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The Fire Refuge Value of Patches of a Fire-Sensitive Tree in Fire-prone Savannas: *Callitris intratropica* in Northern Australia

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ABSTRACT

Patches of fire-sensitive vegetation often occur within fire-prone tropical savannas, and are indicative of localized areas where fire regimes are less severe. These may act as important fire refugia for fire-sensitive biota. The fire-sensitive tree *Callitris intratropica* occurs in small patches throughout the fire-prone northern Australian savannas, and is widely seen as an indicator of low-severity fire regimes and of good ecosystem health. Here, we address the question: to what extent do *Callitris* patches act as refuges for other fire-sensitive biota, and therefore play a broader conservation role? We contrast floral and faunal species composition between *Callitris* patches and surrounding eucalypt savanna, using three case studies. In the first case study, a floristic analysis of 47 *Callitris* patches across Western Australia's Kimberley region showed that woody species in these patches were overwhelmingly widespread, fire-tolerant savanna taxa. No species of special conservation concern occurred disproportionately within *Callitris* patches. Similarly, there was no concentration of fire-sensitive fauna or flora in five *Callitris* patches in the East Kimberley. Finally, there was no difference in ant species composition among 12 *Callitris* patches and surrounding eucalypt savannas in Kakadu National Park, Northern Territory, and there were no fire-sensitive ant species in *Callitris* patches. Our three case studies from throughout the northwestern Australia provide no evidence that *Callitris* patches act as important refuges for fire-sensitive flora or fauna within fire-prone eucalypt savannas. This calls into question the notion that *Callitris* is a strong indicator of general ecosystem health.

Key words: ants; conservation; fire refugia; fire-sensitive biota; reptiles; savannah; small mammals.

Although tropical savannas represent the world's most highly fire-prone biome (Bond *et al.* 2005, Chuvieco *et al.* 2008, Murphy *et al.* 2013), many savanna landscapes include patches of relatively fire-sensitive vegetation that make important contributions to regional biodiversity because of their highly distinctive floral and faunal composition (Russell-Smith & Bowman 1992, Ratter *et al.* 1997, Mittermeier *et al.* 1998, Russell-Smith *et al.* 1998). Such vegetation types include forest patches in the Brazilian cerrado savannas (Ratter *et al.* 1997, Moriera 2000), *Juniperus*/*Quercus* woodland in southern U.S.A. (Fuhlendorf & Smeins 1997, Peterson & Reich 2001, Karnitz & Asbjornsen 2006), and monsoon rain forest (Russell-Smith & Bowman 1992, Russell-Smith *et al.* 2012), riparian gallery forest (Douglas *et al.* 2003, Radford *et al.* 2008), tropical heath (Russell-Smith *et al.* 2002, 2012), and *Acacia* woodlands (Woinarski & Fisher 1995a,b) in eucalypt-dominated savannas of northern Australia.

In addition to harboring unique species, these fire-sensitive vegetation types also potentially play broader roles in savanna ecology and biodiversity conservation by acting as refuges for other fire-sensitive species that are more widely distributed in the savanna landscape. The refuge value of fire-sensitive vegetation types within savannas, however, has been poorly studied. This issue is especially relevant in the vast savanna landscapes of northern Australia, where disruptions to traditional Aboriginal burning practices following European settlement have meant that fire has been largely unmanaged over recent decades in many regions. This has led to an increase in the frequency and extent of higher intensity fires occurring late in the dry season, and there are widespread fears that such changed fire regimes have had a negative impact on savanna biodiversity (Russell-Smith & Yates 2007, Yates *et al.* 2008, Russell-Smith *et al.* 2012). Although much of Australia's savanna biota is highly resilient to fire (Andersen & Muller 2000, Corbett *et al.* 2003, Russell-Smith *et al.* 2003, Lawes *et al.* 2011, Radford 2012), a range of taxa are threatened by severe fire regimes, including small mammals (Andersen *et al.* 2005, Burbidge *et al.* 2009, Woinarski *et al.* 2010, 2011), late-succession reptiles, and invertebrates (*e.g.*, Trainor & Woinarski 1994, Lowe 1995, Taylor & Fox 2001, Barrow 2009), and obligate seeding plant species that can be eliminated by fire-return intervals less than the time required to reach reproductive maturity (Russell-Smith *et al.* 1998, 2002).

One fire-sensitive species that has attracted considerable attention in Australia is the native cypress *C. intratropica* (Cupressaceae; recently synonymized with *C. columellaris* by Farjon 2005, hereafter simply referred to as *Callitris*). This tree occurs patchily

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in Australia's eucalypt-dominated savanna landscapes, often in association with rocky refugia (Bowman & Panton 1993, Bowman *et al.* 2001, Prior *et al.* 2011). *Callitris* populations are associated with areas of reduced grass biomass (Trauernicht *et al.* 2012), which greatly reduces flammability and provides resistance to low-intensity fires from the surrounding savanna landscape. *Callitris*, however, is sensitive to the intense crown-scorching fires that are prevalent in the late dry season of northern Australia (Russell-Smith *et al.* 2012). Observed declines in *Callitris* stand structure across much of northern Australia is seen as a strong signal of increasingly severe fire regimes and reflecting broader declines in regional biodiversity values (Bowman & Panton 1993, Price & Bowman 1994, Graham 2001). Conversely, areas with high concentrations of *Callitris* patches with a diversity of plant size classes are seen as indicative of low-severity fire regimes and good ecosystem health.

The status of *Callitris* as a key indicator of local low-severity fire regimes (Bowman *et al.* 2001) raises the question: To what extent might *Callitris* patches act as important refuges for other threatened fire-sensitive biota? In contrast to the patches of fire-sensitive rain forest that are also embedded in savanna landscapes, and have a highly distinct flora and fauna (Russell-Smith 1991, Gambold & Woinarski 1993, Woinarski 1993, Reichel & Ansersen 1996), the plant and animal species associated with *Callitris* have been poorly documented (though see Trauernicht *et al.* 2012, 2013). If patches of *Callitris* act as refuges for other fire-sensitive savanna species, then such patches could play an important role in the ecology and conservation of fire-prone savanna landscapes.

In this study, we examine the extent to which *Callitris* patches act as fire refuges for other taxa within Australia's savanna landscapes. We ask: are other fire-sensitive biota of high conservation value disproportionately prevalent in *Callitris* patches compared with surrounding savanna? We address this question using three case studies from across northwestern Australia that combine new survey data with existing information on species' distributions. First, we analyze the floristic composition of 47 *Callitris* patches distributed throughout the Kimberley region of far northern Western Australia. Second, we compare species composition of woody plants, mammals, reptiles, and ants inside *Callitris* patches and in adjacent eucalypt savanna habitat in the Ning Bing Ranges of the East Kimberley. Third, we compare ant species composition in *Callitris* patches to adjacent eucalypt-dominated savanna habitat in Kakadu National Park in the Northern Territory. In each case, we seek to identify fire-sensitive species other than *C. intratropica* that occur in *Callitris* patches, but are not well represented in the surrounding, frequently burned eucalypt savannas.

METHODS

STUDY SITES.—*General.*—Both the Kimberley and Kakadu regions (Fig. S1) experience a tropical monsoonal climate, with high temperatures (daily mean maximum >30°C) year-round, and high annual rainfall (*ca* 1000–1200 mm annual) occurring predominantly from November to March. The structure of *Callitris* patches varied from dense to relatively open (Figs. 1, S2A and C). Overall similarities in vegetation structure among *Callitris* patches (low perennial grass cover, low eucalypt cover, high shrub cover, and high plant richness) irrespective of *Callitris* cover, however, consistently differentiated them from surrounding eucalypt savannas (Figs.1 and S2B).

Kimberley-wide survey.—Sites in the broad-scale Kimberley survey were distributed throughout the North and Central Kimberley IBRA (Interim Biogeographic Regionalisation of Australia) bioregions (Fig. S1) (Graham 2001). *Callitris* patches ranged from <100 m^2 to >25 ha, and were subjected to a range of land uses including pastoral and conservation (Graham 2001). Many of the *Callitris* patches included were structurally complex containing a range of size classes (Graham 2001) indicative of locally low intensity fire regimes (Prior *et al.* 2011).

Ning Bing range.—The Ning Bing study was conducted on Carlton Hill Station (15.10°S, 128.68°E). Elevation of all sites was <200 m above sea level. Sites represented a range of *Callitris* and nearby eucalypt savanna habitats (Table 1). Five *Callitris* patches (sites NC1-5) were examined, situated on a range of substrates including deep sands (N = 3), shallow sand on sandstone (N = 1), and limestone-derived clay soils (N = 1) (Table 1). Three additional sites (NS1-3) represented typical vegetation from surrounding eucalypt savanna. Two sites were chosen on deep sand substrates and one (NS3) on limestone-derived clay soil. All sites were situated within 30 km of one another, with the closest sites at least 500 m apart. Patch width ranged from 80 to 300 m (Table 1). All sites were subjected to low levels of grazing by domestic cattle due to their occurrence in relatively low fertility (sand plain and range) areas on the station. We assume that numerous seedling and juvenile *Callitris* present at Ning Bing study sites (Table 1) is indicative of locally low-intensity patchy fire regimes (Prior *et al.* 2011).

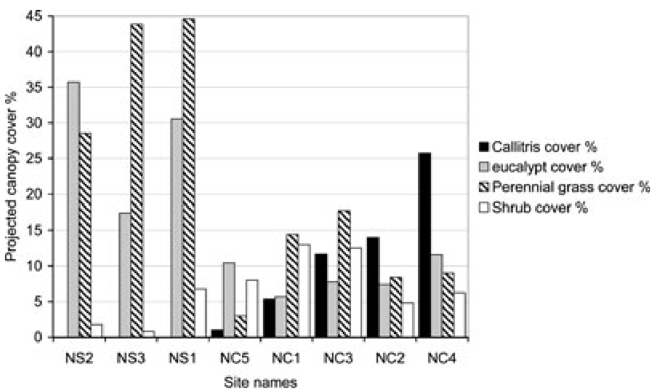

FIGURE 1. Histogram of comparative *Calltiris intratropica*, eucalypt, perennial grass, and shrub-projected canopy cover (%) at five *Callitris* patches and three eucalypt savanna sites in the Ning Bing Ranges of the Kimberley, Western Australia.

TABLE 1. *Summary information on the size and structure of the five Callitris patches studied in the Ning Bing Ranges.*

Patch number	Soil type	Maximum patch diameter (m)	Density (ha^{-1}) Seedlings (<1 m)	Juveniles (1–4 m)	Adult trees (>4 m)	Dead trees
NC1	Clay	120	1600	66	513	43
NC2	Sand	120	242	0	155	320
NC3	Sandstone	200	10000	108	113	79
NC4	Sand	300	6000	250	250	188
NC5	Sand	80	2	1	12	47

Kakadu.—The Kakadu study sites were located on the western Arnhem Land Plateau, with six *Callitris* patches each in the Gunlom and Jim Jim Falls regions (sites G1-6 and J1-6, respectively; Fig. S1) (Trauernicht *et al.* 2012). Elevation ranged from 178 to 436 m above sea level. Patches ranged in size from 50 to 100 m maximum diameter and were separated by at least 500 m. They were located within open sandsheet savannas dominated by *Eucalyptus tetrodonta* and *E. miniata*. There is no commercial grazing of livestock in the region, although very low densities of water buffalos were present in the Jim Jim area. *Callitris* stands in this study included a range of size classes indicative of relatively benign regimes (Trauernicht *et al.* 2012, 2013).

SAMPLING.—*Kimberley-wide survey.*—Vegetation surveys were completed for 143 quadrats among 47 *Callitris* patches, each quadrat 50 m × 10 m in size. Larger *Callitris* patches had two or more quadrats surveyed if they fitted contiguously within the patch. No eucalypt savannas were surveyed in this part of the study. All woody plant species occurring within quadrats were recorded. Taxonomic nomenclature follows Petheram and Kok (2003), Brooker and Kleinig (2004), and Kenneally *et al.* (1996). The conservation status of each species was assessed using information in Nature Map, WA Department of Environment and Conservation (http://naturemap.dec.wa.gov.au/default.aspx).

Ning Bing ranges.—Plant community structure was documented along transects running from the edge toward the center of *Callitris* patches, or through representative vegetation at eucalypt savanna sites. Vegetation was assessed at a minimum of three points along each transect, with each point separated by 20 m. Woody plant cover was estimated by species at each point at three heights: canopy (>4 m), mid-storey (1–4 m), and ground (<1 m). Mean canopy and mid-storey cover and basal area were estimated using the Bitterlich method (Lindsay *et al.* 1958). Additional woody plant species present, but with no cover values, were recorded within 20 × 20 m quadrats adjacent to each transect point. Herbaceous vegetation structure was also recorded in 20 × 20 m quadrats. A point intercept method was used to quantitate herbaceous cover within several cover classes. The method used for selection of point intercepts per quadrat (*N* = 45) was done by random placement of a 1.5 m staff marked with 15 lines spaced 10 cm apart. The staff was placed along the ground three times in each quadrat, with the specific site chosen by pacing random numbers of steps along the diagonal of the quadrat to avoid deliberate site selection. Ground cover was designated under each marked line using the following cover classes: perennial grass (*e.g.*, *Triodia* spp., *Sorghum plumosum*, *Themeda triandra*), annual grass (*e.g.*, *Sorghum stipoidium*), forb, leaf and grass litter, bare ground, and rock.

Trapping grids for sampling reptiles and small mammals were established adjacent to vegetation transects. A 7 × 7 grid of Elliott traps with 20 m spacing, covering an area of 120 × 120 m (1.44 ha), were established at each site to survey mammals. Half the Elliott traps were medium sized (9 × 10 × 33 cm) and half were large (15 × 15.5 × 46 cm). Eighteen funnel traps (20 × 20 × 80 cm) were placed within the grid to sample ground dwelling reptiles, placed in the center of every second grid cell formed by the locations of Elliott traps. All reptile and small mammal traps were opened for four consecutive nights, and checked and cleared early each morning. Species identity and size (total length for reptiles and weight for mammals) was recorded for each animal. Animals captured were all released on-site immediately after identification and measurement.

Ants were sampled using a 5 × 4 grid of pitfall traps with 10-m spacing, located adjacent to the vegetation transect at each site. Pitfall traps were 7-cm-diam plastic vials, partly filled with ethylene glycol as a preservative, and were operated for 48 h. Ants were identified to species through reference to the CSIRO Tropical Ecosystem Research Centre collection in Darwin, which contains the most comprehensive holdings of northern Australian ants. Most species could not be confidently identified, and these were assigned species codes (sp. 1, sp. 2, etc.) that follow those used in previous studies (*e.g.*, Andersen *et al.* 2006, 2010).

All sampling was conducted between May and September (dry season) 2009.

Kakadu study.—Ants were sampled using a 5 × 4 grid of pitfall traps in each of the 12 *Callitris* patches, with this configuration sometimes modified due to irregular patch shape. Spacing between traps was 5 m or 10 m, depending on patch size. In each case, 20 additional traps were located in surrounding eucalypt savanna, regularly spaced around the *Callitris* patch. Eucalypt savanna traps were set within 20 m of the edge of *Callitris* patches to reduce confounding effects of different locations within a patch. Twenty meters was deemed sufficient to separate putative *Callitris*-associated assemblages, given that most ant species have foraging ranges less than 10 m. Traps were 4.5-cm-diam plastic vials, partly filled with ethylene glycol as a preservative. Deployment time varied because of logistic constraints, from 26 to 50 h, but was the same for each *Callitris*/eucalypt savanna pair of sites. Sampling occurred during May and June (dry season) 2011. Ants were identified as described for the Ning Bing study.

ANALYSIS.—Each plant species from the Kimberley-wide survey and the Ning Bing Ranges study was classified according to its post-fire recruitment response (obligate seeder, facultative resprouter, resprouter; Gill & Bradstock 1992) using the Northern Territory Plant Ecological Attributes data base (M. R.Gardner, J.Russell-Smith, D. Albrecht, I. Cowie, K. Brennan, A. Duguid, C. Brock and C. Nano. unpubl. data 2005).

For the Ning Bing Ranges study, differences between mean values at *Callitris* and eucalypt savanna sites were tested and one-way ANOVA was used. Percentage cover data were arc-sine square root transformed prior to analysis and fauna numerical abundance data (counts of individuals and species richness) were $\log_e$ transformed. Animal abundance, species richness, and mean length (mm) of common species were compared between *Callitris* and eucalypt savanna sites and one-way ANOVA was used.

Relationships between the 24 Kakadu plots (12 inside *Callitris* patches, matched by 12 outside) based on ant species composition (abundance) were explored using non-metric multidimensional scaling of species abundance data based on Bray-Curtis similarity (Clarke & Warwick 2001). Analysis of Similarity (ANOSIM), run as a two-factor (location, patch type) model, was used to test for differences in species composition (Clarke & Warwick 2001). Separate analyses were conducted on species presence/absence and abundance data, using PRIMER v5 (Clarke & Gorley 2001). Similar analyses were not conducted on data from the Ning Bing Ranges because there were too few sample plots.

RESULTS

KIMBERLEY-WIDE SURVEY.—A total of 114 plant species were identified in the Kimberley-wide survey of 143 × 500 m^2 quadrats across 47 *Callitris* patches (Appendix 1). Nature Map (http://naturemap.dec.wa.gov.au) shows that the overwhelming majority (95%) of these are common and widespread savanna species. Only one species (*Brachychiton tuberulatus*) is of potential conservation concern, and it has no particular association with *Callitris* patches. Four other species (*Livistona eastonii*, *Eucalyptus brachyandra*, *E. cadophora,* and *E. lirata*) have relatively restricted distributions in the Kimberley region, but none of these is fire sensitive or particularly common in *Callitris* patches. There was only one species (*Glochidion disparipes*) characteristic of rain forest rather than savanna habitats. The generally low representation of fire-sensitive species is further illustrated by only 18 (16%) of the 114 species within *Callitris* patches being obligate seeders (Table S1).

NING BING RANGES.—A total of 44 woody plant species were recorded during the Ning Bing surveys of *Callitris* and eucalypt savanna sites. Forty-one of these species were recorded at the five *Callitris* sites (within 22 × 400 m^2 quadrats) and 20 species were recorded at the three eucalypt savanna sites (in 13 × 400 m^2 quadrats) (Table S2). Mean species richness per quadrat was significantly higher at *Callitris* sites (18.4 cf. 11.7, F [1, 7] = 15.05, P = 0.01). *Callitris intratropica* canopy cover was the only variable differing significantly between *Callitris* and eucalypt savanna sites (Table S2). None of the 44 species is of conservation concern, with all having widespread distributions in a range of habitats independent of *Callitris* patches.

Thirty two (73%) of the plant species were resprouters, nine (20%) were facultative resprouters, two species had unknown fire responses (5%), and only three species (7%) were obligate seeders (Table 2). There were no differences between patch types in the mean richness of any of the fire responses when *C. intratropica* was excluded from analysis. Resprouters had significantly higher canopy cover at eucalypt savanna, however, compared with *Callitris* sites (Table 2). Eucalypt cover, total tree cover, and perennial grass cover were higher at eucalypt savanna sites compared with *Callitris* patches, whereas shrub cover was higher at *Callitris* sites (Table 2).

A total of 80 individuals of 13 reptile species and 8 individuals of two mammal species were captured during vertebrate surveys (Table 3). Trap success was 13.9 percent for reptiles and 0.5 percent for mammals. Fourteen vertebrate species were recorded at *Callitris* sites and 11 at eucalypt savanna sites (Table 3), with no significant difference in mean site species richness (5.5 cf. 5.75, F [1, 7] = 0.08, P = 0.79). The most commonly caught reptiles were the skinks *Ctenotus inornatus*, *C. robustus,* and *Morethia ruficauda*, which were all more abundant in eucalypt savanna than in *Callitris* habitats, but not significantly so (Table 3). Combined catches of the two *Ctenotus* species, however, were significantly higher in eucalypt savanna (F [1, 7] = 6.95, P = 0.04). Both rodent species, *Pseudomys delicat-*

TABLE 2. *Plant structural and functional differences between Callitris patches and Eucalyptus savannas in the Ning Bing ranges. Data are means, and* P *values are from one-way ANOVA (d.f = 1.7; P < 0.05 in bold).*

	Callitris	Savanna
Canopy cover		
Total vegetation cover (%)	35.79	33.38 ns
Obligate seeders (not incl. *Callitris*) (%)	0.04	<0.01 ns
Facultative resprouters (%)	5.50	3.02 ns
Resprouters (%)	12.80	29.61†
Species richness of:		
Obligate seeders (not incl. *Callitris*)	0.60	0.33 ns
Facultative resprouters	2.40	1.67 ns
Resprouters	10.00	7.33 ns
Vegetation structure		
Basal area (m^2/ha)	14.47	12.28 ns
Total woody vegetation cover (%)	35.79	33.38 ns
Eucalyptus/Corymbia cover (%)	8.56	27.87*
Shrub density	37.00	11.82 ns
Shrub cover (%)	8.91	3.10†
Perennial grass (%)	10.51	39.00*
Annual grass (%)	3.94	0.56 ns
Leaf litter (%)	33.94	34.60 ns

*Statistically significant (P < 0.01).
†statistically significant (P < 0.05).
ns, not statistically significant (P > 0.05).

TABLE 3. *Mean catches of reptiles (72 trap-nights per site) and mammals (196 trap-nights per site) in Callitris patches and in adjacent Eucalyptus savanna in the Ning Bing Ranges.*

	Animals per site	
Species	*Callitris*	Savanna
Mammals		
Muridae		
Pseudomys delicatulus	0.60	0.67 ns
Pseudomys nanus	0.40	0.33 ns
Reptiles		
Agamidae		
Chlamydosaurus kingii	0.40	0 ns
Diporiphora bennettii	0.20	0 ns
Diporiphora lalliae	0.40	0.33 ns
Diporiphora magna	0.40	1.33 ns
Elapidae		
Furina ornatus	0	0.33 ns
Gekkonidae		
Heteronotia binoea	0.20	1.67 ns
Strophurus ciliaris	0.20	0 ns
Scincidae		
Carlia munda	1.20	0.67 ns
Ctenotus inornatus	0.60	2.30 ns
Ctenotus robustus	1.80	2.67 ns
Glaphyromorphus isolepis	0.20	0 ns
Lerista grifini	1.20	1.00 ns
Morethia ruficauda	1.40	2.33 ns

ns, not statistically significant ($P > 0.05$).

TABLE 4. *Mean length (mm) of the most common reptile species in Callitris patches and Eucalyptus savanna sites in the Ning Bing Ranges.*

Species	*Callitris*	Savanna
Carlia munda	88.0	103.5 ns
Ctenotus spp.	131.4	192.2*
Diporiphora magna	177.5	187.5 ns
Lerista grifini	106.7	76.7*
Morethia ruficauda	75.0	65.0*

*Statistically significant ($P < 0.05$).
ns, not statistically significant ($P > 0.05$).

ulus and *P. nanus*, had similarly low capture rates (<1 animal per site) at *Callitris* and eucalypt savanna sites (Table 3). All vertebrates were widespread, common species, with none being of conservation concern.

There was no significant difference in mean weight of the rodent *Pseudomys delicatulus* between *Callitris* patches (7.67 g) and eucalypt savanna (5.50 g) sites (F [1, 4] = 2.54, $P = 0.21$), nor were there differences in length for the lizards *Carlia munda* or *Diporiphora magna* (Table 4). Large skinks of the genus *Ctenotus* (*C. inornatus* and *C. robustus*, total length up to 380 mm), however, were significantly shorter in *Callitris* patches, whereas the small skinks *Lerista grifini* and *Morethia ruficauda* were both longer (Table 4).

A total of 53 ant species from 13 genera were collected in pitfall traps (Table S3). The richest genera were *Monomorium* (12 species), *Melophorus* (10), *Iridomyrmex* (8), and *Rhytidoponera* (6), and the most common ants were species of *Iridomyrmex*, *Monomorium,* and *Rhytidoponera*. Site species richness ranged from 11 to 35, and was significantly higher at *Callitris* (mean of 24.6) than eucalypt savanna (14.3) sites (F [1, 7] = 5.78, $P = 0.05$). All ant species commonly recorded in *Callitris* patches were also common outside, and no ant species from *Callitris* patches are known to be fire-sensitive or of conservation significance.

KAKADU STUDY.—A total of 112 ant species from 26 genera were recorded in the Kakadu study, with the richest genera being *Monomorium* (18 species), *Meranoplus* (13), *Camponotus* (11), *Rhytidoponera* (10), *Melophorus* (10), *Pheidole* (7), *Iridomyrmex* (6), *Tetramorium* (5), and *Polyrhachis* (5) (Table S4). As in the Ning Bing Ranges, the most common ants were species of *Iridomyrmex*, *Monomorium,* and *Rhytidoponera*, and many of the most common species (*e.g.*, *Iridomyrmex pallidus*, *I. sanguineus*, *I. reburrus*, *Iridomyrmex* sp. 1, *Monomorium* sp. 13) were shared. The total number of species recorded in *Callitris* patches (91) was very similar to that of outside (95), and mean site species richness was not significantly different (28.3 vs. 29.0; $P = 0.567$, paired t-test).

NMDS results were very similar for species presence/absence and abundance data, and so only the former are presented. There was strong differentiation in species composition between sites from the Gunlom and Jim Jim Falls locations (ANOSIM Global $R = 0.26$, $P = 0.01$), with plots from the same site within a location also strongly clustered (Fig. 2). There was no significant differentiation between *Callitris* patches and adjacent eucalypt savanna (ANOSIM Global $R = 0.034$, $P = 0.32$, Fig. 1). As was the case in the Ning Bing Ranges, we were unable to identify any species from *Callitris* patches that might be regarded as fire-sensitive or otherwise of particular conservation significance.

DISCUSSION

Our two Kimberley case studies showed that *Callitris* patches were structurally different from surrounding eucalyptus savannas, with higher richness and cover of shrubs, and lower cover of perennial grasses. Such structural differences have also been shown for *Callitris* patches in central and western Arnhem Land in the Northern Territory (Trauernicht *et al.* 2012, 2013). Nevertheless, we found no evidence of a concentration of fire-sensitive (obligate seeder or facultative resprouter) plant species, and virtually all plant species occurring in *Callitris* patches in our study have widespread distributions and broad habitat ranges. Only three species (*Alstonia spectabilis, Glochidion disparipes,* and *Calytrix exstipulata*) could be considered characteristic of fire-sensitive vegetation, and all are very common and widespread across northern Australia.

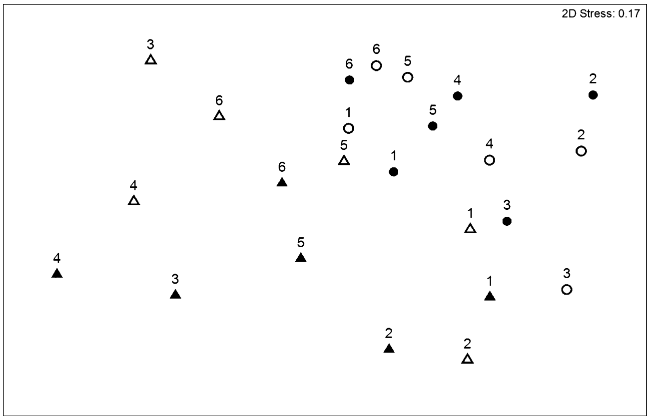

FIGURE 2. NMDS ordination of Kakadu plots based on ant species occurrence. Circles and triangles represent plots from the Gunlom and Jim Jim regions, respectively, with plots inside and outside *Callitris* patches indicated by filled and open symbols, respectively. Numbers indicate site numbers (*i.e.*, 1–6 from each location, each with a plot inside and outside a *Callitris* patch).

Trauernicht *et al.* (2013) found that (fire-sensitive) obligate-seeder plant species contributed about 25 percent of stems and species in intact *Callitris* patches in Arnhem Land, which was far higher than we recorded in the Kimberley. It is not clear if these regional differences reflect differences in fire regimes, edaphic conditions, or regional floras. Notably, however, the fire-sensitive species with higher prevalence in intact *Callitris* patches in Arnhem Land are regionally common and widely distributed outside *Callitris* patches (Trauernicht *et al.* 2013), and there is no evidence that *Callitris* patches make a significant contribution to the conservation status of any of them.

Our results suggest that *Callitris* patches do not support a particular concentration of fire-sensitive animal species, either in the Kimberley or Arnhem Land. Our Ning Bing Ranges study found no reptile species common in *Callitris* patches that were not also common in surrounding eucalypt savanna. Indeed, *Ctenotus robustus*, which is known to be fire-sensitive based on documented fire responses (Trainor & Woinarski 1994, Corbett *et al.* 2003), was less abundant, and individuals were on average smaller, within *Callitris* patches than in surrounding, frequently burnt, eucalypt savanna. Only two small mammal species were recorded in the Ning Bing Ranges, and each was equally uncommon in *Callitris* and eucalypt savanna. Previous studies suggest that these species have contrasting responses to fire in eucalypt savanna, with *P. nanus* decreasing (Legge *et al.* 2008) and *P. delicatulus* increasing in response to fire (Corbett *et al.* 2003), but both are among the most widespread and common small mammals across northern Australia (Legge *et al.* 2008, 2011, Woinarski *et al.* 2010, Radford 2012). Despite extensive *Callitris* stands (Bowman *et al.* 2001, Trauernicht *et al.* 2013), there have been dramatic declines in fire-sensitive small mammals across central and western Arnhem Land (Woinarski *et al.* 2010), which further suggests a lack of significant fire refuge value of *Callitris* patches. We recorded no specialist ant species characteristic of long-unburnt habitat (Andersen *et al.* 2006, Andersen & Hoffmann 2011) in either the Ning Bing Ranges or Kakadu National Park. In short, we were unable to identify any animal species from *Callitris* patches that might be regarded as fire-sensitive or otherwise of particular conservation significance.

The lack of response of fire-sensitive fauna suggests that *Callitris* patches represent unsuitable habitat for such species despite low fire severity. Fire-sensitive animal species in Australian savannas tend to be associated with particular habitat structures such as complex leaf litter, structurally diverse ground-layer vegetation, or a well-developed mid-storey of fleshy fruit-producing trees (Braithwaite & Griffiths 1996, Corbett *et al.* 2003, Andersen *et al.* 2006, 2012, Firth *et al.* 2006), and these are notably lacking in *Callitris* patches. Indeed, the simplified grass layer characteristic of *Callitris* patches likely explains why fire-sensitive groups such as the large *Ctenotus* skinks are actually less common than in surrounding eucalypt savanna. More particularly, such habitat structure is not favorable for the suite of small mammal species that have undergone marked population declines over recent decades (Woinarski *et al.* 2011). An additional factor mitigating against fire-sensitive small mammals using *Callitris* as fire refuges is small patch size. Most of our study patches were less than three hectares, whereas threatened mammal species such as the northern brown bandicoot (*Isoodon macrourus*) and northern quoll (*Dasyurus hallucatus*) need larger areas (Oakwood 2002, Pardon *et al.* 2003, Cook 2010, Cook *et al.* 2010). *Callitris* patches of this size are dwarfed by surrounding eucalypt savanna landscapes, which cover millions of hectares, and so for most individuals, the patches are unable to offer even short-term refuge during the fires themselves.

Callitris intratropica appears to be functionally similar in terms of fire response to fire-sensitive species of *Acacia*, such as lancewood (*A. shirleyi*), that form extensive monospecific stands in more arid regions of northern Australia (Beadle 1981). Lancewood stands likewise support a depauperate and poorly defined assemblage of vertebrate species, which, although distinct from surrounding savanna, does not include fire-sensitive species (Woinarski & Fisher 1995a,b). As in *Callitris* patches, these stands of fire-sensitive *Acacia* species lack the complex habitat structures required by fire-sensitive animal species.

CONCLUSION

Stands of *Callitris* can play an important role as indicators of the severity of local fire regimes. *Callitris* patches also presumably play additional roles in savanna landscapes unrelated to their fire sensitivity (*e.g.*, as hosts for specialist herbivores). Our results, however, suggest that they do not act as important refugia for other fire-sensitive species. We could find no evidence that *Callitris* patches are indicative of broader ecosystem health. In terms of identifying fire refugia for conserving species threatened by prevailing fire regimes, management attention would be better directed at other habitats such as rocky outcrops, sandstone heathlands and rain forest/riparian forest, which are known to harbor fire-sensitive species (Russell-Smith & Bowman 1992, Woinarski *et al.* 1992, Russell-Smith *et al.* 1998, Burbidge & Manly 2002, Radford 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Woody plant species recorded from 143 quadrats across 47 Callitris patches occurring throughout the Kimberley region.*

TABLE S2. *Woody plant species occurring in* Callitris *patches and in adjacent* Eucalyptus-*dominated savanna in the Ning Bing ranges.*

TABLE S3. *Abundance of ant species collected in pitfall traps in* Callitris *patches and* Eucalyptus *savanna sites in the Ning Bing Ranges.*

TABLE S4. *Ant species collected inside and outside* Callitris *patches in the Gunlom and Jim Jim Falls regions of Kakadu National Park.*

FIGURE S1. Location of the Ning Bing, Jim Jim and Gunlom study regions in northwestern Australia.

FIGURE S2. Adjacent *Callitris* and *Eucalyptus* savanna sites in the Ning Bing Ranges, and site J2 in Kakadu National Park.

LITERATURE CITED

ANDERSEN, A. N., G. D. COOK, L. K. CORBETT, M. M. DOUGLAS, R. W. EAGER, J. RUSSELL-SMITH, S. A. SETTERFIELD, R. J. WILLIAMS, AND J. C. Z. WOINARSKI. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecol. 30: 155–167.

ANDERSEN, A. N., T. HERTOG, AND J. C. Z. WOINARSKI. 2006. Long-term fire exclusion and ant community structure in an Australian tropical savanna: Congruence with vegetation succession. J. Biogeogr. 33: 823–832.

ANDERSEN, A. N., AND B. D. HOFFMANN. 2011. Biodiversity value of low fire frequency in tropical savannas: Ants in monsoonal northern Australia. Austral Ecol. 36: 497–503.

ANDERSEN, A. N., J. LANOUE, AND I. RADFORD. 2010. The ant fauna of the remote Mitchell Falls area of tropical north-western Australia: Biogeography, environmental relationships and conservation significance. J. Insect Conserv. 14: 647–661.

ANDERSEN, A. N., AND W. J. MULLER. 2000. Arthropod responses to experimental fire regimes in an Australian tropical savannah: Ordinal level analysis. Austral Ecol. 25: 199–209.

ANDERSEN, A. N., J. C. Z. WOINARSKI, AND C. L. PARR. 2012. Savanna burning for biodiversity: Fire management for faunal conservation in Australian tropical savannas. Austral Ecol. 37: 658–667.

BARROW, P. H. 2009. The role of fire in the ecology of Leichhardt's grasshopper (*Petasida ephippigera*) and its food plants, *Pityrodia* spp. Ph.D Thesis, Charles Darwin University.

BEADLE, N. C. W. 1981. The vegetation of Australia. Cambridge University Press, Cambridge.

BOND, W. J., F. I. WOODWARD, AND G. F. MIDGLEY. 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165: 525–538.

BOWMAN, D. M. J. S., AND W. J. PANTON. 1993. Decline of *Callitris intratropica* R. T. Baker, H. G. Smith in the Northern Territory: Implications for pre- and post-European colonization fire regimes. J. Biogeogr. 20: 373–381.

BOWMAN, D. M. J. S., O. PRICE, P. J. WHITEHEAD, AND A. WALSH. 2001. The 'wilderness effect' and the decline of *Callitris intratropica* on the Arnhem Land Plateau, northern Australia. Aust. J. Bot. 49: 665–674.

BRAITHWAITE, R. W., AND A. D. GRIFFITHS. 1996. The paradox of *Rattus tunneyi*: Endangerment of a native pest. Wildl. Res. 23: 1–21.

BROOKER, M. I. H., AND D. A. KLEINIG. 2004. Field guides to eucalyptus: Volume 3 Northern Australia. Bloomings Books, Melbourne.

BURBIDGE, A. A., AND B. F. J. MANLY. 2002. Mammal extinctions on Australian Islands: Causes and conservation implications. J. Biogeogr. 29: 465–473.

BURBIDGE, A. A., N. L. MCKENZIE, K. E. C. BRENNAN, J. C. Z. WOINARSKI, C. R. DICKMAN, A. BAYNES, G. GORDON, P. W. MENKHORST, AND A. C. ROBINSON. 2009. Conservation status and biogeography of Australia's terrestrial mammals. Aus. J. Zool. 56: 411–422.

CHUVIECO, E., L. GIGLIO, AND C. JUSTICE. 2008. Global characterization of fire activity: Toward defining fire regimes from Earth observation data. Glob. Change Biol. 14: 1488–1502.

CLARKE, K. R., AND R. N. GORLEY. 2001. Primer v5: User manual/tutorial. Primer-e. Plymouth Marine Laboratory, Plymouth, UK.

CLARKE, K. R., AND R. M. WARWICK. 2001. Change in marine communities: An approach to statistical analysis and interpretation. Primer-e. Plymouth Marine Laboratory, Plymouth, UK.

COOK, A. 2010. Fire effect on habitat use and home-range of the northern quoll, *Dasyurus hallucatus*. Masters of Science Thesis,University of Western Austalia.

COOK, A., I.RADFORD , R.BENCINI , AND H. R.MILLS . 2010. Habitat use and home-range of the northern quoll, *Dasyurus hallucatus*: Effects of fire. Australian Wildlife Management Society Conference – Poster. Sydney.

CORBETT, L. C., A. N.ANDERSEN, AND W. J.MULLER . 2003. Terrestrial vertebrates. In: A. N. Andersen, G. D. Cook, and R. J. Williams (Eds.). Fire in tropical Savannas: The Kapalga experiment. pp. 126–152. Springer-Verlag, New York.

DOUGLAS, M. M., S. A. TOWNSEND, AND P. S. LAKE. 2003. 5. Streams. In: A. N. Andersen, G. D. Cook, and R. J. Williams (Eds.). Fire in tropical Savannas: The Kapalga experiment. pp. 59–78. Springer-Verlag, New York.

FARJON, A. 2005. Monograph of Cupressaceae and Sciadopitys. Royal Botanic Gardens, Kew. pp. 507–513.

FIRTH, R. S. C., E. JEFFERYS, J. C. Z. WOINARSKI, AND R. A. NOSKE. 2006. The diet of the brush-tailed rabbit-rat (*Conilurus penicillatus*) from the monsoonal tropics of the Northern Territory, Australia. Wildl. Res. 32: 517–523.

FUHLENDORF, S. D., AND F. E. SMEINS. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. J. Veg. Sci. 8: 819–828.

GAMBOLD, N., AND J. C. Z. WOINARSKI. 1993. Distributional patterns of herpetofauna in monsoon rain forests of the Northern Territory, Australia. Aust. J. Ecol. 18: 431–449.

GILL, A. M., AND R. A. BRADSTOCK. 1992. A national register for the fire responses of plant species. Cunninghamia 2: 653–660.

GRAHAM, G. 2001. An assessment of the distribution and status of Arnhem Cypress pine Callitris intratropica in the Kimberley region. Unpublished Report to the National Reserve Systems Program, Environment Australia, Canberra, Western Australia.

KARNITZ, H., AND H. ASBJORNSEN. 2006. Composition and age structure of a degraded tallgrass oak savanna in Central Iowa. Nat. Areas. J. 26: 179–186.

Kenneally, K. F., D., Choules Edinger, and T., Willing. 1996. Broome and Beyond: Plants and people of the Dampier Peninsula, Kimberley. Western Australian Department of Conservation and Land Management, Como, Western Australia.

Lawes, M. J., H. Adie, J. Russell-Smith, B. Murphy, and J.J. Midgley. 2011. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. Ecosphere 2: 1–13.

Legge, S., M. S. Kennedy, R. Lloyd, S. A. Murphy, and A. Fisher. 2011. Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. Austral Ecol. 36: 791–799.

Legge, S., S. Murphy, J. Heathcote, E. Flaxman, J. Augusteyne, and M. Crossman. 2008. The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. Wildl. Res. 35: 33–43.

Lindsay, A. A., J. D. Barton, and S. R. Miles. 1958. Field efficiencies of forest sampling methods. Ecology 39: 428–444.

Lowe, L. 1995. Preliminary investigations of the biology and management of leichhardt's grasshopper, Petasida ephippigera white. J. Orthoptera Res. 4: 219–221.

Mittermeir, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conserv. Biol. 12: 516–520.

Moriera, A. G. 2000. Effects of fire protection on savanna structure in Central Brazil. J. Biogeogr. 27: 1021–1029.

Murphy, B. P., R. A. Bradstock, M. M. Boer, J. Carter, G. J. Cary, M. A. Cochrane, R. J. Fensham, J. Russell-smith, G. J. Wiliamson, and D. M. J. S. Bowman. 2013. Fire regimes of Australia: A pyrogeographic model system. J. Biogeogr. 40: 1048–1058.

Oakwood, M. 2002. Spatial and social organization of a carnivorous marsupial Dasyurus hallucatus (Marsupialia: Dasyuridae). J. Zool. 257: 237–248.

Pardon, L. G., B. W. Brook, A. D. Griffiths, and R. W. Braithwaite. 2003. Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. J. Anim. Ecol. 72: 106–115.

Peterson, D. W., and P. B. Reich.2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecol. Appl. 11: 914–927.

Petheram, R. J., and B. Kok. 2003. Plants of the Kimberley Region of Western Australia. University of Western Australia Press, Perth.

Price, O., and D. M. J. S. Bowman. 1994. Fire-stick forestry: A matrix model in support of skilful fire management of *Callitris intratropica* R.T. Baker by North Australian Aborigines. J. Biogeogr. 21: 573–580.

Prior, L. D., W. L. McCaw, P. F. Grierson, B. P. Murphy, and D. M. J. S. Bowman. 2011. Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change. For. Ecol. Manage. 262: 252–262.

Radford, I. J. 2012. Threatened mammals become more predatory after small-scale prescribed fires in a high rainfall rocky savanna. Austral Ecol. 37: 926–935.

Radford, I. J., and A. C., GriceB. N., Abbott, D. M., Nicholas, andL., Whiteman. 2008. Impacts of wet and dry season prescribed burning on invasive *Cryptostegia grandiflora* populations and on associated tropical woodland, and riparian forest in north Queensland, Australia. Austral Ecol. 33: 151–167.

Ratter, J. A., J. F. Ribeiro, and S. Bridgewater. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Ann. Bot. 80: 223–230.

Reichel, H., and A. N. Ansersen. 1996. The rainforest ant fauna of Australia's Northern Territory. Aus. J. Zool. 44: 81–95.

Russell-Smith, J. 1991. Classification, species richness, and environmental relations of monsoon rainforest vegetation in the Northern Territory. J. Veg. Sci. 2: 259–278.

Russell-Smith, J., and D. M. J. S. Bowman. 1992. Conservation of monsoon rainforest isolates in the Northern Territory, Australia. Biol. Conserv. 59: 51–63.

Russell-Smith, J., A. C. Edwards, and O. F. Price. 2012. Simplifying the Savanna: The trajectory of fire-sensitive mosaics in northern Australia. J. Biogeogr. 39: 1303–1317.

Russell-Smith, J., P. G. Ryan, and D. C. Cheal. 2002. Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: Frequency, intervals, patchiness. Biol. Conserv. 104: 91–106.

Russell-Smith, J., P. G. Ryan, D. Klessa, G. Waight, and R. Harwood. 1998. Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. J. Appl. Ecol. 35: 829–846.

Russell-Smith, J., P. J. Whitehead, G. D. Cook, and J. L. Hoare. 2003. Response of Eucalyptus-dominated savanna to frequent fire: Lessons from Munmarlary 1973-1996. Ecol. Monogr. 73: 349–375.

Russell-Smith, J., and C. P. Yates. 2007. Australian savanna fire regimes: Context, scale, patchiness. Fire Ecol. 3: 48–63.

Taylor, J. E., and B. J. Fox. 2001. Assessing the disturbance impact on vegetation and lizard communities of fluoride pollution interacting with fire and mining in eastern Australia. Austral Ecol. 26: 321–337.

Trainor, C. R., and J. C. Z. Woinarski. 1994. Responses of lizards to three experimental fires in the savanna forests of Kakadu National Park. Wildl. Res. 21: 131–148.

Trauernicht, C., B. P. Murphy, T. E. Portner, and D. M. J. S. Bowman. 2012. Tree cover –fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna. J. Ecol. 100: 958–968.

Trauernicht, C., B. P. Murphy, N. Tangalin, and D. M. J. S. Bowman. 2013. Cultural legacies, fire ecology, and environmental changes in the Stone Country of Arnhem Land and Kakadu National Park, Australia. Ecol Evol 3: 286–297.

Woinarski, J. C. Z. 1993. A cut-and-paste community - birds of monsoon rain forests in Kakadu National Park, Northern Territory. Emu 93: 100–120.

Woinarski, J. C. Z., M. Armstrong, K. Brennan, A. Fisher, A. D. Griffiths, B. Hill, D. Milne, S. Ward, M. Watson, S. Winderlich, and S. Young. 2010. Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. Wildl. Res. 37: 116–126.

Woinarski, J. C. Z., and A. Fisher. 1995a. Wildlife of lancewood (Acacia shirleyi) Thickets and Woodlands in Northern Australia. 1. Variation in vertebrate species composition across the environmental range occupied by lancewood vegetation in the Northern Territory. Wildl. Res. 22: 379–411.

Woinarski, J. C. Z., and A. Fisher. 1995b. Wildlife of lancewood (Acacia shirleyi) Thickets and Woodlands in Northern Australia. 2. Comparisons with other environments of the region (Acacia woodlands, Eucalyptus Savanna woodlands and Monsoon rainforests). Wildl. Res. 22: 413–443.

Woinarski, J. C. Z., S. Legge, J. A. Fitzsimmons, B. J. Traill, A. A. Burbidge, A. Fisher, R. S. C. Firth, I. J. Gordon, A. D. Griffiths, C. Johnson, N. L. McKenzie, C. Palmer, I. Radford, B. Rankmore, E. Ritchie, S. Ward, and M. Ziembicki. 2011. The disappearing mammal fauna of northern Australia: Context, cause, and response. Conserv. Lett. 4: 192–201.

Woinarski, J. C. Z., R. W. Raithwaite, K. A. Menkhorst, S. Griffin, A. Fisher, and N. Preece. 1992. Gradient analysis of the distribution of mammals in Stage III of Kakadu National Park, with a review of the distribution patterns of mammals across north-western Australia. Wildl. Res. 19: 233–262.

Yates, C. P., A. C. Edwards, and J. Russell-Smith. 2008. Big fires and their ecological impacts in Australian savannas: Size and frequency matters. Int. J. Wildland Fire 17: 768–781.