Forest Ecology and Management 419–420 (2018) 146–159

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Leigh-Ann Woolley[a,*], Brett P. Murphy[a], Ian J. Radford[b], John Westaway[c,d,1], John C.Z. Woinarski[a,d,2]

[a] NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia
[b] Department of Biodiversity, Conservation and Attractions, PO Box 942, Kununurra, WA 6743, Australia
[c] Department Agriculture and Water Resources, PO Box 37846, Winnellie, NT 0821, Australia
[d] Parks and Wildlife Commission of the Northern Territory, PO Box 496, Palmerston, NT 0831, Australia

ARTICLE INFO

Keywords:
Tree cavities
Hollow-bearing trees
Eucalypt woodland
Disturbance ecology
Arboreal fauna

ABSTRACT

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.

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

* Corresponding author.
E-mail address: leigh-ann.woolley@cdu.edu.au (L.-A. Woolley).
[1] Current address: Department Agriculture and Water Resources, PO Box 37846, Winnellie, NT 0821, Australia.
[2] Current address: NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia.

https://doi.org/10.1016/j.foreco.2018.03.034
Received 1 February 2018; Received in revised form 16 March 2018; Accepted 17 March 2018

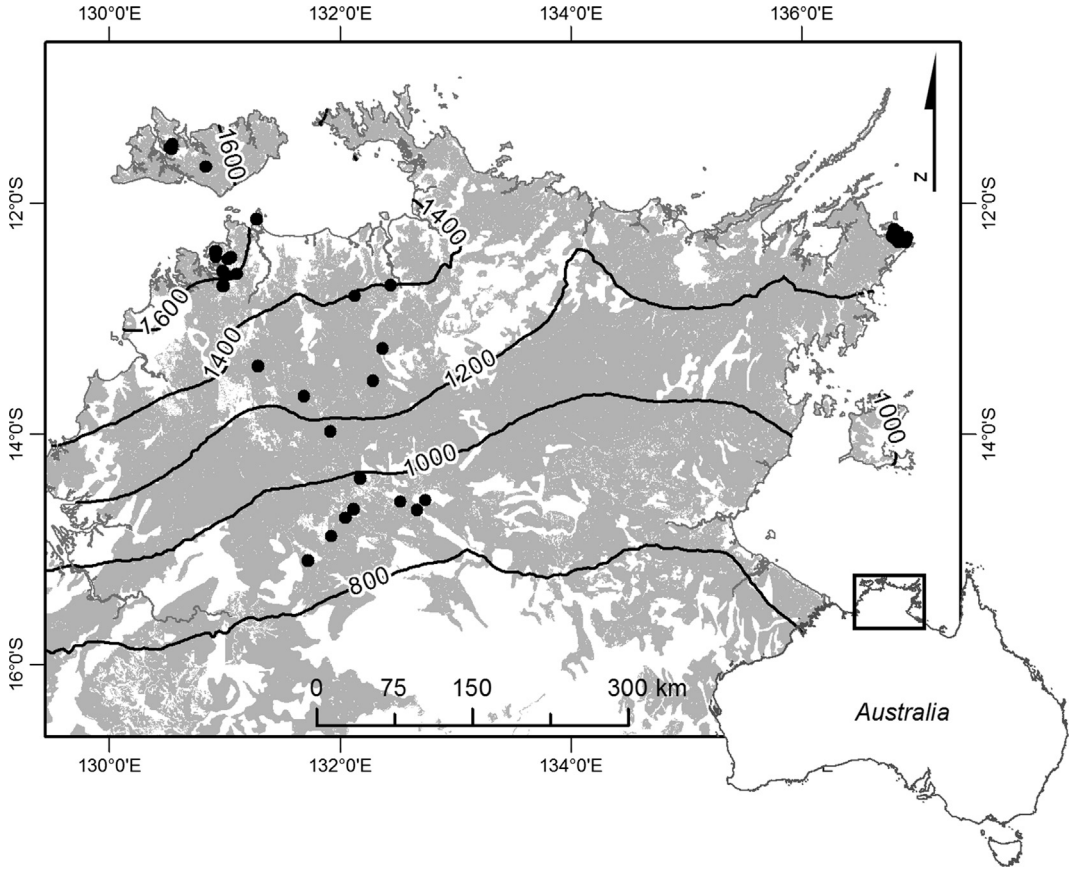

Fig. 1. Location of sample sites within eucalypt-dominated savanna (grey shading) across the Northern Territory, Australia (above ca. 800 mm mean annual rainfall). The contour lines represent mean annual rainfall isohyets.

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