gradients (annual rainfall, soil depth). Key disturbances – 33 cyclones, fire, and termites – substantially disrupted these relationships and led to high 34 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<sup>-1</sup>, 35 hollows > 10 cm: 23 ha<sup>-1</sup>) and greatest in high rainfall areas (associated with the abundance 36 37 of large eucalypts). Many arboreal mammal species in northern Australia have now 38 contracted to higher rainfall parts of their former range (where hollows are at highest 39 density); however such higher rainfall areas are also more likely to be affected by stochastic 40 cyclonic events that can severely reduce the abundance of hollows. Hollow abundance was 41 also affected by recent fire history and, in many areas, the current regime of frequent, high 42 intensity fires will lead to marked reduction in this resource.

# 43 Key words

44 Tree cavities; hollow-bearing trees; eucalypt woodland; disturbance ecology; arboreal fauna

#### 45 **1. Introduction**

Tree hollows are a critical resource for many animal species across the globe (e.g. Blakely et 46 47 al. 2008, Lindenmayer and Wood 2010, Ouellet-Lapointe et al. 2012, Altamirano et al. 2017). 48 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, 49 50 survival, and breeding success of many hollow-dependent species (e.g. Du Plessis 1995, 51 Sedgeley 2001, Robles et al. 2011, Bonaparte and Cockle 2017, Lindenmayer et al. 2017). 52 In Australia, many vertebrate and invertebrate species rely on tree hollows (Taylor et 53 al. 2003, Goldingay 2009, 2012). The co-evolution of Australia's eucalypts (family: 54 Myrtaceae) and its diverse fauna has created the opportunity for many hollow-using species 55 to co-exist in the forests and woodlands across the continent (Woinarski et al. 1997), and 56 even in the absence of avian excavators such as woodpeckers, hollows are often abundant in 57 many Australian forests and woodlands (Gibbons and Lindenmayer 2002, Remm and 58 Lõhmus 2011). This is primarily due to eucalypt propensity for hollow formation by 59 microbial decay of heartwood, especially after mechanical disturbance, e.g. wind, water, fire, 60 termites (Gibbons and Lindenmayer 2002, Harper et al. 2005, Taylor and Chisholm 2005, Adkins 2006). 61

62 Many studies have documented the abundance of hollows in temperate Australia, and 63 the factors influencing this abundance, with hollow availability found to be reduced by broad-64 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 65 in temperate Australia, hollow availability is limiting for hollow-dependent species, and 66 67 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, 68 69 Manning et al. 2013).

70 In contrast, little is known about hollow availability and the factors that influence it in 71 woodlands of the tropical savannas of northern Australia, whose environmental and 72 disturbance factors show some distinct differences to that of temperate Australia (Bowman 73 1988). For example, less than 2% of the savanna woodlands in the region considered here 74 have been cleared (Woinarski 2004), substantially less than for Australian forests and 75 woodlands generally (Bradshaw 2012). Furthermore, in the north Australian savannas, 76 timber-harvesting has been limited and focused almost exclusively on two tree species, 77 *Callitris intratropica* and *Erythrophleum chlorostachys*, both favoured for timber because they are relatively termite-resistant (Hanssen and Wigston 1989, Woinarski and Dawson 78 79 2004). However, the savanna woodlands of northern Australia are now subject to increasing 80 intensification of land use and marked changes in fire regime (Woinarski et al. 2007): such 81 changes may be expected to increasingly influence hollow availability and hence habitat 82 suitability for many hollow-dependent species.

83 Of the nine mammal species that have declined markedly in northern Australia since 84 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, 85 the decline occurred earlier (and most severely) in lower rainfall areas (McKenzie 1981, 86 87 Woinarski et al. 2011, Start et al. 2012, Ziembicki et al. 2015). Despite this recognised 88 decline of hollow-dependent species, there have been very few studies of hollow abundance 89 and the extent to which animals are reliant on hollows in the tropical savannas of northern 90 Australia. Braithwaite et al. (1985) and Taylor and Chisholm (2005) conducted snapshot 91 estimates of hollow prevalence in Kakadu National Park and the Gulf region of the Northern 92 Territory, respectively. Both reported an increase in hollow abundance with tree size 93 (estimated by diameter at breast height, DBH) and significant differences in hollow 94 abundance among tree species, but neither of these localised studies investigated the

95 environmental predictors of hollow abundance. Some more recent studies of single bird or 96 mammal species have demonstrated or inferred that hollows may be limiting, and such 97 limitation may constrain breeding success or abundance of threatened hollow-dependent 98 species in Australian savanna (Kurucz 2000, Pittman 2003, Firth et al. 2010, Brazill-Boast et 99 al. 2011, Hohnen et al. 2015). However, an explicit link between potential hollow limitation 100 and arboreal fauna declines at a landscape scale has not been established. This study does not 101 directly address this issue: rather, we establish a foundation towards future studies on it by 102 describing hollow abundance at a landscape and site scale and the factors (including 103 management issues) that affect such abundance.

104 As in other savannas globally, the vegetation structure and floristic composition of 105 Australia's tropical savannas is controlled by a highly seasonal wet-dry climate and frequent 106 fires (Sankaran et al. 2005, Staver et al. 2011, Lehmann et al. 2014) Furthermore, a distinct 107 combination of factors are operating in this tropical, mesic savanna including high monsoonal 108 summer rainfall, low soil fertility, low human population density, and disturbance such as 109 cyclones and very frequent fires (Bowman 1988, Woinarski et al. 2007). Across the area 110 sampled in this study, the fire regime is approximately bi- or triennial in frequency with 111 around two-thirds of burnt area occurring in the late dry season, when fires are of highest 112 intensity and impact (Edwards et al. 2018). Arboreal termites are also abundant in these 113 woodlands, resulting in a high incidence of piping and hence hollow formation in eucalypt 114 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)

120 compare characteristics of hollow abundance in these environments with those in temperate 121 forests and woodlands, and (iv) consider how the observed abundance of hollows in this 122 environment, and the factors that affect that abundance, may affect hollow-dependent fauna 123 and its management.

124

### 125 **2. Methods**

126 2.1 Field procedures

127 Tree hollow abundance was assessed for 1809 trees on 43 sites in eucalypt woodlands in the 128 monsoonal tropics of the Northern Territory (Fig. 1). All sample sites were in woodlands 129 dominated or co-dominated by the tree species *Eucalyptus miniata* and *E. tetrodonta*. 130 Woodlands dominated by either or both of these species are the most extensive and characteristic woodland types in northern Australia, comprising ca. 180,000 km<sup>2</sup> of 131 continuous, intact savanna in the Northern Territory (Woinarski 2004) and ca. 445,000 km<sup>2</sup> 132 133 across northern Australia (Fox et al. 2001). Sites were selected to sample broadly across the 134 rainfall, edaphic, disturbance and topographic range spanned by these woodlands, and every 135 site was situated in a relatively homogenous environment. Typical of the region, no sites 136 sampled had been subject to timber-harvesting, and no cut stumps indicative of previous 137 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 145 evaluated per hectare. Trees smaller than 20 cm DBH were excluded given they were 146 unlikely to contain hollows (Kurucz 2000, Taylor and Chisholm 2005), with this exclusion 147 consistent with precedents of previous hollow availability studies (Wormington et al. 2005). 148 Hollows were counted from the ground (using binoculars where required) for each 149 tree within the transects at a site. The presence of a hollow was defined as any entrance that 150 may have depth exceeding the minimum entrance diameter. Every hollow present was 151 categorised into one of four size classes, based on minimum entrance diameter: small (< 5152 cm); medium (5 - 10 cm); large (10 - 20 cm); very large (> 20 cm). At sites where fewer than 153 50 trees occurred in the four belt transects, additional trees were sampled randomly outside 154 the transects where possible, to bring the tally to a minimum of 50 trees per site. These 155 additional trees were included in the tree-level, but not the site-level, analysis. The range of 156 tree characteristics and environmental variables recorded for each tree and site is detailed in 157 Appendix A, with these variables shown in many studies elsewhere to be useful predictors of 158 hollow abundance (Munks et al. 2007, Koch et al. 2008, Fox et al. 2009, Lindenmayer et al. 159 2016, 2017).

160 The reliability of our ground-based hollow counts was assessed by comparing 161 estimates against actual counts for a random selection of 22 trees, of which 14 were climbed 162 by arborists and eight were felled. A hollow was confirmed if hollow depth exceeded 163 minimum entrance diameter. There was a weak tendency (10% difference) to over-estimate 164 hollow numbers from ground counts, although this tendency was evident only when 165 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 166 167 of total hollows per tree were strongly correlated with actual counts (r = 0.75, p < 0.001).

168

169 2.2 Statistical analysis

170 Analysis considered hollow counts at site-level and the level of an individual tree. All models 171 were run using R version 3.4.3 (R Core Team 2017). The density of total hollows (and also 172 density of hollows in the four size classes) was modelled against all possible combinations of 173 predictor variables (Appendix A) using generalised linear models (GLM) at site-level and 174 generalised linear mixed models (GLMM) with site as a random effect at tree-level (R 175 package lme4: Bates et al. (2015), R package glmmADMB: Fournier et al. (2012)). Poisson 176 models were fitted first, but where overdispersion was evident, negative binomial 177 distributions were considered, followed by zero-inflated models (Zuur et al. 2012). Model 178 validation was conducted by evaluation of Pearson residuals plotted against fitted values as 179 well as included and excluded covariates to check for homogeneity, independence and model 180 fit (Zuur et al. 2012). To assess whether Poisson or negative binomial models predicted 181 enough zeros, 10,000 datasets were simulated from the models and the percentage of zeros 182 calculated for each simulated dataset. If the observed versus simulated percentage of zeros 183 was similar, the model was accepted.

184 Due to collinearity between bole height (height of first branch) and tree height, and 185 between bole height and bole:trunk ratio (ratio of bole height to total tree height), bole height 186 was dropped from tree-level models. Tree height and bole:trunk ratio were retained (little 187 collinearity). Grazing was strongly correlated with rainfall, rock cover with soil texture and 188 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, 189 190 however information on their relationships with hollow density is presented in Appendix B. 191 We allowed the effect of continuous variables to be non-linear by introducing a quadratic 192 term into models. All continuous variables were standardised by dividing by two times the 193 standard deviation (Gelman 2008).

194 An information-theoretic approach to model selection was used to identify the best models according to Akaike Information Criterion (AIC) (R package MuMIn: Barton 195 196 (2016)). These best models were used for visualisation of variable effects (R package visreg: 197 Breheny and Burchett (2016)). Log-transformed total area sampled per site was incorporated 198 as an offset variable in site-level models and its inclusion fixed in all models during model-199 averaging. Relationships are presented for highly influential predictors of total hollows per 200 tree or per site, but where additional predictors were important or relationships differed from 201 that of total hollows, figures were presented for hollow size classes.

202

## 203 **3. Results**

Across all sites sampled, we found a mean hollow density of 207 ( $\pm$  22.1 SE) ha<sup>-1</sup>, of which 204 88 (± 11.6) ha<sup>-1</sup> were > 5 cm in diameter and 23 (± 4.8) ha<sup>-1</sup> were > 10 cm (Table 1). These 205 206 values varied by more than an order of magnitude between sites (total hollows: 15 - 735 ha<sup>-1</sup>, Table 1). The mean density of hollow-bearing trees was 73 ( $\pm$  5.8) ha<sup>-1</sup>, and this too varied 207 208 substantially among sites (range: 8 - 200, Table 1). Hollows occurred in 67% of all trees 209 sampled. Trees > 50 cm DBH comprised only a very small proportion (4%) of all trees, with mean density of 5.3 ( $\pm$  1.2) ha<sup>-1</sup> (range 0 – 40 ha<sup>-1</sup>). The densities of such large trees were 210 highest on high rainfall sites (>1300 mm mean annual rainfall), with a mean density  $(ha^{-1})$  of 211 212 8 ( $\pm$  1.4) trees > 50 cm DBH and 23 ( $\pm$  3.2) trees > 40 cm DBH on high rainfall sites 213 compared with 2 ( $\pm$  0.4) trees > 50cm DBH and 15 ( $\pm$  1.9) trees > 40 cm DBH on lower rainfall sites. Woody stand basal area averaged 9.0 ( $\pm$  0.6) m<sup>2</sup>.ha<sup>-1</sup> (range 2.2 – 32.2 m<sup>2</sup>.ha<sup>-1</sup>) 214 215 across all sites (Table 1). There was a strong relationship between stand basal area and total 216 hollow density, with rainfall and cyclone impact the strongest predictors of stand basal area 217 and stand density (Appendix B).

219 3.1 *Tree-level* 

220 At a per tree level, hollow abundance increased continuously with tree size (Table 2, Fig. 2a). 221 Although only 17% of all trees sampled were large (> 40 cm DBH), 95% of these were 222 hollow-bearing (Fig. 3a) and these trees contributed disproportionately (39%) to the total 223 number of hollows counted (Fig. 3b). Most hollows were classed as small (59% < 5 cm) or 224 medium (31% 5-10 cm) and were dispersed across tree sizes (Fig. 3c, d), but only 10% of all 225 hollows in the landscape were large (8% 10-20 cm, 2% > 20 cm, Fig. 3e, f). These large 226 hollows were most commonly (80%) associated with large (> 40 cm DBH) euclypts (68%) 227 or stags (entirely dead trees; 12%). 228 Eucalypts (family: Myrtaceae, i.e. Eucalyptus and Corymbia spp.) contained the most 229 hollows per tree (Fig. 2b, Appendix C). Eucalyptus miniata and E. tetrodonta were the 230 dominant tree species in the vegetation type sampled, and hence most common species 231 sampled: they contained a mean 2.3 ( $\pm$  0.1) and 1.7 ( $\pm$  0.1) hollows per tree respectively. 232 These two eucalypts also had the highest frequency of larger (> 10 cm) hollows (Appendix 233 C). From modelling, the minimum DBH at which one hollow >10 cm would be expected in 234 *E. miniata* is 38 cm and *E. tetrodonta* is 39 cm; and a very large hollow (> 20 cm) at 45 and 235 47 cm DBH respectively. Large E. miniata trees (> 40 cm DBH) contained a mean of 5.1 (± 236 0.3) hollows per tree (17% were > 10 cm in diameter). Large *E. tetrodonta* contained a mean 237 of 4.4 ( $\pm$  0.2) hollows per tree (18% were > 10 cm in diameter). Large trees of other species 238 supported relatively fewer hollows; 2.9 ( $\pm$  0.2) hollows per tree (9% were >10 cm in 239 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).

248

249 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).

253 The disturbance factors most strongly affecting hollow abundance were cyclone 254 impact and fire history (Table 2, Fig. 4c-e). There were fewer medium hollows at sites 255 exposed to more frequent fire, and relatively few large hollows at sites with a higher 256 incidence of late dry season fire (Table 2, Fig. 4d, e). Hollow abundance was relatively low at 257 cyclone-impacted sites, and cyclone impact was an important predictor of a decreasing 258 abundance of smaller-sized (< 10 cm) hollows (Table 2, Fig. 4c). Cyclone impact had a 259 strong effect on the underlying relationship between hollow abundance and rainfall, and at 260 sites sampled after 33 years of regrowth following a severe cyclone the abundance of hollows 261 remained low (Fig. 5). Hollow density at high rainfall (>1300 mm) sites was reduced from a mean of 236 ( $\pm$  2.6) hollows ha<sup>-1</sup> at sites unaffected by cyclones to 179 ( $\pm$  2.2) hollows ha<sup>-1</sup> 262 with moderate cyclone impact, and 71 ( $\pm$  1.0) hollows ha<sup>-1</sup> on severely impacted sites. 263 264

# 265 **4. Discussion**

266 Cyclones, fire, and termites – the primary disturbance drivers affecting vegetation structure in

267 northern Australian tropical savannas – substantially perturbed the predictability of

268 relationships between tree hollow abundance and broad underlying environmental gradients.

269 In this tropical savanna environment, stand basal area was greatest and hence large trees and 270 tree hollows were generally more abundant at high rainfall (> 1300 mm) sites and sites with 271 deeper soils (> 10 cm), consistent with studies identifying the dominant effects of rainfall and 272 soil properties on tree basal area in Australian savanna (Williams et al. 1996, Lehmann et al. 273 2014, Murphy et al. 2015). An individual tree was most likely to contain numerous hollows if 274 it was a large (> 40 cm DBH, > 15 m height) eucalypt. Large eucalypts contributed 275 disproportionately to total hollow abundance across all hollow size classes and particularly to 276 the abundance of large hollows. Therefore it is the abundance of eucalypts and their size 277 distribution which is the proximate controller of hollow abundance. At a landscape scale, this 278 is evident in a strong correlation between stand density (and stand basal area) and hollow 279 density. However, rainfall and cyclone impact were the ultimate drivers of both stand 280 density/basal area and total hollow density. The underlying relationship of hollow abundance 281 with the landscape-scale factors of rainfall and soil depth, as well as tree size and species, 282 was markedly disrupted by disturbance factors (cyclone impact, frequent fires, termite 283 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

294 increased mortality of large trees (Liedloff and Smith 2010, Bond et al. 2012, Murphy et al. 295 2015). Reduced densities of small and medium hollows could be associated with the loss of 296 small trees and branches over the short-term (Murphy et al. 2010). Our data showed that 297 increased frequency of late dry season fire (i.e. higher intensity fires) was associated with 298 lower density of large hollows, suggestive of the direct loss of large trees with high intensity 299 fires, consistent with the findings of Williams et al. (1999) and Edwards et al. (2018). The 300 incidence of fire scars on a tree (indicative of an intense fire in the recent past) was associated 301 with fewer large hollows, again suggesting that high-intensity fires reduce the number of 302 large hollows.

303 High termite activity generally resulted in more hollows per tree, highlighting the 304 importance of the contribution of termites to hollow formation, especially in eucalypts 305 (Werner and Prior 2007). Termites are abundant in these tropical savanna environments, and 306 most trees in northern Australian savannas have hollow cores or pipes due to termite activity, 307 with this frequency significantly higher for eucalypts (82% of *E. tetrodonta*, 97% of *E.* 308 miniata) than non-eucalypts (27%) (Werner and Prior 2007). The termite species most 309 commonly responsible is Coptotermes acinaciformis and is most likely to enter a tree from 310 underground or aboveground points of mechanical or fire injury (Andersen et al. 2005). In 311 Australian tropical savanna, microbial decay is accelerated by moisture and termite intrusion 312 (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

319 may be exceptionally intense due to unusually high fuel loads attributable to fallen limbs and 320 trees (Bowman and Panton 1994) and increases in fire frequency may occur due to increased 321 grass biomass in areas where cyclones have reduced the canopy cover (Hutley et al. 2013). 322 There may also be interactive impacts of fire and termites on hollow formation and longevity 323 in northern Australian savannas, and in other savannas globally, as fire may access the 324 internal structure of the tree at termite mound entrances and cause external openings to 325 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 326 327 et al. 2009, N'Dri et al. 2011, N'Dri et al. 2014).

328 In Australian tropical woodlands, trees are generally smaller than those of the forests 329 of temperate Australia (Ball et al. 2011). Despite this, we found that the mesic tropical 330 savannas of Australia's Northern Territory support greater densities of hollows than those in 331 many temperate eucalypt woodlands and forests populated by trees of much larger stature, 332 and densities of larger hollows may approach similar levels to that of long unburnt, unlogged, 333 intact forests in particular temperate regions (Table 1). This is most likely because tropical 334 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 335 336 temperate woodlands (Gibbons and Lindenmayer 2002)). In turn, this higher density of 337 hollow-bearing trees in the tropical woodlands is because termite prevalence causes hollow 338 formation to occur in much smaller trees than those of temperate eucalypt forests (Table 1) 339 (Braithwaite et al. 1985, Taylor and Chisholm 2005, Rayner et al. 2014, Cheesman et al. 340 2017, Lindenmayer et al. 2017).

As is typical with studies of hollow abundance (Braithwaite et al. 1985, Bennett et al.
1994, Kurucz 2000, Lindenmayer et al. 2000, Whitford 2002, Taylor and Chisholm 2005,
Wormington et al. 2005, Munks et al. 2007, Koch et al. 2008, Goldingay 2009, Lindenmayer

344 et al. 2011, Goldingay 2012, Rayner et al. 2014, Treby and Castley 2015), we found that most 345 hollows in this system are small, and that large and very large hollows are much rarer. In 346 many temperate eucalypt forests, small hollows are unsuitable for most vertebrates (Gibbons 347 et al. 2002), however many small reptile and frog species in the region of our study are 348 hollow-dependent (Taylor et al. 2003), so it is likely that many small hollows are used by 349 vertebrates. However, most birds and mammals, including many declining species, in this 350 region require large or very large hollows (Kurucz 2000), so the abundance of these may be a 351 critical conservation resource. Taylor et al. (2003) estimated that there are more species of 352 hollow-using mammal and reptile species in northern Australian savannas than in woodlands 353 in temperate southern Australia, and some studies indicate tree hollows may be a limiting 354 resource in northern Australian savannas for at least some species that have specialised 355 hollow requirements (Kurucz 2000, Pittman 2003, Firth et al. 2010, Brazill-Boast et al. 2011, 356 Hohnen et al. 2015). However, far less information on habitat quality and the link to fauna 357 occupancy is available for Australia's tropical north than for the temperate south where tree 358 hollow limitation has been linked to hollow suitability, e.g. only 5% of potential hollows 359 were suitable for wildlife in a sample of mature trees in Tasmania (Stojanovic et al. 2014). 360 Indeed, a key question now is whether the seeming abundance of hollows in northern 361 Australian tropical savannas meets the requirements of the suite of hollow-using species 362 occurring there, or whether these species may be limited by the availability of suitable (large) 363 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,

369 such as the assessment of mammal survival and density at paired sites with and without 370 provision of artificial hollows, may be required to consider whether hollows are limiting in 371 this environment, and hence whether there is a need to attempt to manage those controllable 372 factors influencing hollow availability (most notably fire). The coastline of northern 373 Australia is likely to experience frequent disturbance by storms and tropical cyclones during 374 the monsoonal wet season and has a significantly higher risk of cyclones than inland regions 375 more than 100 km from the coast (Cook and Goyens 2008). There is thus a relatively high 376 likelihood for severe disturbance to reduce hollow abundance in these areas, placing hollow-377 dependent fauna at particular risk to potential impacts of hollow limitation and raising further 378 concerns over the threats to the declining mammal populations in these coastal zones.

379

# 380 **5. Conclusion**

381 Large hollow-bearing trees are keystone habitat structures in northern Australia's mesic 382 tropical savannas, as they are in other savannas globally (Remm and Lõhmus 2011, Shannon 383 et al. 2011, Lindenmayer et al. 2014, Pringle et al. 2015). Hollows are abundant in this 384 system, especially in eucalypts and in higher rainfall areas. However, further research is 385 required to establish whether hollow availability may be adequate to retain hollow-dependent 386 fauna species, particularly a set of threatened and declining mammals. Management can 387 affect hollow availability, with a particular priority to reduce the frequency of high-intensity 388 (i.e. late dry season) fires (Russell-Smith et al. 2013), especially in high rainfall coastal zones 389 where the risk of marked reduction in hollows due to synergistic effects of disturbance factors 390 following cyclones is greatest.

391

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405

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**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).

Study	Region	Hollows ha <sup>-1</sup>	Hollow-bearing trees	Proportion of trees with	h hollows	Stand basal area	Max
		(mean (range))	ha <sup>-1</sup> (mean (range))	at 30 cm DBH at 50 cm DBH		$(\mathbf{m}^2 \cdot \mathbf{ha}^{-1})$ (mean (range))	DBH (cm)
Current study	Tropical savanna, Northern Territory	88 (5–395) for hollows >5cm; 207 (15–735) for all hollows	42 (5–155) for hollows >5cm; 73 (8–200) for all hollows	0.56 for hollows >5cm; 0.72 for all hollows	0.89 for hollows >5cm; 0.97 for all hollows	9.0 (2.2–32.2) for stems >20cm DBH	65
Ball et al. (2011)	Tropical eucalypt woodland, central Queensland coast (remnant woodland)	13 (2–36) for hollows >4cm	40 (11–92) for hollows >4cm	0.63 for hollows >4cm	0.90 for hollows >4cm	N/A	94
Eyre (2005)	Dry sclerophyll forest, SE Queensland	~ 20 for hollows >10cm	5.9 (1–19) for hollows >10cm	0–0.06 for hollows >10cm	0.02–0.5 for hollows >10cm	N/A	80+
Wormington et al. (2005)	Dry sclerophyll forest, SE Queensland	N/A	1.8–20 for hollows >2cm and stems >20cm DBH	0 for hollows >2cm and stems >20cm DBH	0 for hollows >2cm and stems >20cm DBH	8–30 for stems >10cm DBH	100+
Eyre et al. (2010)	Dry sclerophyll forest, SE Queensland	N/A	4 (0–23) for hollows >10cm and live stems >20cm DBH	0.01–0.03 for hollows >10cm and live stems >20cm DBH	0.05–0.18 for hollows >10cm and live stems >20cm DBH	N/A	185
Harper et al. (2005)	Dry sclerophyll forest, urban SE Australia	N/A	5.8 (0–21) for hollows >5 cm	N/A	0.1–0.3 for hollows >5 cm	N/A	100+
Treby and Castley (2015)	Wet sclerophyll forest, urban SE Queensland	88 (1–165) for hollows >10cm	37.5 (1–86) for hollows >10cm	N/A	N/A	N/A	80+
McLean et al. (2015)	Wet sclerophyll forest, New South Wales	80–140 intact forest; 30–50 logged forest (for hollows >2cm)	40–50 intact forest; 10–20 logged forest (for hollows >2cm)	N/A	N/A	24–29 intact forest; 10–20 logged forest (for stems >15cm DBH)	N/A
McLean et al. (2015)	Dry sclerophyll forest, New South Wales	90–130 intact forest; 50–90 logged forest (for hollows >2cm)	30–50 intact forest; 18–30 logged forest (for hollows >2cm)	N/A	N/A	18–28 intact forest 16–18 logged forest (for stems >15cm DBH)	N/A
Rayner et al. (2014)	Dry sclerophyll woodlands, central W New South Wales	82 for hollows >1cm	17 for hollows >1cm	0.02–0.35 for hollows >1cm, four common eucalypts	0.3–0.75 for hollows >1cm, four common eucalypts	N/A	200+
Croft et al. (2016)	Open eucalypt forests and woodlands, SE New South Wales	61 frequently burnt; 110 long unburnt (for all hollows)	29 long unburnt (for all hollows)	N/A	N/A	N/A	N/A
Gibbons et al.	Mountain forests, SE	N/A	22 (10 – 30) intact	0-0.15	0-0.2	20-120	300+

(2000)	Australia		forest (for hollows >2cm)	for hollows >2cm	for hollows >2cm	for live eucalypts	
Whitford (2002)	Wet sclerophyll forests (Jarrah), SW Western Australia	25–30 for hollows >2cm	N/A	N/A	N/A	N/A	180+
Munks et al. (2007)	Dry eucalypt forests, Tasmania	24–55 for hollows >3cm	14–33 for hollows >3cm	0 for hollows >3cm	0 for hollows >3cm	N/A	150+
Gibbons and Lindenmayer (2002)	Range of studies in temperate forests	N/A	13–27	N/A	N/A	N/A	N/A
Gibbons and Lindenmayer (2002)	Range of studies in temperate woodlands	N/A	7–17	N/A	N/A	N/A	N/A

**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 ( $w_+$ ) 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  $w_+ \ge 0.73$  (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<sup>2</sup> is the conditional goodness-offit pseudo-R<sup>2</sup> (not supported for zero-inflated model classes) of the best model which included only highly influential variables (Nakagawa and Schielzeth 2013).

Response variable	Model distribution	<b>W</b> <sub>+</sub>								$\mathbf{R}^2$
		DBH	Tree height	BT ratio	Tree health	Species group	Cyclone	Fire scar	Termite	
Tree-level analysis										
Total hollows	Poisson	1.00	1.00	1.00	1.00	1.00	0.94	0.25	1.00	0.56
Small (<5cm)	Poisson	1.00	1.00	1.00	1.00	1.00	1.00	0.05	0.59	0.46
Medium (5-10cm)	Poisson	1.00	0.98	0.59	1.00	0.98	0.24	0.87	1.00	0.43
Large (10-20cm)	Zero-inflated negative binomial	1.00	0.28	0.94	1.00	1.00	0.49	0.55	0.76	N/A
Very large (>20cm)	Zero-inflated negative binomial	1.00	0.30	0.30	1.00	0.36	1.00	0.73	0.95	N/A
							Fino	Late dry		
Site-level analysis		Rainfall	Soil depth	Soil texture	Slope	Cyclone	frequency	frequency		
Total hollows	Negative binomial	1.00	0.27	0.01	0.35	0.96	0.35	0.25		0.32
Small (<5cm)	Negative binomial	1.00	0.24	0.01	0.27	0.99	0.25	0.20		0.34
Medium (5-10cm)	Negative binomial	1.00	0.15	0.01	0.49	1.00	0.73	0.21		0.41
Large (10-20cm)	Negative binomial	0.40	0.47	0.01	0.27	0.11	0.25	0.82		0.19
Very large (>20cm)	Negative binomial	0.31	0.80	0.20	0.23	0.05	0.19	0.30		0.16



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 ( $\Delta$ ) 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

732 Table 3). The black line is model fit and the grey band represents 95% confidence interval. Codes for categorical 733 variables: Species group (E.min = Eucalyptus miniata, E.tet = E.tetrodonta, RBB = Rough/thick-barked bloodwoods, 734 SBB = Scaly/thin-barked bloodwoods, Eryth = Erythrophleum chlorostachys, Acacia = Acacia spp., Non-euc = Non-735 eucalypt spp.); Tree health (Nil/few = no/few dead branches, Some/many = some/many dead branches, Entirely = 736 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; 737 738 Much = extensive/cambial trunk fire scarring); Termite activity (Nil = No sign of termite activity, Tracks = termite 739 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<sup>-1</sup>) 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

750 definitions.



Figure 5. (a) Relationship between hollow density per hectare (ha<sup>-1</sup>) 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

772 773

brackets)) for continuous variables.

Coding **Parameter** Comment Sample median (and range) or total sample size per category Tree-level analysis Diameter at breast height (DBH) Continuous, standardised Diameter (cm) of main stem measured at 1.3m from the ground 28 (20-65) Tree height Continuous, standardised Total tree canopy height (m) 15 (2-32) Bole height Continuous, standardised Height (m) from the ground to the first branch that was at least 25% 8 (1-25) of the diameter of the trunk at the branching point Assessment of tree shape given by the ratio of bole height to Continuous, standardised Bole:trunk (*BT ratio*) 0.53 (0.1-1.0) canopy height Species group Categorical (Eucalyptus Species included in Rough/thick-barked bloodwoods (RBB) = E.miniata 657, E.tetrodonta 822, (includes half-barked) C.confertiflora, C.dunlopiana, C.ferruginea, miniata, E.tetrodonta, Erythrophleum chlorostachys 133, C.nesophila, C.polycarpa, C.polysciadia, C.porrecta, C.setosa; RBB 106, SBB 43, Acacia spp. 18, Erythrophleum chlorostachys, Rough/thick-barked Scaly/thin-barked bloodwoods (SBB) = C.bleeseri, Other non-eucalypt spp. 30 bloodwoods, Scaly/thin-C.dichromophloia, C.foelscheana, C.latifolia; Acacia spp. = Acacia auriculiformis, A.lamprocarpa; Other non-eucalypt spp. = Alstonia, barked bloodwoods, Acacia spp, Other non-eucalypt spp) Brachychiton, Buchanania, Ficus, Gardenia, Lophostemon, Owenia, Petalostigma, Syzygium, Terminalia, Xanthostemon spp. Categorical (Nil = no evidence The extent to which the trunk showed evidence of fire scarring Nil 391, Fire scar of trunk fire scar. Some = depending on height of fire scar and depth of scarring Some 1305. superficial/minimal trunk fire Note: Fire scar height on the trunk and depth of tissue damage can Much 113 scar; Much = indicate whether a tree has experienced an intense fire in the recent extensive/cambial trunk fire past, with greater height and depth indicative of greater intensity scarring) fire Tree health Categorical (No or few dead The extent of tree mortality No/few 1064, branches, Some or many dead Some/many 576, branches, Entirely dead) Entirely dead 169 *Termite* sign Categorical (Nil = none, The extent of termite activity on the tree Nil 852, Tracks = signs of termite Tracks 534, tracks on trunk. Mound = Mound 423 termite mound present at base of tree) Categorical (No, Yes) Cyclone damage to canopy The presence or absence of cyclone damage to canopy No 1665, Yes 144

Site-level analysis			
Mean annual rainfall	Continuous, standardised	Estimate of mean annual rainfall (mm) per site from lat/long location sourced from ANUCLIM (Houlder et al. 2000)	1333 (868-1674)
Fire frequency	Continuous, standardised	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, www.firenorth.org.au)	0.5 (0-1.0)
Late dry season fire frequency	Continuous, standardised	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, www.firenorth.org.au) Note: Late dry season fire frequency approximates frequency of high intensity fires due to accumulation of cured fuel load in the late dry season and consequential greater fire intensity compared with early season fires (Williams et al. 1999)	0.125 (0-0.5)
<i>Cyclone</i> impact	Categorical (No discernible impact, Moderate, Severe)	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	None 26, Moderate 11, Severe 6
Slope	Continuous, standardised	Estimate of slope (degrees)	1 (0-15)
Soil depth	Categorical (0-10cm, 10- 40cm, >40cm)	Measure of soil depth (cm), average from three sample points per site	0-10cm 4, 10-40cm 10, >40cm 29
Soil texture	Categorical (sand, sandy- loam, loam, clay-loam)	Field or hand-texturing estimate of soil texture (McDonald et al. 1998), average from three sample points per site	Sand 8, Sandy-loam 23, Loam 10, Clay-loam 2
Rock cover	Continuous, standardised	Estimate of percentage (%) rock cover on the land surface, average from three sample points per site	2 (0-75)
Livestock grazing (See Appendix B)	Categorical (Grazed by livestock, Not grazed by livestock)	Presence or absence of evidence of livestock grazing, based on tenure (i.e. pastoral property or not).	Grazed 7, Not grazed 36
Stand density index (See Appendix B)	Continuous, standardised	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) <sup>1.605</sup>	114.9 (14.3-310.5)
Stand basal area (See Appendix B)	Continuous, standardised	Total basal area of all trees on a site calculated from DBH (m <sup>2</sup> .ha <sup>-1</sup> )	9.0 (2.2-32.2)



775 Appendix B. Relationship between total hollow density per site and (a) stand density index (calculated from number 776 of trees and average stand DBH, see Appendix A), (b) stand basal area, and (e) presence of livestock grazing on a site, 777 and relationship between (f) rainfall and grazing. Modelled relationships between stand density and the most 778 important predictors of stand density (c) rainfall and (d) cyclone impact, derived from model-averaged gamma GLM. 779 In figures (a) - (d) black circles are data points, the black line is model fit, and the grey band represents 95% 780 confidence interval. In figure (e) and (f) median (thick, line), upper and lower quartiles (box), minimum and maximum 781 values (whiskers) and outliers (black circles) are shown. Stand basal area or stand density index may be a valuable 782 field measure as a coarse proxy for direct counts of total hollow density (Pearson's correlation r = 0.63), but this 783 relationship is weaker for large hollows > 10 cm diameter (r = 0.42). Note that grazing was highly correlated with 784 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
- 786 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.