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Short-term responses of reptile assemblages to fire in native and weedy tropical savannah



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ABSTRACT

Fire is frequently used as a management tool to reduce the cover of weeds, to reduce the amount of fuel available for future fires, and to create succession mosaics that may enhance biodiversity. We determined the influence of fire on wildlife, by quantifying reptile assemblage composition in response to fire in a weedy environment characterised by very short-term fire return intervals (<2 years). We used reptiles because they are often understudied, and are only moderately vagile compared to other vertebrates, and they respond strongly to changes in vegetation structure. We repeatedly sampled 24 replicate sampling sites after they had been unburned for two years, just prior to burning (pre-burnt), just after burning (post-burnt), and up to 15 months after burning (revegetated) and monitored vegetation structure and reptile richness, abundance and assemblage composition. Our sites were not spatially auto-correlated, and were covered by native kangaroo grass (*Themeda triandra*), black spear grass (*Heteropogon contortus*), or an invasive weed (grader grass, *Themeda quadrivalvis*). Reptile abundance and richness were highest when sites had been unburned for 2 years, and greatly reduced in all areas post burning. The lowest reptile abundances occurred in sites dominated by the weed. Reptile abundance and richness had recovered in all grass types 15 months after burning, but assemblage composition changed. Some species were present only in before our focus fire in native grass, and their populations did not recover even 15 months post-burning. Even in fire-prone, often-burnt habitats such as our study sites, in which faunal richness and abundance were not strongly influenced by fire, reptile assemblage composition was altered. To maintain faunal biodiversity in fire-prone systems, we suggest reducing the frequency of prescribed fires, and (if possible) excluding fire from weedy invasions if it allows native grasses to return.

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1. Introduction

Fire is often used as a management tool in natural, recreational, and cultivated areas to remove weeds, reduce the build-up of fuel (Price et al., 2012), and to maintain mosaics of habitat for wildlife (Parr and Andersen, 2006; Pastro et al., 2011). Weed removal is a critical activity, because weeds are among the worst threats to native biodiversity. Exotic grasses, for example, can rapidly change ecosystem functions and services (Elton, 1958; D'Antonio and Vitousek, 1992; Zavaleta et al., 2001). Invasive grasses often grow taller and denser and have higher biomass than native perennial grasses (McIvor and Howden, 2000; Vogler and Owen, 2008; Wilsey et al., 2009; Foxcroft et al., 2010; Lindsay and Cunningham, 2012; Alba et al., 2015). Invasive grasses can alter ecosystems directly by altering the dominant vegetation (D'Antonio and Vitousek, 1992). In

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addition, the interaction between fire and weeds can have negative impacts on fauna. For example, fires fuelled by invasive grasses may burn hotter and more intensely than native grass fires (D'Antonio and Vitousek, 1992; Corbett et al., 2003; Setterfield et al., 2010). Hotter fires can consume more vegetation, which may change faunal resource dynamics, reducing availability of food and shelter, and increasing susceptibility to predators of native fauna (Barnard, 1987; Valentine et al., 2007; Pastro et al., 2011; Penman et al., 2011; McGregor et al., 2014). In addition, hotter fires may increase mortality rates of small vertebrates (Griffiths and Christian, 1996; Barlow and Peres, 2004; Smith et al., 2012; Cross et al., 2015). Repeated fires may reduce species ranges, and fire-sensitive species may become locally extinct (Parr and Andersen, 2006; Driscoll and Henderson, 2008; Penman et al., 2011; Russel-Smith et al., 2012).

Some ecosystems are shaped by natural fires and are highly diverse, suggesting that their fauna are resilient to naturally occurring fires (Woinarski et al., 2004; Andersen et al., 2005; Pianka and Goodyear, 2012). Organisms in these habitats are thought to be adapted to high natural fire frequency (Braithwaite, 1987; Friend, 1993; Trainor and Woinarski, 1994; Corbett et al., 2003; Pastro et al., 2011), and may prefer the habitat structure and composition created by fire (Braithwaite, 1987; Friend, 1993; Trainor and Woinarski, 1994; Singh et al., 2002a; Pianka and Goodyear, 2012). In such environments, the influence of fire, weeds and their interactions on native fauna may be reduced, because the fauna is resilient to fire (Pastro et al., 2014). For example, fire had little effect on the assemblage composition of vertebrates in a tropical savanna in Australia and South Africa (Parr and Andersen, 2006). On the other hand, fire did alter the assemblages of lizards in the Simpson Desert, which is a fire-prone grass habitat (Pastro et al., 2011).

Typically, studies investigating the effects of fire compare areas with different fire histories (e.g., Driscoll and Henderson, 2008; Valentine et al., 2012; Nimmo et al., 2013; Pastro et al., 2014). Such studies examine fire succession, and the long-term effects of fire, but are not designed to quantify short-term effects (≤ 2 years). It is, however, of interest to examine the same sampling sites before and after fire, to investigate the rate of recovery of flora and fauna. Here we compared replicate sampling sites, dominated by different types of native grass or an invasive weed, over time to determine the short-term effects of fire on fauna. We sampled the same sites when they had not burnt for 2 years, directly after burning, and up to 15 months after burning, when vegetation cover had returned to pre-burnt levels. The environment we studied often burns more than once per year, due to a combination of wildfire and prescribed burns, especially when weed-infested. Determining the short-term effects of fire longitudinally is highly relevant to such environments (Price et al., 2012).

We examined assemblage composition of reptiles, because they are abundant and typically respond strongly to disturbance (Braithwaite, 1987; Pianka and Goodyear, 2012; Smith et al., 2013; Hacking et al., 2014). In addition, reptiles are small-to medium-sized, and only moderately vagile compared to birds and mammals, making them excellent study organisms in which to study small-scale influences of habitat (Pardon et al., 2003; Mills, 2004; Pianka and Goodyear, 2012). Finally, influences of anthropogenic habitat disturbance on reptiles is often neglected compared to other vertebrates.

2. Methods

2.1. Study system

Our study sites were located in savannah and open woodland at Undara Volcanic National Park in north Queensland, Australia (18°19'29.92"S, 144°36'28.31"E). We used a total of 24 sampling sites with eight replicates, each dominated by a particular grass, either native kangaroo grass (*Themeda triandra*), native black spear grass (*Heteropogon contortus*), or non-native, invasive grader grass (*Themeda quadrivalvis*, see Appendix Figure S1 in supporting information). We monitored these sites as they passed through three different states, when they had not been burnt for 2 years (pre-burnt), directly after burning (post-burnt), and up to 15 months after burning (15 months post-burnt) when vegetation cover was similar to pre-burnt levels.

Briefly, the area was a grazing property until it was made a National Park in 1992. At the time of our study, the entire area had not been grazed for 16 years. Black spear grass and native kangaroo grass grow together in the same land type, and we exploited patches (50 × 50 m) dominated by each grass on small scales at our sampling sites. Grader grass grows in disturbed areas, and was common on the sides of tracks, and in previously cultivated areas at our site, but it also occurred in patches closely associated with, and interspersed with native grasses. We exploited such patches to specifically target differences in the fauna at sites that were influenced in particular by grass species and burning, and not primarily driven by differences in other factors, such as soil type, past history or spatial location. For a more comprehensive description of sampling sites and history see Abom et al. (2015).

Grader grass is native to India, and grows in a sward, emerging as a single stolon, whereas the two native grasses grow in clumps or hummocks (McIvor and Howden, 2000; Keir and Vogler, 2006). Grader grass can grow to 2.5 m, producing high above-ground biomass, whereas these native grasses grow to 1.5 m. A detailed habitat description has been provided elsewhere (Abom et al., 2015), and for a more comprehensive review of grader grass characteristics and biology, see Keir and Vogler (2006).

The rangers at Undara Volcanic National Park implemented prescribed fires in April 2009 and 2010, when environmental conditions were cool enough to allow the fire to self-extinguish in the late afternoons. Sampling sites in the current study had been burnt on rotation every 2 years since 2002, with wildfires also occurring. A wildfire in October 2003 burned the entire park, and one in November 2008 burnt large areas of the park, including some sampling sites (Appendix S1).

2.2. Survey periods and data collection

We trapped reptiles over two years in four distinct trapping periods per year, for a total of eight trapping periods: pre-wet (21 Oct–14 Nov 2008 and 2009), mid-wet (3–26 March 2009 and 2010), early-dry (14 April–6 May 2009 and 2010), and mid-dry seasons (14 July–12 Aug 2009 and 2010) with 19–21 trap-days in each season. We selected our sampling sites (each 50 × 50 m) to ensure that there was no spatial clumping of a particular grass among site locations (Appendix S1). This was possible because of the highly heterogeneous nature of the grasses growing in the area, and because all three grasses were widely and patchily represented at Undara.

We followed the same sites through time, monitoring changes in vegetation cover and structure before and after burning, and then when vegetation cover had returned. We conducted vegetation surveys for each sampling site in each trapping period, using four 50-metre transects at each site, spaced 16.6 m apart, and variables were recorded in linear centimetres on this transect. At each sampling occasion, we recorded the cover of: dominant grass (total number of cm of grader, kangaroo, or black spear grass intercepting the 50 m tape on all 4 transects, converted to % cover), mixed grasses (calculated by summing the % cover of all other grass species), broad-leaf vegetation (% cover of herbaceous plants and legumes), leaf litter, logs, rocks, burnt areas (April to December), exposed soil, and canopy cover above each transect.

We used a 30 × 30 m trapping grid placed in the centre of each of the 24 50 × 50 m survey sites (Appendix S1). Five pitfall traps (20l, straight-sided buckets) were placed in the ground with the lip level with the ground's surface, with one centre bucket and four 'arms' (Appendix S1). Pitfall traps were spaced 10-m apart and connected via a drift fence (50-cm high UV resistant fibreglass drift fence, Cyclone™), which crossed every pitfall trap, and extended a further 5 m beyond the last pitfall trap on each 'arm' of the cross. To reduce desiccation risk and exposure of captured animals, a moistened sponge and a piece of cloth were placed inside each pitfall trap, and the bottom of each trap was lined with a 5-cm layer of leaf litter. Eight funnel traps (dimensions, 180W × 730L × 170H mm) were arranged at each site. Funnel traps were placed on both sides of the drift fence on each arm of the cross, against the 5 m of drift fence projecting past the last pitfall trap on each arm, approximately 2 m from the end, with a shade cloth covering the funnel trap (Appendix S1). To prevent small vertebrates in traps being attacked by ants, we used ant sand (Antex, 2 g/kg Bifenthrin) as a deterrent, sprinkled around the mouth of the pitfall trap and underneath funnel traps. All traps were checked and cleared twice daily, in the early morning (5:30–8:30) and in the late afternoon (16:00–18:00), and captured reptiles were identified to species using Wilson (2005).

2.3. Statistical analyses

2.3.1. Vegetation structure

We described the vegetation cover at each sampling site, pre-burnt, post-burnt, and up to 15 months after burning, comparing the percent cover of each dominant grass (grader, kangaroo, and black spear grass), mixed grass (all other grass species combined), broad-leaf vegetation, logs and branches, rock, leaf litter, burnt area (April to February), exposed soil, and tree canopy cover among sites. Prior to statistical analysis, we relativised vegetation data by dividing the cover of each variable in cm by the maximum cover of that variable at any sampling site (value between 0 and 1), and compared the relativised values using MANOVA with Wilk's lambda as the test statistic, followed by ANOVAs and Tukey's HSD *posthoc* tests when significant differences were detected in habitat cover among the sampling sites (SPSS V.20).

2.3.2. Reptile assemblage composition

We described the reptile assemblage composition over time, first when the sites had not been burnt for 2 years (pre-burnt), then right after fire (post-burnt), and then after they were revegetated. To reduce the influence of rare species, we excluded any species with less than 12 individuals captured. We standardised trapping effort to individuals sampled per 100 trap nights, and to reduce the statistical influence of overly abundant species, prior to statistical analysis, numbers of individuals captured for each species were relativised (as above for vegetation). Reptile species used in all statistical analyses are listed in Table 1. To determine whether reptile richness and abundance varied among grass type and over time in response to burning, we used generalised linear models (GLZM) with Gaussian-error distribution, with an identity link function and followed significant differences with pairwise least significant difference (LSD) comparisons (SPSS V.20).

We used the statistical package PC-ORD to explore reptile assemblage composition (McCune and Mefford, 1999) in relation to vegetation variables. We used Multiple Response Permutation Procedures (MRPP) to create a non-parametric, rank-transformed Sorensen (Bray–Curtis) distance matrix among reptile assemblages in pre-burnt, post-burnt, and revegetated grader, kangaroo, and black spear grass. The MRPP produces an A-statistic from chance-corrected within-group agreement and a *p*-value for each pairwise comparison. We followed this with non-metric multidimensional scaling (NMDS) to show the differences in reptile assemblage composition across burning histories and among grass types ($r^2 < 0.20$) when significant ($P < 0.05$) differences were detected. For the NMDS, we used the autopilot "slow and thorough" with Sorensen distance measures, dimensionality was determined by Monte Carlo test (9999 permutations, significance test of stress in relation to dimensionality of the number of axes in final analysis). We extracted axis and cumulative scores by using Sorensen (Bray–Curtis) dissimilarity indices with original end point selection, city-block projection geometry and calculation of residuals. To illustrate reptile assemblage compositional trends among treatments, we constructed bi-plots from NMDS sites and species scores. Finally, we investigated the response of specific reptile species to pre-burnt, post-burnt,

Table 1

Untransformed catch numbers of 18 common reptile species among pre-burnt (G, K, S), post-burnt (GB, KB, SB), and revegetated (GR, KR, SR)—grader, kangaroo, and black spear grass sites to illustrate trends in species composition with significant indicator species $P < 0.05^*$, $P < 0.01^{**}$ in **bold** and indicator species approaching significance $P = 0.0846^\wedge$ in *italic*.

Species	Unburnt			Burnt			Revegetated		
	G	K	S	GB	KB	SB	GR	KR	SR
<i>Amalosia rhombifer</i>	0	3	2	1	2	2	0	1	1
<i>Carlia schmelzii</i>	13	36	32	0	10	3	9	16	12
<i>Carlia vivax</i>	14	13	12	2	2	5	14	9	6
<i>Cryptoblepharus adamsi</i>	0	11	4	0	2	1	0	9	0
<i>Ctenotus taeniolatus</i>	3	4	11	1	2	3	2	9	12
<i>Delma tineta</i>	1	3	5	0	0	2	4	1	2
<i>Demansia psammophis</i>	4	8	6	0	1	1	2	0	3
<i>Diporiphora australis</i>	3	10	5	0	6	3	1	7	1
<i>Gehyra dubia</i>	3	1	3	2	0	1	1	2	0
<i>Glaphyromorphus cracens</i>	5	16**	11	0	0	0	6	3	4
<i>Heteronotia binoei</i>	0	5	4	1	3	0	1	3	2
<i>Lygisaurus foliorum</i>	5	33**	19	0	6	2	4	17	9
<i>Menetia greyii</i>	2	10	8	5	4	1	11	5	8
<i>Morethia taeniopleura</i>	3	18*	13	1	1	0	2	6	3
<i>Proablepharus tenuis</i>	1	7	5	0	0	1	3	10**	4
<i>Pseudonaja textilis</i>	2	5	8	0	0	0	9 [^]	1	3
<i>Strophurus williamsi</i>	0	3	2	3	2	0	2	0	0
<i>Varanus scalaris</i>	0	10**	3	0	0	1	0	0	0

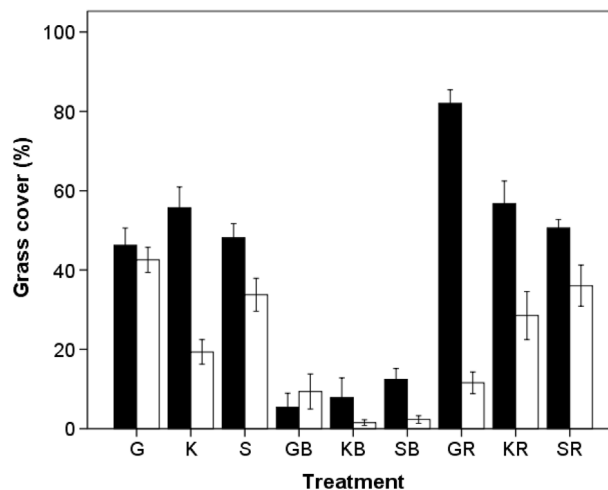


Fig. 1. Mean grass cover (%) in dominant grass (black), and in mixed grass (white bars) cover in pre-burnt, post-burnt, and revegetated grader (G, GB, GR), kangaroo (K, KB, KR), black spear (S, SB, SR) grass sites (MANOVA analysis was performed on relativised data, and error bars $\pm 1SE$).

and revegetated sites; we used the indicator species analysis with Monte Carlo tests of significance of observed maximum indicator values for reptile species with 9999 permutations and random number seed in PC-ORD (McCune and Mefford, 1999).

3. Results

3.1. Vegetation structure

We detected significant variation in vegetation cover among sites when they were pre-burnt, post-burnt, and revegetated, among grass types (MANOVA $\lambda = 0.001$, $P < 0.001$, untransformed means $\pm SE$ in Appendix S2). Dominant grass cover varied significantly (ANOVA $F_{8,37} = 38.340$, $P < 0.001$): revegetated grader grass (15 months post-burning) had significantly more grader grass cover than before burning (pre-burnt) (Tukey's HSD, $P < 0.05$, Fig. 1). Similarly, there was significantly more mixed grass cover in pre-burnt than in revegetated grader grass (ANOVA $F_{8,37} = 17.625$, $P < 0.001$, Tukey's HSD, $P < 0.05$, Fig. 1), whereas the percent cover of dominant and mixed grass cover in the two native grasses did not differ between pre-burnt and revegetated samples. Interestingly, immediately post-burning, the burnt area was significantly greater at sampling sites dominated by grader than black spear grass (Tukey's HSD, $P < 0.05$).

The percent cover of logs differed significantly among the different grass types (ANOVA $F_{8,37} = 6.321$, $P < 0.001$), there were more logs in pre-burnt, post-burnt, and revegetated kangaroo grass than in post-burnt and revegetated grader

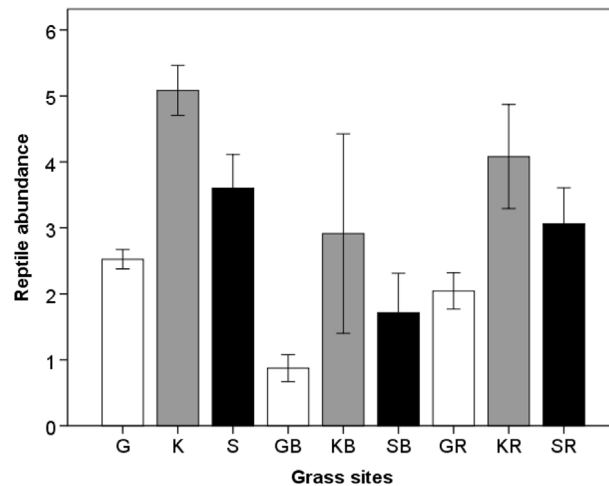


Fig. 2. Untransformed average reptile abundance (GZLM analysis was performed on relativised by maximum reptile abundance data) in pre-burnt (G, K, S), post-burnt (GB, KB, SB), and revegetated (GR, KR, SR) sites in grader (white), kangaroo (grey bars), and black spear (black bars) grass with error bars ± 1 SE.

grass (Tukey's HSD, $P < 0.05$). Also, there were no significant differences in the percent cover of logs among pre-burnt grader, kangaroo, and black spear grass. The cover of leaf litter (ANOVA $F_{8,37} = 4.322$, $P = 0.001$) and exposed soil (ANOVA $F_{8,37} = 5.172$, $P < 0.001$) were significantly higher in pre-burnt kangaroo grass than in revegetated grader grass (Tukey's HSD, $P < 0.05$). Typically, for most variables that differed, vegetation cover and site variables in black spear grass were intermediate to, and not significantly different from, kangaroo and grader grass. Percent cover of broad-leaved vegetation, (ANOVA $F_{8,37} = 1.755$, $P = 0.118$), rock (ANOVA $F_{8,37} = 2.071$, $P = 0.071$), and canopy (ANOVA $F_{8,37} = 0.471$, $P = 0.869$) did not differ among grass types.

3.2. Reptile abundance and richness

We trapped for a total 27,972 trap days, and we captured a total of 795 individuals from 48 species, including 9 families. We selected the 18 most numerous reptile species (range of abundances 12–131, $n = 731$) to describe the reptile assemblages (Appendix S3).

We detected significant differences in reptile abundance among pre-burnt, post-burnt, and revegetated samples (GZLM Wald $\chi^2 = 29.566$, $df = 8$, $37 P < 0.001$, Fig. 2), but not reptile richness (GZLM Wald $\chi^2 = 12.066$, $df = 8$, $37 P = 0.148$). Reptile abundances were significantly reduced post-burning in all grass types compared when they were pre-burnt (pairwise comparisons, pre-burnt vs. post-burnt kangaroo grass, LSD, $P = 0.007$, pre-burnt vs. post-burnt black spear grass LSD, $P = 0.029$). In grader grass, abundance was very low initially, and the trend for reduced abundance right after burning was only marginally significant (pre-burnt vs. post-burnt grader grass, LSD, $P = 0.055$, Fig. 2). We did not detect any significant differences in reptile abundances between pre-burning and revegetation, or post-burning and revegetation, in any grass type (LSD, $P > 0.05$).

3.3. Reptile assemblage composition

Differences in assemblage composition of reptiles in grader, kangaroo, and black spear grass before burning are described elsewhere (Abom et al., 2015). Reptile assemblage composition varied significantly among pre-burnt, post-burnt and revegetated grass states (MRPP: $A = 0.1740$, $P < 0.001$). In grader grass, which was depauperate, the reptile assemblage composition differed significantly between pre-burnt and post-burnt samples ($A = 0.133$, $P = 0.025$), but not from revegetated samples, which were similar to, and overlapped both the pre-burnt and post-burnt assemblages. Similarly, the reptile assemblage in black spear grass pre-burning was significantly different from post-burning samples ($A = 0.148$, $P = 0.002$), while revegetated samples were similar to pre-burnt samples. The reptile assemblage composition in kangaroo grass prior to burning was significantly different from post-burnt ($A = 0.143$, $P = 0.002$), and revegetated ($A = 0.101$, $P = 0.044$) samples. Cross comparisons showed that the reptile assemblage composition in kangaroo grass pre-burning differed significantly from that in grader grass ($A = 0.139$, $P = 0.016$), but not black spear grass. Interestingly, there were no differences detected in reptile assemblage composition among the different types of grass immediately post-burning ($P > 0.05$). Reptile assemblages differed significantly between revegetated kangaroo and grader grass ($A = 0.194$, $P = 0.011$), while spear grass assemblages were intermediate. Like abundance, the reptile assemblage in kangaroo grass prior to burning was similar to the other native grass (pre-burnt black spear grass, $P = 0.822$), but differed significantly from all other grass states ($P < 0.05$).

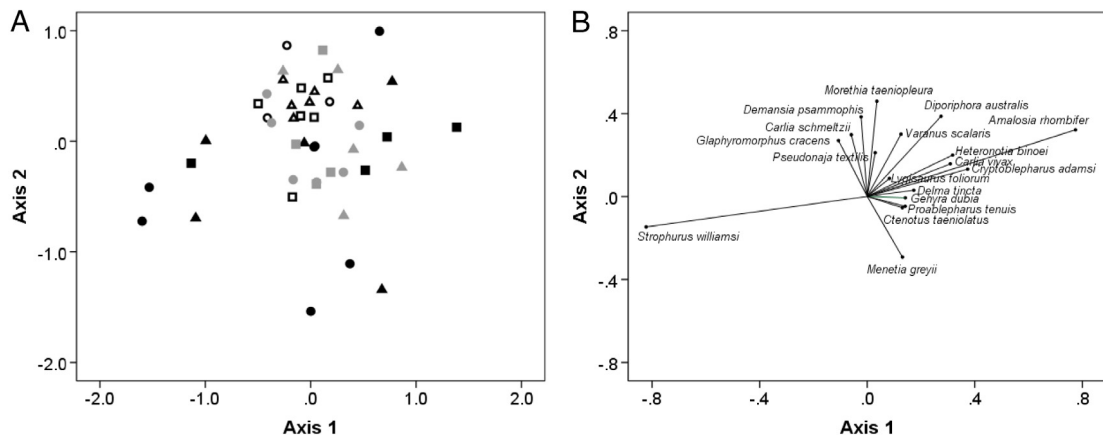


Fig. 3. Two dimensional NMDS ordination (stress = 0.180) with the 18 reptile species (data relativised by maximum). (A) Open symbols = pre-burnt grass, filled black symbols = post-burnt, and filled grey symbols = revegetated grass sites with grass symbols, circles = grader, triangles = kangaroo, and squares = black spear grass, (B) correlations ($r^2 > 0.20$) with the 18 reptile species.

Table 2

Indicator species (relativised by maximum) analyses with observed indicator value (IV), mean indicator value from randomised groups (± 1 SD) at level of significance with species significantly associated with pre-burnt kangaroo* grass sites, one species significantly associated to revegetated kangaroo^o grass sites with one species[§] approaching significant level in revegetated grader grass sites.

Species	IV	Mean \pm SD	P-value
<i>Glaphyromorphus cracens</i> *	35.2	16.2 \pm 4.81	0.0005
<i>Lygisaurus foliorum</i> *	28.5	17.2 \pm 4.10	0.0099
<i>Morethia taeniopleura</i> *	30.9	16.4 \pm 5.03	0.0145
<i>Proablepharus tenuis</i> [^]	39.8	17.6 \pm 6.10	0.0066
<i>Pseudonaja textilis</i> [§]	25.3	16.4 \pm 6.01	0.0836
<i>Varanus scalaris</i> *	59.8	18.0 \pm 9.43	0.0017

We found a stable, three-dimensional NMDS solution accounting for 65.68% of the variance (first axis = 30.90%, second axis = 17.68%, and third axis = 17.11%) with a final stress of 0.180 (Fig. 3(a)). Pre-burnt and revegetated samples formed two distinct groups, while there were no clear patterns among sites after burning, which were more scattered, indicating high variation in the reptile composition among the post-burnt samples (Fig. 3(a)). Pre-burnt and revegetated native samples grouped more clearly than did grader grass samples.

3.4. Indicator species associated with pre-burnt and post-burnt sites

The indicator species analysis indicated that we captured more reptiles in pre-burnt samples than in post-burnt and revegetated samples, and that reptiles were, on average, more strongly associated with native than invasive grasses. The scincid lizards *Glaphyromorphus cracens*, *Lygisaurus foliorum*, *Morethia taeniopleura*, and goanna *Varanus scalaris* were significantly associated with pre-burnt kangaroo grass, while the skink *Proablepharus tenuis* was significantly associated with revegetated kangaroo grass (Tables 1 and 2). A venomous elapid, the eastern brown snake *Pseudonaja textilis*, was the only reptile that showed a strong association to grader grass and approached significance as an indicator of revegetated grader grass (Tables 1 and 2). *G. cracens*, *L. foliorum*, *M. taeniopleura* and *V. scalaris* were encountered more than 40% more frequently in pre-burnt kangaroo grass than in revegetated kangaroo grass, and were encountered more than 75% more frequently in pre-burnt compared to post-burnt kangaroo grass (Table 1). *P. tenuis* was the only lizard significantly associated with revegetated kangaroo grass, and was encountered 50% more frequently in revegetated than in pre-burnt kangaroo grass with an 80% higher encounter rate in revegetated compared to post-burnt kangaroo grass (Table 1).

4. Discussion

Reptiles were more abundant in native grasses before they were burned (or after 2 years without burning) than in similar sites invaded by grader grass. The lowest abundances of reptiles were observed in grader grass after fire, but burning immediately reduced the abundance of reptiles in all grasses. Overall abundances recovered to pre-burnt levels in revegetated grasses. Some species returned to abundances similar to their pre-burnt levels as revegetation occurred, but many remained absent or less abundant even after revegetation in this study. Thus, the reptile assemblage composition changed with fire, and remained different, especially in kangaroo grass sites after revegetation, even in our extremely fire-prone habitat.

4.1. Structural effects of burning

The percentage of dominant and mixed grass cover was similar in the two native grasses before the fire that was the focus of our study, and after they were revegetated. However, grader grass cover was higher, and mixed grass cover lower, in grader grass after it was revegetated than before it burned, indicating that grader grass grew back more vigorously after fire, replacing other grasses. During fires we observed that, flames in grader grass were higher than flames in native grass (R. Abom personal observations). As with grass cover, there was no change in log cover in the two native grasses, before and after our focus fire, but the percent cover of logs in grader grass was reduced post-burning. This suggests that fires in grader grass were hotter than in native grass, consuming more logs, and negatively influencing habitat for fauna, contributing to the low abundance and diversity in the weed. Similarly, fires in invasive gamba grass (*Andropogon gayanus*) were hotter than those in native grasses, causing greater damage to woody vegetation, which reduced the availability of refuges such as logs and tree hollows for fauna (Setterfield et al., 2010). These results illustrate the interaction between weeds and fire, thought to drive the negative effects of fire on fauna.

4.2. Reptile assemblage patterns in relation to fire

Reptile abundances varied greatly in our samples before the focus fire, immediately after it, and into revegetation which was interesting, because our study sites have been burnt so frequently. Thus, the reptile assemblage in our study area was probably biased towards less fire-sensitive species. If our assemblage was completely composed of fire-insensitive species, however, we should have seen little change in abundance and species composition of the reptile communities following fire (e.g., McCoy et al., 2013), and yet we did observe changes. Similarly in fire prone grassland systems in Argentina, Iberian Peninsula, South Africa, and USA have also shown changes to the faunal assemblage composition with frequent fires (Parr and Andersen, 2006; Cano and Leynaud, 2010; Santos and Poquet, 2010; Hulton VanTassel et al., 2015).

Vegetation structure is often correlated with reptile abundance (Abom et al., 2015), and therefore the responses of reptiles to fire may have been driven by their responses to vegetation structural change (Valentine and Schwarzkopf, 2008; Valentine et al., 2012). At least some reptiles inhabiting naturally fire-prone systems may prefer the vegetation cover and structure created by frequent grass fires (Braithwaite, 1987; Friend, 1993; Trainor and Woinarski, 1994). On the other hand, they may simply persist as long as the specific habitat features they require are present (Singh et al., 2002a). Even closely related species may differ in their responses to fire. For example, two closely related agamid lizards responded to fires in opposite directions (Pianka and Goodyear, 2012). In our study system, a species of small agamid lizard declined the least of any lizard (40%) in native grass after burning, suggesting that they are relatively tolerant to fire. Most other species in our study declined much more than 40% post-burning, and they did not return to pre-burning abundances as vegetation cover returned. Decline without complete recovery 15 months after fire suggests that these reptile species may always have relatively small populations in these extremely fire prone environments. The abundances of many reptile species increase with increasing time since fire in comparisons with longer post-fire intervals (Letnic et al., 2004; Valentine and Schwarzkopf, 2008; Valentine et al., 2012; Nimmo et al., 2013; Smith et al., 2013).

Fires reduce accumulated leaf litter deposits, and species that are strongly correlated with leaf litter often occur in lower abundances following fire (Braithwaite, 1987; Friend, 1993; Singh et al., 2002b; Legge et al., 2008; Valentine and Schwarzkopf, 2008; Price et al., 2010; Martin and Murray, 2011; Valentine et al., 2012; McCoy et al., 2013). In our sites, leaf litter was reduced by up to 75% between the pre-burnt period and revegetation. Several leaf-litter-associated skinks were significantly associated with kangaroo grass before our focus fire, and declined between 50 and 80% in revegetated native grass, and did not recover. Other species may follow the abundance trends of these lizards, for example specialist predators of lizards were most common in kangaroo grass before our focus fire, much reduced post-burning, and absent in revegetated kangaroo grass (*Demansia psammophis*, Table 1). Small predaceous monitor lizards show similar trends, in this and other studies (Mott et al., 2010). Reduced numbers of lizard predators such as snakes and monitors after fire may be due to a combination of altered vegetation properties (i.e. fewer logs) and lower overall prey abundance following fire.

In our study, only one lizard species increased significantly in revegetated kangaroo grass, and it is not clear why. Similarly, only one snake (eastern brown snakes) was associated with grader grass, and they increased by 75% in revegetated grader grass, and declined between 60% and 80% in the two revegetated native grass sites. Revegetated grader grass has higher seed loads than pre-burning (Vogler and Owen, 2008). Native mice were abundant in revegetated grader grass, which may explain why we detected higher numbers of rodent-eating snakes in these locations (unpublished data).

Our sites were quite small, and fairly close together, and movement among sites might have influenced the abundance of different species in our study. We marked individuals, however, and had very low recapture rates between sites (3.4%). We are confident, therefore, that the trends we observed were real changes in abundance, rather than simple movement away from our sites.

4.3. Reptiles and fire management

Land managers use fires to reduce weeds and lessen the impact from wildfires (Price et al., 2012), but fires occurring in the same location may increase the burnt area (Alba et al., 2015), and frequent fires ($1 < 2$ years) alter the vegetation structure

(Burgess et al., 2014; Griffiths et al., 2015). Many studies report that reptile abundance and richness are unaffected by fires, whereas others report lower reptile abundance and richness in frequently burnt areas, and even fire-insensitive reptiles often occur in higher abundances in habitats with longer time since fire (Woinarski et al., 2004; Perry et al., 2012; McCoy et al., 2013). We found that, overall, reptile abundance and richness were similar before our focus fire and once it had been revegetated. More importantly, however, we detected a significant difference in the composition of the reptile assemblage before and after revegetation in native grass, demonstrating that to detect the influence of fires, especially in fire-adapted communities, it may be important to analyse community structure as well patterns of abundance and richness.

The community structure of reptiles in our study area was still different 15 months after our focus fire, and therefore it may be beneficial to wildlife to allow longer fire-free intervals to allow community structure to recover before repeated fires are implemented for management. Very importantly, the weed we studied was encouraged by fire, and frequent burning did not cause weed reduction in our study, instead both encouraging the weed, and increasing (not reducing) its detrimental effects on the depauperate reptile assemblage that used the weed.

5. Conclusion

The reptiles inhabiting the weed in our study were a depauperate subset of the species inhabiting native grasses; no reptile species were significantly associated with any burning state of the weed. Reptile abundances were also always lower in grader grass than in the two native grasses, regardless of burning state. The lowest abundance of any treatment occurred in grader grass after the focus fire, while with revegetation, abundances returned to the same low levels as were recorded before the focus fire. Native grasses had significantly higher reptile richness and abundances than grader grass, regardless of fire state, and overall abundances of reptiles in native grasses returned to similar levels after revegetation had occurred. The lowest reptile abundances were detected immediately after burning, probably because there was such reduced vegetation cover. In contrast to abundance, reptile assemblage composition in native kangaroo grass did differ between before our focus fire and after revegetation. Four species were significantly associated with kangaroo grass before the fire, and many species occurred in much reduced abundances in the two native grasses after revegetation. We found no evidence that burning the weed created a more hospitable habitat for reptiles. Instead, we found that burning grader grass simply allowed it to flourish, and to support the same depauperate community of reptiles present in grader grass left for longer periods. Our study site has been burnt so frequently that it is difficult to draw inferences regarding reptile assemblage composition in areas not burnt every 2 years or more. However, even in these extremely fire-prone, often-burnt environments, reptile numbers in native grass declined after fire, and failed to return with revegetation, suggesting that longer periods without burning may be beneficial to reptile assemblages, even in very fire-prone systems. The responses of reptiles to burning seemed to be plausibly driven by changes in vegetation structure, although this hypothesis could be more rigorously tested with experiments manipulating vegetation structure.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.02.002>.

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