

Fauna and vegetation responses to fire and invasion by toxic cane toads (*Rhinella marina*) in an obligate seeder-dominated tropical savanna in the Kimberley, northern Australia

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Abstract

Context. Changed fire regimes are an important threatening process to savanna biodiversity. Fire-sensitive vegetation such as pindan and its fauna may be particularly susceptible to fire impacts. Invasion by alien species is an additional threatening process. The toxic anuran *Rhinella marina* is a well publicised invader of savannas. Little is known of impacts in many habitats.

Aims. To test the hypotheses (1) that fire responses among pindan fauna are greater than general savanna responses, and (2) that cane toad-invasion impacts will be reduced relative to riparian habitats.

Methods. Reptiles, frogs, invertebrates and mammals were surveyed seven times from 2008 to 2012, four times before and three times following *R. marina* invasion. Time since last fire was recorded during each survey. Vegetation change was measured.

Key results. Pindan vegetation structural recovery took 4–5 years, whereas fauna recovery took only 1 year. Ground active agamids, combined Scincidae, fossorial skinks and ground-layer invertebrates responded positively to recent fire. Skinks of *Ctenotus* spp. declined in size after fire. Short-term fauna responses reflect rapid re-establishment of herbaceous cover. Fauna responses were detected following *R. marina* invasion, including increases in frogs of *Uperoleia* spp. and skinks of *Carlia* spp., and decreases in *Lerista griffini* and ground-layer invertebrates. Insufficient data were available to test for responses among large predators; however, >50% lower *Varanus* spp. trap success occurred post-invasion. No invasion response was detected among small mammals.

Conclusions. Pindan fauna fire responses were similar to those of savannas. Fauna responses to *Rhinella marina* invasion were relatively minor compared with those previously reported in riparian habitats and this may be related to the lower abundance of the invader here than in previous studies in riparian or more fertile habitats.

Implications. The dominant obligate seeding tree in pindan woodland, *A. tumida*, requires >4 years with no high-intensity fires for re-establishment of the dominant tree. Fire management should aim to minimise extensive fires to reduce impacts on fire-sensitive fauna. Persistence of large predators after cane-toad invasion suggests possible refuge value of low-productivity pindan savannas.

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Introduction

Fire responses among plant communities and their faunas are highly variable. Fire responses range from radical change in vegetation and fauna community structure followed by extended post-fire recovery (e.g. Fox 1982; Masters 1996; Letnic *et al.* 2004), through to plant and animal communities that have little apparent fire response, or have extremely rapid recovery (Williams *et al.* 1999; Andersen and Muller 2000; Corbett *et al.* 2003; Russell-Smith *et al.* 2003; Andersen *et al.* 2005; Andersen *et al.* 2010; Radford 2012).

Generally, it would be expected that post-fire succession would be more pronounced and diverse in climatic zones and vegetation types where recovery time is slower. Thus, flammable-desert or -heath vegetation that requires many years to recover

‘climax’ vegetation or particular vegetation structures may be expected to have a greater range of plant- and animal-assemblage successional stages (Fox 1982; Masters 1996; Haslem *et al.* 2012), than do vegetation types that rapidly recover after fire (Andersen *et al.* 2005; Radford and Andersen 2012; Andersen *et al.* 2014a). However, there can be a disconnect between floral and faunal community fire responses, or among taxa within communities, such that different successional trajectories are observed among different taxonomic groups independently of vegetation recovery (Andersen *et al.* 2005, 2012; Clarke 2008; Taylor *et al.* 2013).

Fire-response differences among taxa probably relate directly to the habitat attributes that particular taxa respond to. So ants and other invertebrate groups that respond positively to open

savanna habitat may be unaffected by fire because they perceive savanna as open irrespective of whether the site is recently burnt or not (Andersen and Muller 2000; Andersen *et al.* 2010, 2014a). In contrast, larger fauna such as mammals may be severely affected by the same fire regime (Andersen *et al.* 2005, 2012; Legge *et al.* 2008). Differences in recovery rates and post-fire seral stages may be important for conservation management because particular species or groups may respond only to a subset of post-fire seral stages or habitat attributes (Andersen *et al.* 2012, 2014b; Radford *et al.* 2015).

Savanna vegetation, as one of the more regularly flammable vegetation types with development of an annual fuel load, might be expected to have rapid recovery of flora and fauna after fire events. And, in fact, many elements of the flora and fauna of tropical savannas are highly resilient to regular fires (Andersen and Muller 2000; Corbett *et al.* 2003; Russell-Smith *et al.* 2003; Andersen *et al.* 2005; Radford 2012), namely, plants through high percentages of resprouting species in frequently burnt savannas that rapidly recover pre-fire above-ground biomass (Clarke *et al.* 2015) and animals, presumably, through the rapid recovery of their habitat structures and resource bases (Radford 2012; Radford and Andersen 2012). However, not all savanna vegetation types are so rapid in their recovery of pre-fire condition. There are several vegetation components making up a small proportion within the savanna matrix that take much longer to recover after fire. These include vegetation components dominated by obligate-seeder species the adult stands of which are killed by canopy scorch. Such elements of savanna vegetation in northern Australia include *Callitris intratropica* (Bowman *et al.* 2001; Prior *et al.* 2011), tropical heath communities (Russell-Smith *et al.* 1998) and savanna woodlands dominated by *Acacia* spp. (Woinarski and Fisher 1995a, 1995b). Aside from a small number of one-off descriptive studies of floral and faunal communities associated with these savanna subelements (Woinarski and Fisher 1995a, 1995b; Trauernicht *et al.* 2013; Radford *et al.* 2013), little is known of the dynamics of fire responses among most of these vegetation types and their associated biota (Russell-Smith *et al.* 2010).

The present study primarily aims to describe fire responses of terrestrial animal assemblages and vegetation structure associated within pindan (*Acacia tumida*) savanna woodlands of the wet–dry tropical Kimberley region of northern Western Australia, so as to inform fire management. *Acacia tumida* is an obligate seeder with distributions across the tropical Kimberley. Much of the pindan woodland area is thought to be degraded in terms of biodiversity values through exacerbation of fire regimes, particularly through large areas of the western Kimberley (McKenzie 1981; Kenneally *et al.* 1996). Truncation of fire regimes are thought to threaten the vegetation type itself because, being an obligate seeder, this species requires a minimum time interval to reproduce before the next fire. Despite apparent threats to this vegetation type, there has been little investigation of fire responses among component biota. Description of fauna composition of a similar lancewood (*Acacia shirleyi*) woodland in the Northern Territory suggested that the biota was made up predominantly of fire-resilient savanna taxa (Woinarski and Fisher 1995a, 1995b). This is similar to the finding by Radford *et al.* (2013) that, despite being a fire-sensitive vegetation type (dominated by a fire

killed species), *Callitris intratropica* stands were found to harbour predominantly fire-resilient fauna.

It is unclear whether similar fauna would be present in pindan woodlands of the Kimberley region, or what the dynamics of their fire responses might be. We postulate that delayed recovery of pre-fire vegetation structures in this woodland (obligate seeding) will lead to more gradual recovery of fauna assemblages than in a more typical resprouter-dominated savanna. The present study aims to fill this gap in knowledge to inform fire managers of any specific fire-regime requirements, and also to add to the sum total of fire-response data for little known subelements within savanna vegetation (Radford *et al.* 2013).

Another significant threat to savanna biodiversity in northern Australia is invasion by the toxic anuran *Rhinella marina* (the cane toad; Shine 2010; Woinarski *et al.* 2011; Ziembicki *et al.* 2015). This species has several documented impacts among savanna ecosystems (Shine 2010). These include reductions among top predators as a result of poisoning (Shine 2010; Pearson *et al.* 2014), evolution of changed morphology in response to selective pressures through toad-related mortality (Phillips and Shine 2005), reduced invertebrate abundance (Greenlees *et al.* 2006) and cascading ecosystem responses, such as increases in meso-predator numbers, to functional loss of top predators (Doody *et al.* 2006, 2013). However, impacts by cane toads are variable, with inconsistent responses being recorded among different habitats and even among sites for particular species (Shine 2010; Ujvari *et al.* 2011). Many savannas with documented impacts have been associated with higher productivity or riparian habitats (e.g. Greenlees *et al.* 2006; Doody *et al.* 2009). It is unclear whether impacts would be generally less pronounced in areas with lower incidence of and carrying capacity for cane toads. Timing of invasion by cane toads in 2011 during this fire-response study has allowed the opportunity to address the question of whether pindan fauna are adversely affected by cane-toad invasion in a drier and less productive savanna type compared with other habitats.

Materials and methods

Study area and sites

The study was conducted inside and adjoining Mirima National Park near Kununurra, in the East Kimberley region of Western Australia. The region experiences a tropical monsoonal climate, with high temperatures year round (daily mean maximum 29.6–36.0°C), and medium rainfall (913 mm annual rainfall) occurring predominantly from November to April. Pindan woodlands are characterised by varying dominance of *A. tumida* and *A. platycarpa* in the mid-storey, with a sparse emergent top-storey of eucalypt (e.g. *Eucalyptus tetradonta*, *E. miniata*, *Corymbia polycarpa*) and non-eucalypt tree species (e.g. *Erythrophleum chlorostachys*, *Gevillea agrifolia*, *Adansonia gregori*) on sand or loamy sand substrates. The grass layer is co-dominated by annual *Sorghum stipoidium* and perennial hummock and/or tussock grasses, including *Triodia* spp. and *Aristida* spp. Pindan woodland forms the dominant vegetation type in non-rocky habitats within Mirima National Park (Kununurra).

Surveys

Ground-layer fauna was surveyed repeatedly at 10 pindan sites from October 2008 through to November 2012. Seven fauna surveys were conducted during the study, taking place in October–December 2008, March–May 2009, April–May 2010, November–December 2010, March–April 2011, February–April 2012 and October–December 2012. All surveys were undertaken during the hot, humid periods, either approaching the start of the wet season, or during or just after wet season, so that reptile, frog and invertebrate activity would be greatest. Sites were established between 100 m and 1700 m apart, which, for most small ground-dwelling vertebrates and invertebrates found in surveys (<100 mm in length or <100 g in weight), makes site survey data independent because few individuals were likely to travel among sites. Survey sites were initially chosen in 2008 to represent a range of post-fire intervals (0 years, 1 year and ≥ 2 years post-fire; Table 1). With the occurrence of annual fires throughout the study period, site-specific post-fire interval changed frequently during the study, with 21 survey observations of 0 years post-fire, 18 surveys for 1 year, 19 surveys for 2 years, 7 surveys for 3 years, 3 surveys for 4 years and 2 surveys 5 years post-fire (Table 1). Fire regime was characterised not only by years since the most recent fire (post-fire interval), but also fire intensity (high intensity for tree-crown scorch or low intensity where tree crowns were not scorched). Fire events before and during survey periods ranged from low-intensity prescribed fires (scorch height <3 m and <100% grass-layer vegetation consumed, Williams *et al.* 1999) during wet–dry transition periods (May 2008, April 2011), to high intensity late dry-season wildfires (August, October 2008, October 2012) (scorch height >12 m, 100% consumption of grass layer; Williams *et al.* 1999; Table 1). Prescribed management fires, either to protect or to burn particular sites before surveys, or as part of the greater fire management of the area, were applied in April–May 2009, November–December 2010 and March–April 2011 (Table 1). All other fires were savanna wildfires either caused by arson or accident.

Vegetation structure

Vegetation was assessed during five of the seven trapping sessions. During all vegetation measurements, total projected tree (>4 m) and shrub (1–4 m) canopy cover was recorded as a percentage using the bitterlich method (Lindsey *et al.* 1958). In addition, herbaceous ground-layer vegetation cover was

assessed using a point-intersect method on a pre-marked staff. Vegetation cover was classified at point intercepts according to the ground-cover categories perennial grass (*Triodia* spp., *Aristida* spp.), annual grass (annual *Sorghum*), dicot (forbs and subshrubs), leaf and woody litter and bare ground. Estimation was based on placement of a 1.5-m graduated stick with 10-cm increments at 16 within-site locations (240 points). Locations for placement of the stick were chosen on the diagonal from each of the four corners of the trapping grid, and were placed five paces in a line from the corner of the plot towards the next diagonal trap placement (4 in a line from each corner). Ground-cover categories were then calculated on the basis of percentages derived from intercept points.

Reptile, frog and ground-layer invertebrates

Reptiles, frogs and large ground-dwelling invertebrates (>5 mm long) were sampled using funnel traps during all seven surveys. In total, 18 funnel traps (15 × 15 × 70 cm, with 5-cm entrance diameter) were placed in a 6 × 3 trapping grids, each trap 20 m apart (grid area 0.6 ha). Each funnel was placed in a shallow (10–20 cm deep) trench 6 m long that attracted and guided fauna into the funnel trap from either end as per Radford (2012). This worked in a way similar to drift fences. Traps were opened for seven nights for the first two surveys and for four nights thereafter. Traps were checked daily as soon as possible after sunrise during surveys, to avoid heat stress- or desiccation-related deaths among captured animals. Shade from hessian sacks, branches or grass tufts were also used on top of each trap to reduce fauna mortality resulting from overheating. In very hot dry weather, funnel traps were watered (3–5 L every day) to prevent heat-related deaths in traps through evaporative cooling. Percentage trap success (number of captures/number of trap-nights × 100) was used for all fauna-abundance comparisons, with individual animals being marked using permanent marker pens so that recaptures were not included in totals. Reptiles and frogs were identified to species using standard fauna keys (Storr *et al.* 1983, 1999, 2002; Wilson and Swan 2003). Invertebrates were identified to class (Chilopoda (centipedes)), order (e.g. Coleoptera (beetles), Blattodea (cockroaches), Scorpiones (scorpions), Araneae (spiders)), suborder (e.g. Caelifera (grasshoppers), Ensifera (crickets)) or to family (e.g. Carabidae (carabid beetles)) where readily recognisable in the field). All fauna was measured for combined head and body length and reptiles were measured for snout–vent length and nose–tail length as

Table 1. Number of wet seasons since the last fire at pindan woodland sites at each survey date
Underlined 0 denotes high-intensity fires; bold and italic ***0*** indicates a prescribed management fire

Survey date	MA	MB	MC	MD	ME	MF	MG	MH	MI	MI
October–December 2008	<u>0</u>	<u>0</u>	0	2	<u>0</u>	2	<u>0</u>	<u>0</u>	2	1
April–May 2009	1	1	1	<i>0</i>	1	<i>0</i>	1	1	<i>0</i>	2
March–April 2010	2	2	2	1	2	1	2	2	1	3
November–December 2010	<u>0</u>	3	2	1	2	1	2	2	<u>0</u>	3
March–April 2011 ^A	1	4	3	2	3	2	3	<i>0</i>	1	<i>0</i>
February–March 2012 ^A	2	5	1	1	4	3	4	1	2	1
September–November 2012 ^A	2	5	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>

^ADenotes dates when cane toads were present at survey sites.

a measure of animal size. All animals were released on-site after processing.

Mammals were sampled during the latter five fauna surveys using Elliott and pit-fall traps. Eighteen Elliott traps (9 medium (9 × 10 × 33 cm) and 9 large (15 × 15.5 × 46 cm)) were placed near each funnel trap, making up a duplicate mammal-trapping grid. Elliott traps were baited with a mixture of peanut butter and oats and left open for four nights as per funnel traps. Four pit-fall traps were set up in the four corners of each survey site. Each pit-fall trap was made up of a 20-L bucket buried flush with the ground. Four shallow trenches (10–20 cm deep and 4 m long) radiating into pit-falls were used to direct animal movements into the traps. Like funnel traps, Elliott traps were shaded from the sun by using hessian sacks or leaf material to prevent overheating. Artificial shade was provided in pit traps in the form of loose, moist soil and polystyrene trays to reduce direct sun exposure. All traps were checked as soon as possible after sunrise to reduce risk of heat-related injury/death among trapped animals. Mammal weight, head length, pes length and, in the case of rodent species, combined head–body and tail length were measured to facilitate species identification. Mammal identification was based on Menkhorst and Knight (2004). Mammals were earmarked using permanent marker pens to allow accurate counts of individuals of each species per survey to be made. Although reptiles, frogs and invertebrates were also captured in pit-fall traps, only mammal records from pits are included in this analysis.

Statistical analysis

Nested repeated-measures ANOVA (general linear model; MINITAB 14, Minitab Inc. U.S.A.) was used to test for differences in univariate measures of vegetation, habitat attributes and fauna groups among sites, post-fire intervals, pre- and post-invasion (by toxic cane toads) and among survey dates. Because we were using repeated survey of permanent sites that were burnt periodically throughout the study, post-fire interval was nested within sites for these analyses. Fauna data were divided into surveys before and after cane-toad invasion, and survey date was nested within these periods for analysis. Additional factors, including the intensity of site fires before survey (high intensity with *A. tumida* tree leaf scorch; low intensity with ground-layer vegetation scorched) and rainfall in the 3 months before survey (fauna only) were included within the ANOVA as covariates. Because of the non-independence of repeated site measurements and post-fire interval in a nested design, the ANOVA error term could not be used to calculate sums of squares. All variables except for mammal data were arcsin (square-root) transformed to homogenise variances for percentage data.

Results

Vegetation

Pindan savanna woodlands at survey sites had a mean tree cover of 18.8% and perennial grass cover of 18.7%, shrub cover of 4.7%, annual grass cover of 8.7%, forb cover of 9.1% and leaf and woody litter cover of 37.3%. Time since most recent fire ranged from 0 to 5 years, with a mean time since last fire (TSLF) of 1.7 years. The trees and shrubs making up the greatest components of canopy cover were *Acacia tumida* (13.8%),

followed by *Eucalyptus tetrodonta* (2.7%), *E. miniata* (1.6%), *Erythrophleum chlorostachys* (1.4%), *Grevillea agrifolia* (1.3%) and *Scaevola browniana* (1.1%).

Exothermic fauna

During seven surveys at 10 sites over a total of 6120 trap-nights, 1085 reptiles, 194 frogs and 1375 invertebrates were trapped. Exothermic vertebrate trap success (TS) was 20.8%. The most common component of vertebrate assemblages were species of Scincidae, with a combined trap success of 12.8% (and 61.3% of captures). *Lerista griffini* (sand swimmer skink), *Carlia* spp., *Ctenotus* spp., *Eremiascincus isolepis* and *Morethia ruficauda* were the most common taxa. Frogs were the next most common vertebrate group, with 3.4% TS, and made up 16% of animals captured. The most common frogs were *Platyplectrum ornatum* and *Uperoleia* spp. Gekkonidae (2.2% TS) and Agamidae (1.6% TS) were also common groups, making up 10.8% and 7.9% of vertebrates, respectively. *Heteronotia binoei* was the most common gecko and *Diporiphora magna* and *D. pindan* were the most common agamids. Larger reptiles including *Varanus* spp. ($n=24$), Elapidae ($n=25$), Pygopodidae ($n=1$) and Ramphotyphlops ($n=2$) were trapped rarely (<0.8% TS) and made up 3.8% of vertebrate captures. Small numbers preclude this latter group from formal analysis of trends. Total exothermic vertebrate species richness was 6.2 sites survey⁻¹. Invertebrates had combined TS of 22.5%, with the most common groups being carabid Coleoptera (27.4% of invertebrates captured), Blattodea (21.4%), Chilopoda (20.0%), Araneae (5.9%), Gryllidae (5.6%), other non-carabid Coleoptera (5.0%) and Scorpiones (4.4%).

Mammal fauna

During five surveys and 4240 trap-nights (Elliotts plus pit-fall traps), 80 small mammals were captured (1.8% TS) in total. The most common species was the rodent *Pseudomys delicatulus* ($n=52$). Other rodents captured included *Rattus tunneyi* ($n=12$), *P. nanus* ($n=10$) and *Zyzomys argurus* ($n=3$). Three small dasyurid species *Planigale ingrami* were also recorded during the study ($n=3$).

Fire responses of vegetation structure

Vegetation structure and assemblage were significantly influenced by site, TSLF and survey date, but there was no effect of fire intensity on structural composition (Table 2). Tree cover, perennial grass cover and forb cover were influenced by TSLF (Table 2). Tree and forb cover were influenced by fire intensity (Table 2). Tree and perennial grass cover increased with post-fire interval from zero to 5 years (Figs 1a, 2, Table 2). Forb cover increased from zero in the year of the fire to 1 year post-fire and then declined 4 and 5 years post-fire (Fig. 1b, Table 2). Tree cover was greater at sites experiencing low-intensity fires, whereas forb cover was higher at these sites (Fig. 1a, b, Table 2). Tree cover after high-intensity fire attained values of sites affected only by low-intensity fire after 4 or 5 years post-fire (Fig. 1a). Additional factors significantly affecting pindan vegetation and habitat structure included site-specific (edaphic) effects (e.g. on percentage of bare ground) and survey date (annual grass, forb cover) relating to seasonal change (wet–dry transition or buildup season and rainfall; Table 2). In all,

Table 2. *F*-values and statistical significance of differences for vegetation structural attributes among sites, sample times and time-since-fire nested within sitesGLM, general linear model. *** $P < 0.001$; ** $0.01 < P < 0.001$; * $0.05 < P < 0.01$; n.s., $P > 0.05$ (ANOVA)

Parameter	Covariate (fire intensity)	Site	Years post-fire (site)	Time
MANOVA GLM (Wilks)				
d.f.	8,7	72,50	168,67	32,27
Structure (%)	2.663	2.975***	1.804**	1.947*
d.f.	9,3	81,28	216,45	36,12
Species (%)	1.203	13.761***	2.957***	3.925**
ANOVA GLM				
d.f.	1,14	9,14	21,14	4,14
Woody plants				
Tree canopy cover	8.57*	2.14	6.22**	1.76
Shrub cover (>1 m)	<0.01	0.45	1.32	0.78
Ground-layer shrub cover	0.06	1.03	1.79	0.33
Herbaceous layer				
Perennial grass cover	2.54	1.97	6.94***	0.56
Annual grass cover	4.02	1.21	1.10	6.01**
Forb cover	5.84*	1.88	3.99**	7.72**
Ground layer				
Tree litter	1.34	2.43	0.62	0.81
Bare ground	4.39	3.09*	0.71	0.35
Dominant plant species				
Trees				
<i>Acacia tumida</i>	7.88*	1.01	3.41*	2.09
<i>Corymbia polycarpa</i>	0.03	2.13	2.46	2.13
<i>Erythrophleum chlorostachys</i>	0.74	1.68	2.00	7.17**
<i>Eucalyptus miniata</i>	1.35	9.20***	1.64	0.55
<i>Eucalyptus tetradonta</i>	9.22*	15.37***	2.31	4.72*
Shrubs				
<i>Grevillea agrifolia</i>	1.53	9.98***	1.53	0.81
<i>Persoonia falcata</i>	0.17	3.40**	1.15	1.30
<i>Petalostigma pubescens</i>	0.76	4.47**	0.69	4.90*
Subshrubs and forbs				
<i>Crotalaria cunninghamii</i>	1.44	1.90	3.18*	2.25
<i>Scaevola brownii</i>	1.74	2.48*	3.45*	2.33

4 of 10 common plant species in pindan woodland were significantly affected by fire (Table 2). Cover of the dominant tree species, *A. tumida*, was significantly influenced by post-fire interval and fire intensity (Table 2). *Acacia tumida* cover was reduced almost to zero after intense fire (because of tree mortality) and increased with post-fire interval after both high- and low-intensity fires (Fig. 1c). *Acacia tumida* cover had fully recovered after a high-intensity fire 4–5 years post-fire (Fig. 1c) and, by this stage, trees were mature and able to produce seeds. Covers of the forbs *Crotalaria cunninghamii* and *Scaevola brownii* were influenced by post-fire interval (Table 2), with both attaining maximum cover at intermediate post-fire intervals (2 years post-fire; Fig. 2). In addition to fire-related effects, the covers of *E. miniata*, *E. tetradonta*, *G. agrifolia*, *Persoonia falcata*, *Petalostigma pubescens* and *S. cunninghamii* were significantly related to site-specific factors (edaphic). Cover of 3 of 10 common plant species was influenced by survey date, indicating seasonal effects (rainfall and season; Table 2).

Fauna fire response

Greatest responses among fauna groups were to temporal or seasonal variability (survey date) and spatial variability

(site-related factors) rather than to either fire or invasion (Table 3). Nonetheless, fire responses were detected. Unlike vegetation, fauna groups did not show a gradual or successional response to post-fire intervals from zero to 5 years post-fire ($P > 0.05$). Instead, fauna groups for which fire responses were evident partitioned differences between the year of the burn and all other TSLF (Table 3). Fire-response groups included two agamid species (*D. magna* and *D. pindan*), combined Scincidae, combined reptiles, Araneae, Blattodea and combined invertebrates (Table 3, Fig. 3a, b). In all cases, abundance (trap success) was higher at sites in the year of the fire than at all other TSLF (Fig. 3a, b). The exception to this were skinks of *Ctenotus* spp. (*C. inornatus* and *C. robustus*), which, although present at similar abundance in the year of a fire and at other times, were on average smaller (shorter snout–vent length) in the year of the fire (Table 3, Fig. 3c).

Invasion response

Combined fauna assemblages differed between surveys before and after toad invasion (Table 3). Mean trap success of the burrowing skink *Lerista griffini*, Coleoptera, Gryllidae, and total invertebrates was lower post-invasion, whereas abundance of

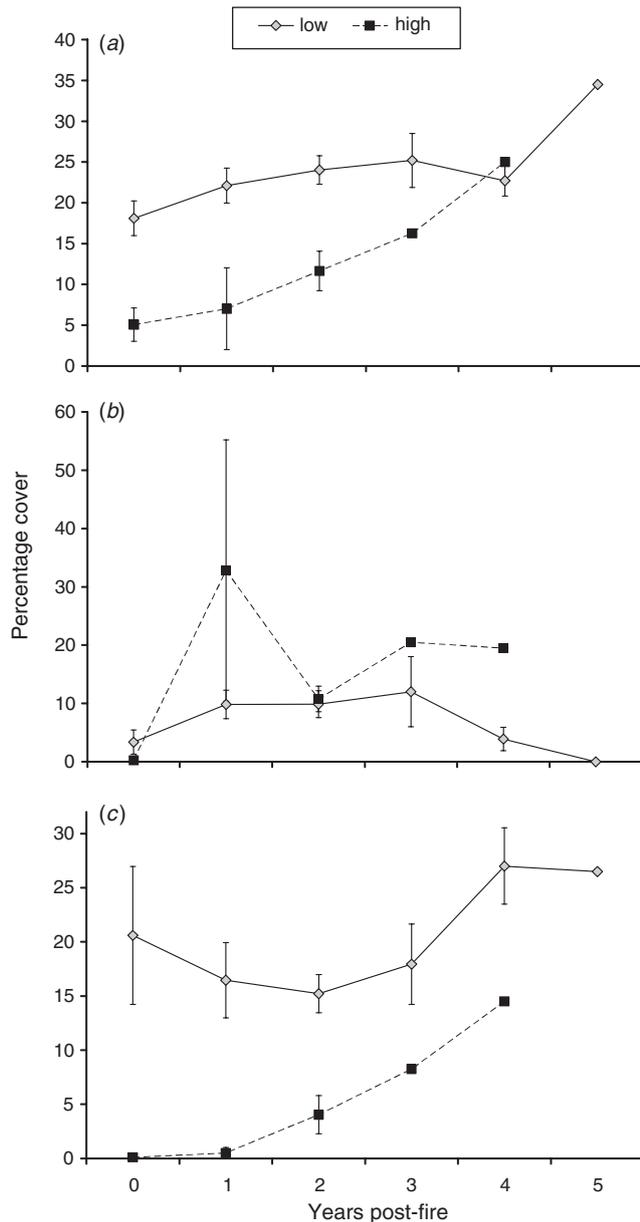


Fig. 1. Mean percentage projected ground cover with post-fire interval and after high-intensity (black squares) and low-intensity (grey diamonds) fires for (a) tree (>4 m) canopy cover (%), (b) forb cover and (c) *Acacia tumida* cover. Vertical bars represent the standard errors of the mean values.

skinks of *Carlia* spp., frogs of *Uperoleia* spp. and *Rhinella marina* (cane toad) was higher (Table 3, Fig. 4). Inter-survey variability was high within pre- and post-invasion periods (Fig. 4). *Lerista griffini* and invertebrate trap success was greatest during the first two pre-invasion surveys (2008/2009) and was generally lower thereafter, irrespective of pre- and post-invasion intervals (Fig. 4). Similarly, high mean TS of *Carlia* spp. and *Uperoleia* spp. occurred only during a single post-invasion survey, rather than generally across all post-toad surveys (Fig. 4).

Statistical analysis of trends among large predators including *Varanus* spp. (i.e. *V. gouldii* (10 pre-/4 post-invasion),

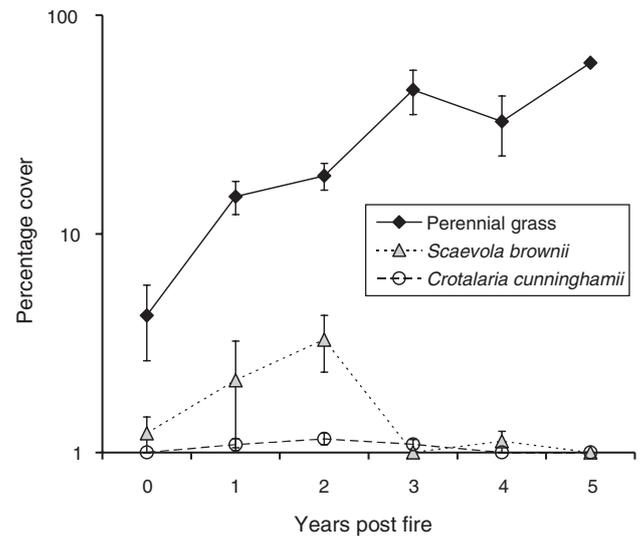


Fig. 2. Mean percentage cover (on logarithmic scale) for perennial grass and the species *Scaevola brownii* and *Crotalaria cunninghamii* with years post-fire (0–5 years). Vertical bars represent the standard error of the mean values.

1 *V. acanthurus* (5/1) and *V. mitchelli* (0/1), *V. scalaris* (1/0), *V. tristis* (2/0)) and snakes (*Brachyurophis roperi* (9/1), *Pseudonaja nuchalis* (2/3), *Pseudechis australis* (1/5), *P. weigeli* (0/1), *Acanthophis praelongus* (1/0), *Suta punctata* (2/0)) was precluded by low number of captures throughout the study. However, trap success for total *Varanus* spp. was reduced by >50% (from 0.56% to 0.27%) after *R. marina* had established at survey sites. In contrast to *Varanus*, total snake trap success was identical in pre- and post-invasion surveys (0.46%), although the burrowing snake *Brachyurophis roperi* had a >80% reduction in trap success (from 0.28% to 0.05%) and mulga snakes *Pseudechis* spp. actually increased by 86% post-invasion (from 0.03% to 0.28%).

Discussion

Vegetation fire response

Australian savannas, generally, are dominated by resprouting species (Clarke *et al.* 2015). Dominance by resprouting trees and shrubs has resulted in relative structural and compositional resilience in Australian savannas (Williams *et al.* 1999; Russell-Smith *et al.* 2003; Radford *et al.* 2008), although long-term absence of fire can result in major changes (Woinarski *et al.* 2004). In contrast to resprouter-dominated savannas, more fire-responsive elements within savanna vegetation, including obligate seeders, have more pronounced responses. *Callitris intratropica* is often cited as a species declining within the savanna matrix because of its inability to resprout after canopy scorch with high-intensity fire (Bowman *et al.* 2001; Trauernicht *et al.* 2013). Obligate-seeder heath species on the Arnhem Land Plateau are also considered under threat from high frequency fire regimes where maturation periods exceed interfire intervals (Russell-Smith *et al.* 2003).

In the present study, the dominant tree, *A. tumida*, was killed by high-intensity fires (scorch >8 m) and seedling emergence

Table 3. Statistical significance using ANOVA for differences in the abundance of fauna among sites, post-fire intervals, before and after cane-toad invasion and survey dates within these periods

Only commonly represented fauna groups and species (present >33% surveys) were included. Percentage trap-success data was arc-sin (square-root) transformed before analysis. GLM, general linear model; S.V.L., snout vent length. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	Site	Burnt or unburnt (site)	Pre- or post-invasion	Time (pre or post)
Abundance				
MANOVA GLM (Wilks)				
d.f.	198,211	220,233	22,23	110,117
Species	1.357*	1.099	7.059***	2.985***
d.f.	207,204	230,226	23,22	115,112
Functional groups	1.767***	1.256*	4.042**	2.756***
ANOVA GLM				
d.f.	9,44	10,44	1,44	5,44
Total Reptilia	1.56	2.35*	<0.01	5.81***
Agamidae				
<i>Diporiphora magna</i>	1.47	2.41*	2.05	3.71**
<i>Diporiphora pindan</i>	2.96**	3.45**	0.51	2.52*
Gekkonidae				
<i>Heteronotia binoei</i>	2.53*	1.11	<0.01	5.53***
Scincidae				
	1.96	2.47*	0.12	6.41***
<i>Carlia</i> spp.	2.66*	1.08	7.86**	3.98**
<i>Ctenotus inornatus</i>	0.73	1.19	3.50	4.39**
<i>Ctenotus robustus</i>	1.09	0.63	1.83	2.98*
<i>Eremiascincus isolepis</i>	2.68*	1.00	0.04	2.10
<i>Lerista griffini</i>	0.57	1.24	27.53***	3.31*
<i>Morethia ruficauda</i>	1.34	1.30	2.22	0.48
Amphibians				
<i>Platyplectrum ornatum</i>	2.26*	0.39	0.12	1.36
<i>Uperoleia</i> spp.	2.02	1.74	13.14**	5.02**
<i>Rhinella marina</i> (toad)	0.88	0.78	10.74**	2.69*
Rare species	1.23	1.29	1.88	4.05**
Invertebrates				
	3.03**	3.13**	6.07**	4.81**
Araneae	1.34	2.49*	2.31	3.31*
Carabidae	3.69**	1.94	0.95	6.17***
Chilopoda	1.32	0.83	0.26	2.17
Non-carabid Coleoptera	0.73	1.05	15.76***	4.15**
Blattodea	1.66	3.22*	1.20	2.59*
Gryllidae	1.30	2.05	4.63*	4.12**
Scoriones	2.56*	1.35	3.09	1.97
Species richness	2.97**	1.26	2.45	3.33*
Size				
d.f.	9,115	9,115		6,115
S.V.L. <i>Ctenotus</i> spp.	1.63	3.25**		2.74*
Mammals				
d.f.	9,27	9,27		4,27
<i>Pseudomys delicatulus</i>	0.91	0.59		5.43***
Total mammals	1.38	1.02		3.42*

occurred in the following wet season, making this an obligate-seeding species (Clarke *et al.* 2015). This species, and also *A. platycarpa*, another characteristic pindan species with basal regrowth, are largely absent from the tree canopy for 3–5 years after fire. Other dominant pindan species were predominantly epicormic resprouters, and either re-established canopies within a single year (e.g. *Eucalyptus tetradonta*, *E. miniata*, *Erythrophleum chlorostachys*, *Petalostigma pubescens* and *Adansonia gregori*) or in the case of some shrubs (e.g. *Grevillea agrifolia*, *Persoonia falcata*) were able to re-establish from basal regrowth within 1 or 2 years.

Re-establishment of pre-fire perennial hummock and tussock grass canopies, like that for *A. tumida* trees, took ~3 years. In the interim period (1–2 years post-fire), forbs (e.g. *Spermacoce* spp., *Gomphrena canescens*) and subshrubs (e.g. *Crotalaria cunningghamii*, *Scaevola brownii*) increased their cover values, presumably taking advantage of increased light and reduced competition for soil resources. Annual *Sorghum* grass, although it did not increase in cover, increased in height and biomass (no data collected) in the period from 1 to 2 years post-fire and before tree canopy and perennial grass re-establishment. Pindan woodlands, therefore, followed distinct successional

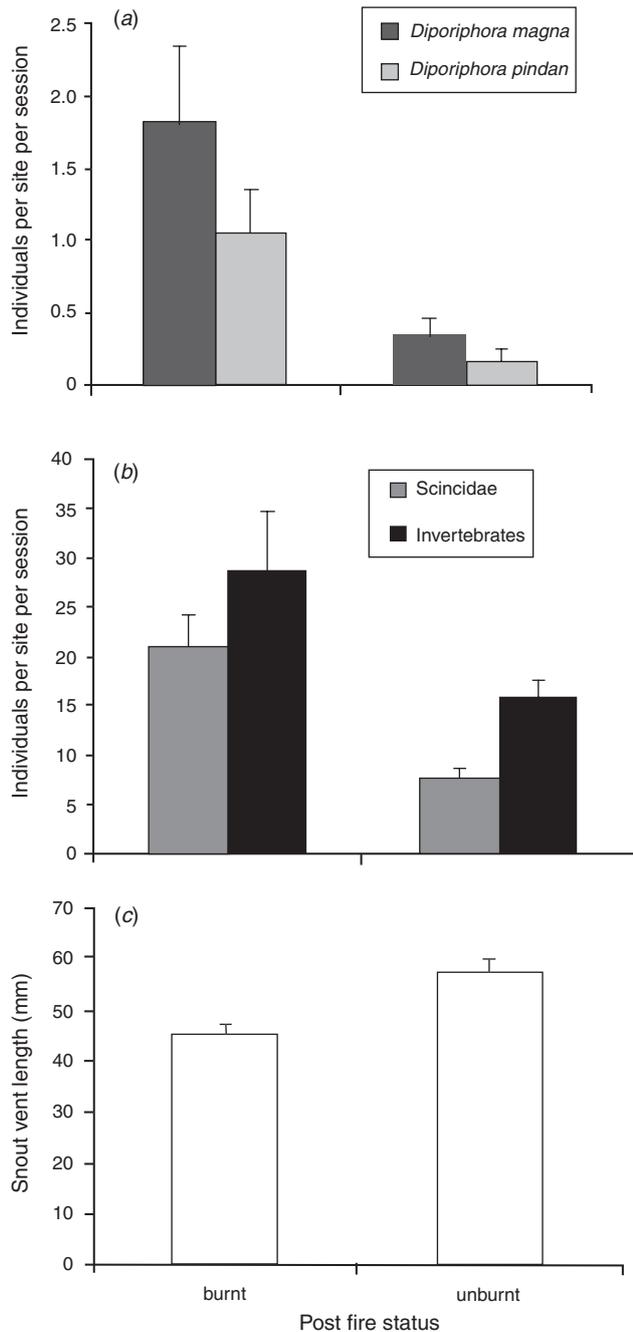


Fig. 3. Trap success of (a) *Diporiphora magna* and *D. pindan*, (b) total Scincidae and invertebrates and (c) snout-vent length of skins of *Ctenotus* spp. in burnt (zero years since fire) and unburnt (1–5 years since fire) survey sites. Vertical lines about columns represent standard errors of the means.

stages post-fire, with initial increases in biomass and cover of annual grasses and forbs, and mass emergence of *A. tumida* seedlings, 1–2 years post-fire, followed by re-establishment of the perennial grass layer, shrub and tree canopies between 3 and 5 years, and an associated decline in forb and annual grass cover. This successional pattern is similar, although more rapid to that seen in central Australian arid grasslands (Masters 1996; Letnic

et al. 2004). This 3–5-year post-fire succession differs from typical resprouter-dominated savannas in northern Australia where pre-fire tree and perennial grass cover is largely re-established 1 or 2 years after fire (Williams *et al.* 1999; Cook 2003).

It should be noted here that the present study cannot claim to elucidate patterns of vegetation or structural development of pindan woodlands beyond 5 years post-fire. This is due to the absence of any longer-term unburnt sites in the study. Observation of long-unburnt pindan woodland at Derby in the western Kimberley with >40 years without fire suggested that there is a gradual loss of perennial grass cover and annual grass biomass as *A. tumida* and shrub canopies develop over time (I. J. Radford, unpubl. data). There is also an increase in some forb species (e.g. *Pterocaulon* spp.). One of the more prominent features of long-unburnt pindan sites is the development of a dense *Calytrix exstipulata* shrub layer (I. J. Radford, unpubl. data). This is a fire-sensitive species killed by canopy scorch and, therefore, usually restricted to fire-sheltered habitats (Radford *et al.* 2013). It is not known whether long-unburnt pindan woodland contains unique botanical biodiversity. However, similar long-term unburnt *Callitris intratropica* stands (another fire-sensitive species) were found to contain no higher species richness of fire-sensitive plants (aside from *C. exstipulata*) than were surrounding savannas (Radford *et al.* 2013). Although *C. intratropica* stands elsewhere reportedly contain high plant diversity compared with surrounding savannas (Trauernicht *et al.* 2013), long-unburnt fire-sensitive savannas appeared to contain no particular concentration of fire-sensitive, threatened or non-savanna (e.g. rainforest) taxa (Radford *et al.* 2013). This latter study was conducted in the same East Kimberley region as the present study.

Fauna fire responses

Savanna faunas both in Australia (Andersen and Muller 2000; Corbett *et al.* 2003; Andersen *et al.* 2005, 2010, 2014a, 2014b; Radford 2012; Radford and Andersen 2012) and elsewhere worldwide (Gillon 1983; Parr and Chown 2003; Parr *et al.* 2004) are often thought to be relatively fire resilient, consistent with fire being intrinsic to this biome (Bond *et al.* 2005). Despite this, some savanna groups are more fire-sensitive than others, for instance, small mammals (Andersen *et al.* 2005; Woinarski *et al.* 2010, 2011) and granivorous finches in northern Australia (Woinarski and Legge 2013). The few known fauna records from fire-sensitive savanna vegetation in northern Australia suggest that they contain typical savanna fauna, rather than specialised assemblages characterised by rainforest or fire-sensitive taxa (Woinarski and Fisher 1995a, 1995b; Radford *et al.* 2013). Pindan fauna documented in the present study were also found to be predominantly typical savanna species (e.g. Trainor and Woinarski 1994; Corbett *et al.* 2003; Radford 2012).

The predominance of typical savanna species in the present study may explain the apparently minor and short-lived fire responses documented here. Establishment of some vegetation ground cover by forbs and annual grasses after a single wet season apparently provided sufficient habitat for recovery of the majority of these species of fauna. In the year of the fire, ground-active

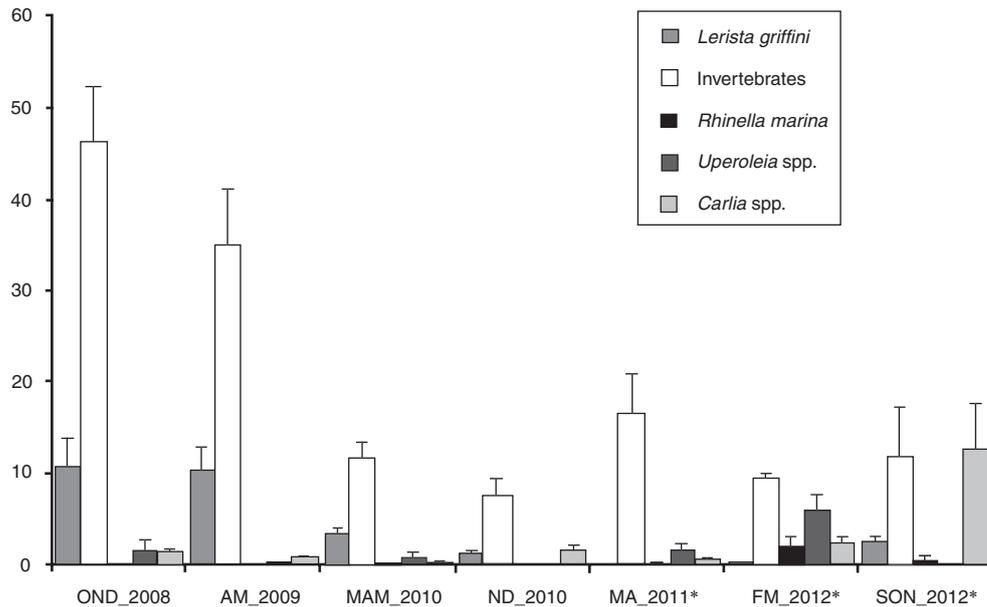


Fig. 4. Variation in the number of *Lerista griffini*, *Uperoleia* spp., *Carlia* spp. and invertebrates among trap sessions before and after cane-toad invasion (latter denoted by *). Vertical lines represent standard errors of the mean values.

running predators, such as *Diporiphora* spp., may benefit from increased hunting efficiency through the loss of herbaceous-layer vegetation, leading to their increased trap success. Increased predator activity after fire removal of vegetation cover has often been observed in savannas. Species including raptors (Braithwaite and Estbergs 1987; Corbett *et al.* 2003), the frilled lizard (Corbett *et al.* 2003), native mammals including *Dasyurus hallucatus* and *Isoodon auratus* (Radford 2012) and introduced mammalian predators *Felis catus* and *Canis dingo* (McGregor *et al.* 2014; Leahy *et al.* unpubl. data) are known to respond positively to removal of ground-layer vegetation by fire. Similar post-fire increases in ground-active reptilian predators have been observed in central Australian spinifex grasslands, although this was for more extended periods due to the more gradual re-establishment of ground-layer vegetation in arid environments (Masters 1996; Letnic *et al.* 2004; Haslem *et al.* 2012).

Increased post-fire activity among other ground-dwelling reptiles, skinks and invertebrates (e.g. spiders, beetles, cockroaches, crickets) soon after fire may reflect changes in trap encounters owing to changes to habitat structure, rather than population trends. There was little time for population responses to fire during surveys, which took place as few as 2 days after fire. It is likely that reduced vegetation complexity and cover at ground level soon after fire increased the ease of movement of many of these small ground-dwelling fauna, leading to more frequent trap encounters. Similar increases among skinks and some invertebrates have been observed previously (Gillon 1983; Andersen and Muller 2000; Radford 2012). However, like many other fire-ecology studies from Australian savannas, no major compositional changes were detected among fauna either in the year of the fire (Andersen and Muller 2000; Corbett *et al.* 2003; Andersen *et al.* 2005; Radford and Andersen 2012), or over longer periods necessary for full recovery of woody vegetation structures.

Higher predator activity post-fire, and also exposure to greater heat stress with low ground cover, may explain a reduction in the mean size (length) of large species of *Ctenotus* skinks (*C. robustus* and *C. inornatus*) after fire. Skinks of *Ctenotus* spp. are large, often attaining total lengths of >300 mm, with individuals as long as 380 mm being observed. Such animals would be more visible to predators in post-fire environments than are smaller skinks and invertebrates, and may be subject to heightened predation levels (Radford 2012). In addition, some *Ctenotus* spp. have strong habitat preferences for high-cover habitats (Masters 1996), possibly to balance their thermodynamic requirements as well as to avoid predators (Bennett and John-Alder 1986). Such requirements may make immediate post-fire environments hostile to large skinks and result in a temporary loss of larger individuals from the population. However, as with other fire responses among pindan fauna, mean size increased back to pre-fire levels after a single wet season.

The present study may have under-estimated fire impacts for some elements of the pindan fauna. One of the key groups identified in northern Australia as having predominantly negative responses to fire is the group of small and medium-sized mammals including rodents and marsupial species up to 5 kg in size (Andersen *et al.* 2005; Woinarski *et al.* 2010, 2011; Ziemicki *et al.* 2015). However, small mammals made up only a small component of pindan survey captures, reflecting generally low abundance and diversity of mammals in this rainfall zone (<1000 mm) across the Western Australian Kimberley region (Radford *et al.* 2014). As is typical for most habitats in this rainfall zone (Radford *et al.* 2014), only rodent species and small dasyurids (<35 g) were recorded at pindan sites. Historical loss of many of these mammals as a functional component of savannas, plus low numbers captured in the study, means that we may have under-estimated the true impact of fire on the

original mammal assemblages in pindan woodlands. We may have under-estimated responses of pindan fauna characteristic of arboreal habitats. Arboreal specialists are likely to respond to loss of habitat after intense fire because of the loss of *A. tumida* and *A. platycarpa* trees, which make up a major component of the tree canopy. Frequent fires may have negative effects on the availability of larger trees with nest hollows (Williams *et al.* 1999; Russell-Smith *et al.* 2003; Radford *et al.* 2008) and associated hollow-dependent fauna (Firth *et al.* 2006; Brazill-Boast *et al.* 2010, 2011, 2013), although this was not assessed at survey sites in the present study. Pindan specialist fauna, for instance, invertebrates that feed exclusively on *A. tumida* and *A. platycarpa*, are likely to be negatively affected by high-intensity fires causing widespread tree mortality but were not recorded in the present study. Finally, we were unable to document long-term responses (>5 year) to an absence of fire because we surveyed no older sites. A long-term absence of fire in savannas is known to result in radical assemblage responses among some fauna (e.g. forest-specialist ants; Woinarski *et al.* 2004; Andersen *et al.* 2012, 2014b). However, the only known data that detail fauna assemblages from long-unburnt (>40 years) pindan woodland (C. Palmer, unpubl. data, 2001) indicate a generalist savanna fauna similar to that documented in the present study at more frequently burnt sites. Specialist survey of these additional fauna groups (e.g. arboreal species, specialist *Acacia* spp. feeders) would be required to more fully assess the longer-term effects of the absence of fire in pindan woodlands.

Response of pindan fauna to cane-toad invasion

Cane-toad invasion has led to a range of impacts among different savanna fauna across northern Australia and internationally; however, impacts have often been inconsistent (Shine 2010; Ujvari *et al.* 2011). Post-invasion impacts have been recorded for invertebrates (Greenlees *et al.* 2006), adult frogs (Catling *et al.* 1999; Greenlees *et al.* 2007, 2010) and tadpoles (Crossland *et al.* 2008) from several separate studies. Toad invasion is generally thought to cause major impacts on large predatory varanid lizards and elapid snakes (Phillips *et al.* 2003; Smith and Phillips 2006; Shine 2010; Pearson *et al.* 2014). Cascading effects on medium-sized predators such as agamid lizards have also been recorded after poisoning of top predators (e.g. *V. panoptes*) in some instances (Doody *et al.* 2013).

Some post-invasion changes to assemblages of pindan fauna were observed in the present study, but these differed from previous studies in the taxa apparently affected. Ground-layer invertebrates and *Lerista griffini*, a fossorial skink that dominated pre-invasion vertebrate faunas, both decreased in abundance after cane-toad invasion, whereas skinks of *Carlia* spp. and frogs of *Uperoleia* spp. increased in abundance. Given design restrictions of the present study (an absence of non-invaded experimental control sites), it is impossible to fully separate invasion from temporal effects. Several of the changes to fauna documented here may be attributable as much to particular seasonal conditions (for instance, the highest *Uperoleia* spp. trap success was recorded during a period of very high rainfall) as to impacts of invasion. In addition, high inter-survey variation within both pre- and post-invasion periods makes it difficult to determine whether variation is

stochastic or directional. Nonetheless, the possibility remains that changes observed here are actually related to perturbations to trophic interactions caused by the arrival of cane toads. Although it is hard to identify the precise trophic pathways leading to declines or increases among particular fauna in the present study, the results are consistent with those of previous studies (e.g. Doody *et al.* 2009, 2013) and our own anecdotal observations (see below), namely, that apparent impacts on large predators such as varanids could lead to cascading effects on pindan faunas. In this case, reductions among varanids could lead to a reduced predation pressure on prey species (e.g. skinks of *Carlia* spp. and *Uperoleia* spp.). In turn, increases among prey groups could lead to cascading effects on availability of resources for invertebrate species and fossorial species (the skink *L. griffini* and snake *B. roperi*) relying on inputs from ground-layer trophic interactions.

Obviously these hypotheses are highly speculative and would require manipulative tests to demonstrate. Nonetheless, we would predict that if these trophic cascades are operating in pindan savannas as a response to cane-toad invasion, future surveys should continue to record similarly altered assemblages as long as cane toads remain at a similar abundance. Alternatively, continued stochastic changes among components of fauna over time would indicate a much more chaotic ecosystem governed by seasonal conditions. Unlike other studies, which have documented short-term changes associated with the timing of invasion from single surveys (Catling *et al.* 1999), the present study with multiple pre- and post-invasion surveys should have greater ability to discriminate between seasonal variation and directional trends. However, as noted by Ujvari *et al.* (2011), replication of impact assessment both spatially and temporally is necessary if we are to gain a full appreciation of impacts of cane toads across highly variable tropical savannas across northern Australia. Further surveys into medium and long-term time scales (5–10 years) may be necessary for us to demonstrably elucidate post-invasion impacts of cane toads in savanna ecosystems.

Despite repeated documentation of cane-toad impacts on large predatory varanids and elapids from several studies (e.g. Phillips *et al.* 2003; Smith and Phillips 2006; Shine 2010; Pearson *et al.* 2014), we were unable to detect any differences in abundance of these groups post-invasion. This is, to a large extent, due to very small numbers of these larger animals captured during our surveys (total $n=49$). Small numbers are partially due to the relatively small size of traps (funnels 15 cm wide and 70 cm long compared with *Varanus* spp. and Elapidae being up to 140 cm long), but also to large home ranges of top predators probably reduce trap encounters in these low-productivity environments. Notwithstanding this important caveat, we can make several observations relevant to impacts by cane toads on these larger predators. Appearance of toads at survey sites and within trap records coincides with several apparently uninjured varanids (*Varanus gouldii*) and elapids (*Pseudechis australis*) being observed dead at survey sites. This supports repeated observations that initial appearance of toads is often associated with mortality events through lethal poisoning on attempted ingestion (Pearson *et al.* 2014). Large varanids and elapids as a group continued to be recorded during post-invasion surveys; however, fewer than half as many varanids were captured

post-invasion as pre-invasion (accounting for differences in trap effort). This suggests that there was a negative, if a muted, impact, of toad invasion at least on varanid species.

Low numbers of cane toads trapped in pindan surveys (only 27 toads captured during 2160 trap-nights) may have mitigated invasion impacts relative to other studies. Studies documenting invasion impacts, such as on the Daly River (Doody *et al.* 2006, 2013) or the Kakadu floodplains (Greenlees *et al.* 2006), may have had greater impacts simply because of the much greater number of cane toads present in these wetter and more productive riparian habitats. The small number of toads observed and captured during pindan surveys contrasts with observations of extremely high densities attained during invasion in many tropical areas (Freeland 1986; Lever 2001; Shine 2010) and very large numbers of toxic prey in these habitats could easily account for much greater impacts among predators. In contrast, pindan savannas that provide little access to permanent or ephemeral water and very low habitat productivity owing to sandy soils may simply not be able to support high cane-toad densities. Results presented here confirmed findings by Shine (2010) and Ujvari *et al.* (2011) that impacts are not consistent across habitat types. Low apparent invasion impacts in low-productivity non-riparian savanna habitats, including pindan woodlands, may play an important role in the persistence of toad-susceptible species, including varanids, by providing refuge habitat with low toad densities and, therefore, low toad-encounter rates.

Management implications

Being an obligate seeder-dominated vegetation type that takes 4–5 years for re-establishment of mature reproductive trees, pindan woodland needs to have a minimum interval of 5–6 years between intense canopy-killing fires. Although seed banks are not necessarily depleted after a single post-fire re-establishment event (I. J. Radford, unpubl. data), continued inter-fire intervals of <4 years will inevitably deplete the regenerative capacity of pindan woodland. Because of the frequency of fires in surrounding vegetation, the most prudent way to achieve longer fire intervals in this vegetation is through annual low-intensity patchy fires in pindan habitat. Such fires can be ignited during wet-season and very early dry-season periods (when fires self-extinguish overnight) because of the presence of highly flammable grasses of *Triodia* spp. and senescent perennial grasses from the previous dry season if fires did not occur. Low-intensity fire did not kill mature *A. tumida* trees, allowed continued seed production and mitigated the effects of late-season fires by reducing fire extent and intensity.

Despite requirements for longer inter-fire intervals for pindan woodland itself, specialised fire management of pindan fauna is not required on the basis of fire responses. Fauna responses here were more typical of responses of savanna fauna generally, than of responses of fauna in slower-regenerating vegetation such as arid grasslands (Masters 1996; Letnic *et al.* 2004). Fauna responses here appeared to be muted and somewhat similar to generalised responses of savanna faunas (Andersen and Muller 2000; Corbett *et al.* 2003). This reflects findings among similar fire-sensitive savanna types including *Callitris intratropica* (Radford *et al.* 2013), *A. shirleyi* and *A. tumida*

woodlands (Woinarski and Fisher 1995a, 1995b) where faunas were predominantly savanna generalists, rather than obligate woodland specialists. However, savanna fire management, generally, should aim to minimise the burning of extensive areas during any single fire. Recent evidence suggests that reducing fire size and/or extent, and retaining key vegetation-cover attributes is probably the most important feature of fire mosaics to maintain threatened biodiversity including mammals (Lawes *et al.* 2015; Radford *et al.* 2015). Although many of the species (e.g. critical weight-range mammals) identified as benefiting from retention of ground-vegetation cover and low-intensity patchy fires no longer persist as major functional elements in savannas in the medium- and low-rainfall Kimberley region (Radford *et al.* 2014), refuge populations occur in some fire-protected habitats (e.g. *Isoodon macrourus* occurs in the outskirts of Kununurra adjacent to pindan woodlands and *Dasyurus hallucatus* exists in some gorges). Such populations provide regional foci for re-establishment of populations under more benign fire regimes or abatement of other threatening processes.

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