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Title

Rapid increase of Australian tropical savanna reptile abundance following exclusion of feral cats

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Short Title: Reptile abundance and feral cats

Abstract

Feral cats have been responsible, in part, for the extinction of many species of mammal, bird and reptile globally, especially on islands. Whilst there is extensive evidence of the predatory impacts of cats on mammals and birds, far less is known about their ecological impacts on reptiles, especially in continental situations. We conducted a field experiment to evaluate the impact of feral cats on terrestrial vertebrates in tropical savanna environments of northern Australia. Three experimental treatments were applied to six 64 ha plots to compare and contrast responses of reptile abundance and species richness to predator exclusion and the additive effects of frequent fire. Replicated pitfall-trapping was undertaken in each plot on seven sampling occasions between November 2013 and November 2015. We analysed relative abundance and species richness data using generalized linear mixed models. There was a significant increase in the abundance of reptiles over a two year period in cat-excluded plots with reptile abundance increasing at twice the rate in cat-exclusion plots compared with cat-accessible plots and there was an additive effect of time-since-fire. Cat exclusion had a positive effect on reptile species richness over time, however the evidence for this pattern was weak when seasonal variation was taken into account. Predation by cats, in synergy with other disturbance processes, could adversely impact reptile species and communities elsewhere in the world where feral cats have been established and warrants further investigation.

Key words: predator-proof fence, reptile, feral cat, invasive species, predation

1. Introduction

Invasive mammalian predators are significant drivers of biodiversity loss worldwide (Doherty et al. 2016). In particular, feral cats have caused high rates of mortality for many bird and mammal species (Loss et al. 2013), and for the extinction of at least 18 species of island-endemic vertebrates (Medina et al. 2011; Nogales et al. 2013). Within Australia, predation by feral cats has been identified as a major contributing factor in the marked and widespread declines of northern Australia's mammal fauna in recent decades (Fisher et al. 2014; Woinarski et al. 2011).

Feral cats now occupy the entire Australian mainland and numerous offshore islands (Legge et al. 2016). Their population densities vary considerably across the continent (Legge et al. 2016); however, even at low densities, cats can deplete local populations of small and medium-sized mammals (Vázquez-Domínguez et al. 2004), increasing the risk of extinction to threatened species (Moseby et al. 2015).

Whilst extensive evidence of the predatory impacts of cats on mammals and birds has accumulated (Loss et al. 2013; Medina et al. 2011; Woinarski et al. 2017), far less is known about their ecological impacts on ectotherms. Reptiles and amphibians form a large component of the diet of cats globally (Bonnaud et al. 2010; Medina et al. 2011; Woods et al. 2003) and within Australia (Kutt 2012; Read and Bowen 2001; Woinarski et al. 2018). Several island endemic reptile species have become threatened through predation by introduced cats (Arnaud et al. 1993) and competition for food resources (Donlan et al. 2000). Dietary studies indicate that feral cats prey on a wide taxonomic range of Australian mainland reptile species and are capable of switching prey as preferred species are depleted (Dickman and Newsome 2015; Doherty et al. 2015). However, the broader ecological impacts of cat predation on reptile populations and communities are uncertain.

To assess the ecological effects of feral cat predation, it is necessary to quantify their predatory impact on natural populations and species assemblages, where possible in the context of other environmental influences. An understanding of the impact of predation by feral cats relative to, or in synergy with, other potential drivers of biodiversity loss is desirable in order to make informed decisions about where and how to best direct management interventions. Studies in northern Australia have shown that cats preferentially hunt in landscapes affected by recent wildfire and grazing (McGregor et al. 2017; McGregor et al. 2016) where they have greater hunting success on mammalian prey (Leahy et al. 2016; McGregor et al. 2015). These findings suggest important interactions between feral cat predation and altered fire regimes driving declines of northern Australian small and medium sized mammals. Many Australian reptile species and communities are also sensitive to altered fire regimes (e.g. Hu et al. 2013; Legge et al. 2008; Pianka and Goodyear 2012; Trainor and Woinarski 1994; Valentine and Schwarzkopf 2009). The interactive effects between feral cat predation and altered fire regimes may also impact reptile diversity.

We conducted a field experiment to evaluate the predatory impact of feral cats on northern Australian savanna terrestrial vertebrates. Here we report on the responses of reptiles to experimental exclusion of feral cats. We compared population responses of reptiles in replicated fenced plots that excluded cats to unfenced plots accessible to cats. As fire is a ubiquitous and important component of Australian tropical savanna woodland ecosystems, we attempted to manage fire as part of the experimental design. We predicted, firstly, that if feral cats exert significant predatory pressure on reptile communities, then populations should increase when cats are excluded. Secondly, we predicted that if frequent fire facilitates increased feral cat predation of reptiles, then when exposed to feral cats, populations of reptiles should increase with reduced fire frequency compared to those with frequent fire.

2. Methods

2.1. Study area

The study was conducted in Kakadu National Park (E 132˚22.47, N 12˚38.97) – the largest terrestrial national park in Australia and a World-Heritage Area (Fig. 1). The climate is monsoonal and is characterised by a humid wet season between December and March, during which the majority of the ca. 1500 mm mean annual rain falls. We undertook the study at Kapalga, north-western Kakadu, which consists of lowland open forest dominated by *Eucalyptus miniata* and *E. tetrodonta* on flat topography. The tropical savanna of Kakadu National Park is frequently burnt with fires typically greater than 1 km^2 in extent and return intervals of less than three years: i.e. at least 33 % (and often at least 50 %) of the lowland forests are burnt every year (Russell-Smith et al. 2017). An extensive landscape-scale fire experiment was undertaken at

Kapalga from 1989 to 1995 within large experimental compartments (Andersen et al. 2005). The area has also been the subject of extensive wildlife ecological studies and monitoring (e.g. Braithwaite and Muller 1997; Griffiths et al. 2015; Woinarski et al. 2001). Consequently the faunal assemblage composition and fire history of the area are well documented.

2.2. Experimental design

Six 64 ha square plots with similar habitat and landscape characteristics and comparable fire histories over the previous 10 years (2002 – 2012, MODIS fire scars, 250 m x 250 m resolution, North Australia and Rangelands Fire Information (NAFI), http://www.firenorth.org.au) were selected using topographic maps, satellite imagery, and vegetation mapping (Schodde et al. 1986). Three experimental treatments were applied to the plots to compare and contrast responses of reptile abundance and richness to predator exclusion and the additive effects of frequent fire, as follows:

1. Predator exclusion and fire suppression
2. No predator exclusion and fire suppression, and
3. No predator exclusion and no fire suppression.

A fully balanced design that incorporated a further treatment with ‘predator exclusion and no fire suppression was considered but not included, because of: (i) ethical concerns about lack of escape routes from fire for some animals inside exclosures; (ii) a high likelihood that fire in predator proof exclosures would damage fences directly and indirectly by causing treefalls; and (iii) a lack of availability of suitable locations within the study area for additional fenced sites with similar fire history and vegetation characteristics.

For treatment 1, predator exclusion fences with firebreaks 8 m in width were established around the perimeters of two plots. The fence design followed that successfully used at Arid Recovery in South Australia to exclude feral cats, foxes and rabbits (Moseby and Read 2006). The fences were constructed using 50 mm hexagonal wire mesh, to a height of 1800 mm with a curved floppy section extending 450 mm outward from the top of the fence. Internal and external foot aprons extended 550 mm from the base to prevent animals from digging under the fence. Note that this fencing excluded not only cats, but also other large mammals present in the area (including dog *Canis familiaris*, Asian buffalo *Bubalus bubalis*, horse *Equus caballus*, pig *Sus* *scrofa* and agile wallaby *Notamacropus agilis*), and may have prevented large goannas *Varanus* spp. and large snakes from entering or exiting the fenced plots.

Treatments 2 and 3 were unfenced plots. Firebreaks 8 m wide were established around the perimeters of two plots for treatment 2; the remaining two plots had no fire breaks for treatment 3.

Fire suppression activities were undertaken by Kakadu Park management staff at all four plots with fire breaks, including early dry season fuel reduction burning around most of the external perimeters, and active fire suppression when necessary inside the plots. However, despite these measures, strict fire exclusion in line with the planned design was not achieved. All plots were burnt at least once between the months of May and November over the duration of the experiment (see Table 1).

2.3. Data collection

Initial (baseline) surveys for reptiles in each plot occurred in November 2013, prior to fence completion. After completion of fences in December 2013, each plot was surveyed three times annually in the late wet (March/April), mid-dry (June/July) and early wet (Oct/Nov) seasons until November 2015. Within each plot six transects, 200 m apart and 800 m in length, were established. Four 20 L pitfall trap buckets (290 mm diameter and 400 mm deep, drift fence 10 m long and 0.3 m high) were installed 200 m apart along each transect. Each transect was sampled for a 72 hr period during each sampling session. Half of the transects (alternate transects) in each of three plots, one from each treatment, were sampled concurrently, followed by the second half of the transects over a total period of seven days. This procedure was then repeated for the other three plots, i.e. there was a total sampling effort of 72 pitfall-days per plot per sample event. The order of plots and transects sampled was varied between survey sessions. Traps were checked twice daily (c. 0700 hrs and 1700 hrs) and the species and number of individuals captured were recorded: note that trapped individuals were not marked, so the abundance tally may include recaptures. Unequal trapping effort occurred between some sampling periods due to heavy rain filling buckets and/or meat ant invasions of some buckets. Total trapping effort was > 90 % across all plots except in three sampling sessions. In November 2013, 85% effort was achieved for three of the unfenced sites and 50% effort for one unfenced plot and both fenced plots. In

March 2014, sampling effort in the fenced plots was 80 and 88 %, and unfenced plots ranged from 83 – 85 %. Lastly, in March 2015 two unfenced plots achieved 85 % and 88 % effort while all others were > 90 %.

Both fenced plots, and three unfenced plots, were burnt prior to the completion of the fences and no fire occurred in any plot in 2014. In 2015, one fence and three unfenced plots burned (Table 1). To test for the effects of fire, visual evidence of fire within 10 m of each pitfall was recorded in each sampling session and corroborated using historical fire scar data obtained from NAFI. The month of fire documented by NAFI was also recorded.

To confirm that the fenced plots successfully excluded cats, eight camera traps (HC550 and HC600; Reconyx, Holmen, WI, USA) were spaced 400 m apart along the interior of the fence in each plot. Cameras were mounted on fence pickets approximately 100 cm above the ground and oriented to take photos of animals passing in front of the camera on both the inside and outside of each fenced plot. In addition, five camera traps baited with a peanut butter and oat mixture were placed within each plot concurrently with trapping to detect cat and other mammal activity within plots and these remained deployed for a minimum of 5 weeks (as per Gillespie et al. 2015). We also estimated cat density in the vicinity of the study area by deploying two grids of 48 cameras each in June 2015 (for methods see Stokeld et al. 2016).

2.4. Statistical Methods

Number of individuals and number of species of reptile captured at each pitfall within each sampling session between November 2013 and November 2015 were calculated and used as response variables to model treatment effects. Diversity measures (i.e. Shannon-Weiner index) could not be used at the pitfall level due to excessive zero inflation. We analysed data using generalized linear mixed models (GLMMs; Pinheiro and Bates 2000) with a Poisson error structure and logit-link function to account for repeated measures at pitfalls (24 pitfalls/plot). GLMMs provide a means for the inclusion of random effects; therefore the variance induced by plot-effects could be estimated as a source of random variation in the data. To assess the temporal effect of predator exclusion on reptile abundance and species richness we analysed the data in R (R Core Team 2015) using package *lme4* (Bates et al. 2015) and ‘bobyqa’ optimiser to minimise problems with model convergence.

To account for the minor variation in sampling effort between pitfalls in each sampling session, the number of sampling visits undertaken at each pitfall, in each sampling session, was $_n$log transformed and used as an offset in the models (Zuur et al. 2009). Therefore, the modelled response is the expected number per unit effort. The number of months since a fire (TSF, range: 0 – 54 months) occurred at a pitfall was $\sqrt{(x+1)}$-transformed to improve normality. Seven sampling sessions were undertaken between November 2013 and November 2015, and an integer variable was created to account for the change in response over time.

To examine the effect of cat exclusion a model was built including the fixed effects of time, fence treatment and their interaction, and the additive effect of TSF (a model including the interaction of time, fence treatment and TSF failed to converge). A series of models was run, varying plot and pitfall-level random effects to allow variation in the intercept and slope of the response for each plot. To check the validity of the inclusion of random effects components the log likelihood ratio test was applied to obtain the optimal variance structure for the data (Zuur et al. 2009). Model fit of fixed effects was compared using Akaike Information Criterion (AIC) to select the optimal model. To account for reduced sampling effort across plots in the first sampling session, we also ran the model set on a dataset excluding the first session. There was little difference in results so we opted to retain the full dataset. The best fitting model was checked for over-dispersion. Model residuals were plotted against the fitted values and each explanatory variable to identify violation of homogeneity. A smoother was applied to the TSF variable using the R package *mgcv* (Wood 2004) and plotted against model residuals to check for non-linear patterns. Structured heterogeneity was identified in the residual plots for reptile abundance; therefore a fixed effect of sampling season (3 seasons per year) was added to the models. Although there was no evidence of structured heterogeneity in the richness model, an additional model was run to assess the effect of season of sampling on species richness. We used R package *effects* (Fox 2003) to estimate significant fixed-effects and graphically present condition means and standard error estimates.

We attempted to examine contrasting responses of different groups of reptiles based upon taxonomic family and body size. However, the data were excessively zero-inflated across these groups (> 25 % of groups = 0). We graphically present capture rates, standardised by trap effort, of all species combined and the four most abundant species for fenced and unfenced plots for visual assessment. Trends were examined for the less common species, but capture numbers were so small per session and plot that no consistent pattern was evident. Shannon-Wiener index was calculated for each plot in each sampling session. A two-factor repeated-measures analysis of variance was used to determine if plot-level reptile diversity in each treatment differed over time.

3. Results

A total of 2647 individuals of 31 species of reptile from 8 families were caught across the seven sampling sessions (Fig. 2). The most common species were the agamid *Diporiphora bilineata*, the gecko *Heteronotia binoei*, and the skinks *Ctenotus essingtonii*, *Ctenotus storri* and *Eremiascincus isolepis*. The mean number of individuals captured varied between sampling sessions and between treatments within sampling sessions (Fig. 3), with most captures obtained in the early wet season (Oct/Nov). There was no evidence that plot-level diversity between treatments changed differentially over time ($F_{12,18} = 0.92$, $p = 0.55$).

The best supported model structure for reptile *abundance* incorporated a random intercept for pitfall- and plot-effects, and random slope for plot-effects indicating the response in abundance over time differed for each plot. There was minimal correlation between repeated observations at pitfalls (*intra-class correlation* = 0.001), but model deviance was significantly reduced with pitfall-effect included. The effect of season was added to the model to improve homogeneity of residuals and this significantly reduced deviance ($\chi^2 = 66.7$, $d.f. = 2$, $p < 0.001$). Excluding cats had a positive effect on reptile abundance over time ($\beta = 0.112$, SE = 0.056, $p = 0.044$) and there was an additive effect of time since fire ($\beta = 0.040$, SE = 0.019, $p = 0.039$) (Table 2, Fig. 4). The effect of predator exclusion resulted in a doubling of mean reptile abundance over two years, while mean reptile abundance remained relatively constant at unfenced plots (Fig. 5).

The best supported model structure for reptile *species richness* incorporated a random intercept and random slope for plot effects. There was no correlation between repeated observations at pitfalls (*intra-class correlation* = 0), so the model was re-run without this term. Time-Since-Fire was not a significant variable in the model explaining species richness ($p = 0.56$), so the model was re-run without this term. Predator exclusion had a positive effect on reptile species richness over time ($\beta = 0.091$, $p = 0.031$) (Table 3a). When the fixed effect of season was added to the model, evidence for a positive effect of predator exclusion on species richness was weak (β = 0.075, p = 0.062) (Table 3b). Including season reduced model deviance (χ^2 = 26.0, $d.f.$ = 2, p < 0.001) and therefore had greater support. Species richness within fenced plots was lower than at unfenced plots at the commencement of the experiment, but fenced plots had a higher rate of increase in species richness over time. However, evidence for this pattern was weak when seasonal variation was taken into account.

One cat was removed from a fenced plot within one week following fence completion. No other cats were detected within the fenced plots for the remainder of the experiment. Cats were detected at all non-fenced plots in at least one sampling session between November 2013 and November 2015. Cat density in the study area was estimated at 0.19 cats km^{-2}.

4. Discussion

Experimental exclusion of feral cats resulted in a significant increase in reptile abundance assessed at the pitfall-level over a two year period, relative to comparable unfenced plots. The most abundant species captured followed the same general overall trend. Most of the reptile species sampled in our study area are relatively small and expected to have generation times of one year or less (Scharf et al. 2015). Assuming that changes in trap return rates are generally indicative of relative population density, the change in abundance of reptiles observed within fenced plots represents an effective population rate of increase across species of approximately 2, relative to the rate of increase at control plots. A small change in species richness was also observed at the pitfall-level within the fenced plots; however, evidence for this was weak when seasonal variation was taken into account. There was no evidence that plot-level diversity differed between treatments over time, however this is not surprising given the small sample size which reduces statistical power and ability to account for sources of heterogeneity such as fire frequency. All of the species we surveyed are within the prey size range for feral cats, and cats have been reported to prey on most of the species, or their conspecifics (Kutt 2011). The density of feral cats at our study site was relatively low compared to many other regions of Australia, although not markedly lower than the national average (0.27 cats km^{-2}) (Legge et al. 2016). These findings indicate that, even at relatively low densities, feral cats are exerting considerable predatory pressure on small reptile populations.

Our findings contrast with two studies undertaken elsewhere within Australia. At Arid Recovery Reserve in South Australia reptile abundance was reported to be greater outside predator exclusion areas than within (Moseby et al. 2009). In a manipulative study on Heirisson Prong in Western Australia, no change in reptile capture rates was detected in response to predator control (Risbey et al. 2000). In contrast to our study, these two study areas maintained relatively high densities of populations of translocated mammals which may have had both direct and indirect negative effects on reptile abundance through competition, predation and changes in vegetation structure. In comparison, Olsson et al. (2005) observed an increase in the density of small lizards in small fenced areas in New South Wales which did not hold translocated mammals and from which both foxes and cats were excluded. Foxes occurred at all three of the aforementioned study areas. Although foxes predominantly prey on small and medium mammals rather than reptiles (Sutherland et al. 2011), predation by foxes may have masked the effects of cat predation on the reptile communities in these studies since fox diets in arid areas can contain high numbers of reptiles (Cupples et al. 2011; Paltridge 2002; Read and Bowen 2001). Nonetheless, the population and community-level responses of reptiles to feral cat predation are likely to vary across different bioregions, due to different top-down and bottom-up ecological processes. Compared to arid and semi-arid temperate zones of Australia the tropics are more productive, most reptile species are active all year round, and there is a higher diversity of predators. Reptile life histories may be more highly geared in this environment to respond quickly to ecological release from predation.

Several other predators occur in the study area which could potentially confound our interpretation of the effect of cats. Dingoes occur in the area and were excluded from the fenced plots; however, dingoes mostly prey on mammals and birds in this region and reptiles comprise a marginal component of their diets (Corbett 1989; Stokeld et al. 2018). An analysis of dingo diet undertaken concurrently at the study site revealed that dingoes preyed predominantly on macropods (Stokeld et al. 2018). Northern quolls (*Dasyurus hallucatus*) are important predators of reptiles and other small vertebrates (Oakwood and Eager 1997). Although this species underwent severe declines in Kakadu with arrival of the cane toad (*Rhinella marinus*) (Woinarski et al. 2010) and populations continue to be suppressed through predation by dingoes (Cremona et al. 2017), they persist at low densities at the study site. However, quolls and other medium-sized scansorial mammal species have the ability to scale the fences and were observed on camera trap occasionally moving in and out of the fenced plots. The diets of sand goannas (*Varanus gouldii*) and floodplain monitors (*V. panoptes*) consist, in part, of reptilian prey (Oakwood and Eager 1997; Sutherland et al. 2011). These species also suffered severe population declines following invasion of the cane toad in the early-mid 2000s (Doody et al. 2009), and were rarely detected in our study area. Checking of pitfall-traps involved walking approximately 1500 km of transects across the six plots over the two year period, during which neither species was seen. Only two observations were recorded of floodplain monitors on camera trap at one non-fenced plot. Sub-adults of these species are capable of passing through the fences. Therefore we are confident that the observed increases in small reptile abundance and species richness inside the fenced plots were not a result of reduced predation from these other species. The fences used in this study also prevented access by large herbivores (e.g. Asian buffalo, horse) present in the general area, whilst a small population of agile wallaby persisted inside the fenced plots for the duration of the study. General observations indicated that large herbivores were present in the unfenced area in relatively low densities and were unlikely to have caused reduction in ground layer vegetation to a sufficient extent to affect cat hunting efficiency or habitat suitability for reptile species.

Reptile abundance (but not richness) also increased with time since fire. Studies of fire effects on reptiles in northern Australian savanna woodlands have been limited and results variable depending on the season of burning (Braithwaite 1987; Corbett et al. 2003; Trainor and Woinarski 1994). Legge et al. (2008) observed a short-term decrease in the abundance of some reptile species following high-intensity late-dry season burning. Nicholson et al. (2006) found no change in the abundance or composition of skinks following low-intensity early-season burning in small-scale experimental fire management plots near Darwin, and Kutt and Woinarski (2007) found little evidence of a significant response of reptiles to different fire frequencies. However, Woinarski et al. (2004) found greater reptile abundance and diversity in long-unburnt sites in comparison with frequently burnt sites near Darwin. Furthermore, Valentine and Schwarzkopf (2009) found that fire intervals of less than three years reduced reptile abundance and species richness in a north Queensland tropical savanna by altering availability of resources such as leaf litter and vegetation structure. Our findings are somewhat consistent with those of Valentine and Schwarzkopf (2009) and Woinarski et al. (2004) in that reptile abundance increased the longer sites remained unburnt. However, the effect size was small and may not have been detected with a shorter-term study that did not measure changes through time.

Fires are frequent in the tropical savannas of northern Australia generally and in the lowland woodlands of Kakadu specifically (Russell-Smith et al. 2017). Small reptiles have limited dispersal capabilities and are likely to be affected to some extent by such frequent and large-scale disturbances. Our data were too sparse to examine contrasting responses amongst species or different groups of reptiles; however responses to fire are likely to vary among species depending on the timing and intensity of fires as well as species habitat and life history attributes and habitat requirements (Valentine and Schwarzkopf 2009), and this warrants further evaluation.

The impacts of cat predation and frequent fire on reptile abundance were additive. This result is consistent with other recent studies of cat behaviours and impacts in the tropical savannas of northern Australia. McGregor et al. (2014) found that cats preferentially hunt in areas with little ground-layer vegetation cover, especially heavily grazed areas and areas recently burnt by high intensity fires. Furthermore, the hunting efficiency of cats is significantly increased in open habitats (McGregor et al. 2015), indicating that habitat changes associated with frequent, high intensity fires and livestock grazing may amplify feral cat predatory impacts.

This experiment demonstrated that feral cats are exerting considerable predation pressure on small reptile populations in northern Australian tropical savannas. Albeit to a lesser degree, frequent fire is also suppressing small reptile abundance. Feral cats have received considerable recent attention in Australia due primarily to their contribution to declines and extinctions of mammal (Woinarski et al. 2015) and bird species (Woinarski et al. 2017), and the impact of cats on many of these species may be exacerbated by altered fire regimes (McGregor et al. 2015). Our findings suggest that these factors are similarly impacting small reptile communities.

We found that a comparatively low density of feral cats was capable of suppressing populations of a variety of reptile species. Given the large numbers and diversity of small reptile species consumed by feral cats annually (Woinarski et al. 2018), our findings suggest that feral cat predation may be having a much larger impact on reptile diversity than previously recognised, and could be an important contributing factor to increasing their extinction risk.

In contrast to mammals and birds there has been less documentation of historic and contemporary declines or extinctions of small squamates (Böhm et al. 2016; Smith et al. 2012), especially in continental settings. This difference may reflect, in part, less extensive surveillance and reporting of long-term broad-scale changes in small reptile communities. The effects of feral cat predation on reptile populations may not yet be apparent in long-term monitoring data or through increases in threatened species listings. In this context our findings may be an early warning for threatened species, such as the yellow-snouted gecko (*Lucasium occultum*), or other susceptible species which may be suffering declines that have not been detected with current monitoring approaches.

4.1. Management implications

Eradication, or suppression, of feral cat populations has been identified as a national priority for threatened species conservation in Australia (Commonwealth of Australia 2015). Whilst the imperative for this has been driven by the plight of threatened mammals and birds, such measures are likely to benefit reptile diversity as well. However, it remains challenging for managers to achieve long-lasting and extensive reduction in the density of feral cats, and this has not yet been achieved at any large site in Australia's tropical savannas, nor elsewhere in the world where feral cats are established, apart from small islands (Campbell et al. 2011). Our findings indicate that both feral cat predation and the current prevailing savanna fire regimes are having a significant adverse effect on reptile diversity. It is likely that, in the short term, the most effective mechanism for reducing predation impacts by cats on fauna in tropical savanna regions of Australia will be through intensive fire management, aimed at reducing the extent, frequency and intensity of fire.

For the foreseeable future in Australia and elsewhere, areas targeted for feral cat intervention are likely to be directed by threatened mammal and bird priorities (see Commonwealth of Australia 2015; Nogales et al. 2013). As demonstrated here, feral cat predation can have significant additive impacts on reptile assemblages with respect to fire regimes. How such additive, or potentially synergistic, interactions with other disturbance processes or habitat alteration impact reptile species and communities elsewhere in the world where feral cats are established warrants further investigation. Risk assessments are also needed to evaluate additional priorities for reducing the threat posed by feral cats to threatened reptile species.

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Table 1. Fire history for each plot for the 2013-2015 sampling period. Values represent the proportion of the pitfalls that were burnt within that month.

2013	**Plot**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Treatment 1 (Fence)	a	--	--	--	--	--	--	20%	--	--	50%	--	--
Treatment 1 (Fence)	b	--	--	--	--	--	--	20%	--	--	100%	--	--
Treatment 2 (Firebreak)	a	--	--	--	--	--	30%	--	--	--	--	--	--
Treatment 2 (Firebreak)	b	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 3 (Control)	a	--	--	--	--	--	--	--	--	--	100%	--	--
Treatment 3 (Control)	b	--	--	--	--	--	--	--	--	--	100%	--	--
2014		**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Treatment 1 (Fence)	a	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 1 (Fence)	b	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 2 (Firebreak)	a	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 2 (Firebreak)	b	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 3 (Control)	a	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 3 (Control)	b	--	--	--	--	--	--	--	--	--	--	--	--
2015		**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Treatment 1 (Fence)	a	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 1 (Fence)	b	--	--	--	--	--	--	--	100%	--	--	--	--
Treatment 2 (Firebreak)	a	--	--	--	--	--	--	--	--	--	--	--	--
Treatment 2 (Firebreak)	b	--	--	--	--	--	--	--	--	--	--	33%	--
Treatment 3 (Control)	a	--	--	--	--	70%	--	--	--	--	--	--	--
Treatment 3 (Control)	b	--	--	--	--	--	100%	--	--	--	--	--	--

Table 2. Model results for the fixed effects from a generalised linear mixed model testing the response of mean reptile abundance to predator exclusion over time. The expected abundance is per unit effort. Bold values represent significant terms.

Model:

$$Abundance = exp(B_0 + B_1(Time) + B_2(Treatment) + B_3(Season) + B_4(TSF) + B_5(Time \times Treatment) + (1+Sample|Plot) + (1|Pitfall) + offset({}_n logEffort))$$

	Estimate	*S.E.*	*p-value*
Intercept (Unfenced plots, Dry season)	**-0.965**	**0.167**	**< 0.001**
Time	0.003	0.032	0.935
Fence	**-0.567**	**0.272**	**0.037**
Season: Early Wet	**0.229**	**0.046**	**< 0.001**
Season: Late Wet	**-0.191**	**0.055**	**0.001**
TSF	**0.040**	**0.019**	**0.039**
Time x Fence	**0.112**	**0.056**	**0.044**

Table 3. Model results for the fixed effects from a generalised linear mixed model testing the response of mean reptile species richness to predator exclusion fencing over time. Bold values represent significant terms. Expected richness is per unit effort.

A.

Model:

Species Richness = exp(B0 + B1(Time) + B3(Treatment) + B4(Time x Treatment) + (1|Plot) + (1|Pitfall) + offset(nlogEffort))

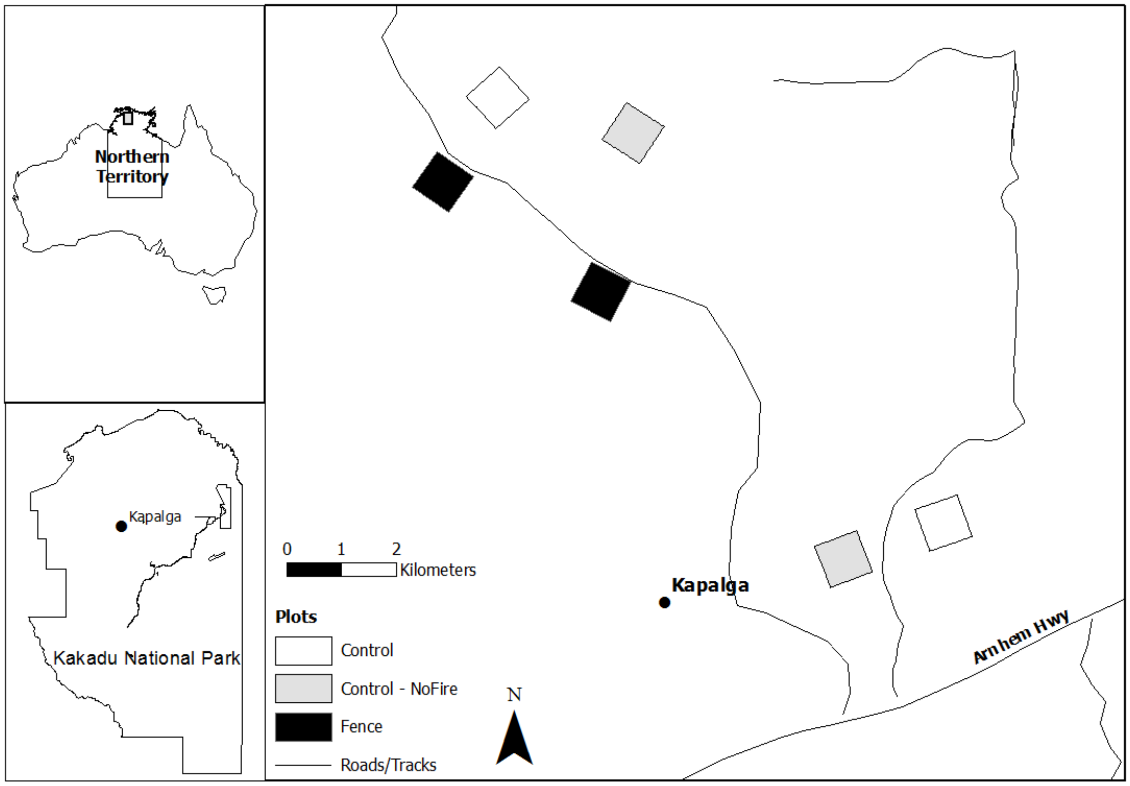
	Estimate	*S.E.*	*p - value*
Intercept (Unfenced plots)	**-1.175**	**0.084**	**< 0.001**
Time	0.031	0.023	0.183
Fence	**-0.467**	**0.163**	**0.004**
Time x Fence	**0.091**	**0.042**	**0.031**

B.

Model:

Species Richness = exp(B0 + B1(Time) + B2(Treatment) + B3(Season) + B4(Time x Treatment) +(1|Plot) + (1|Pitfall) + offset(nlogEffort))

	Estimate	*S.E.*	*p-value*
Intercept (Unfenced plots, Dry season)	**-1.194**	**0.085**	**< 0.001**
Time	0.022	0.022	0.319
Fence	**-0.381**	**0.150**	**0.011**
Season: Early Wet	**0.188**	**0.054**	**0.001**
Season: Late Wet	-0.096	0.064	0.132
Time x Fence	0.075	0.040	0.062



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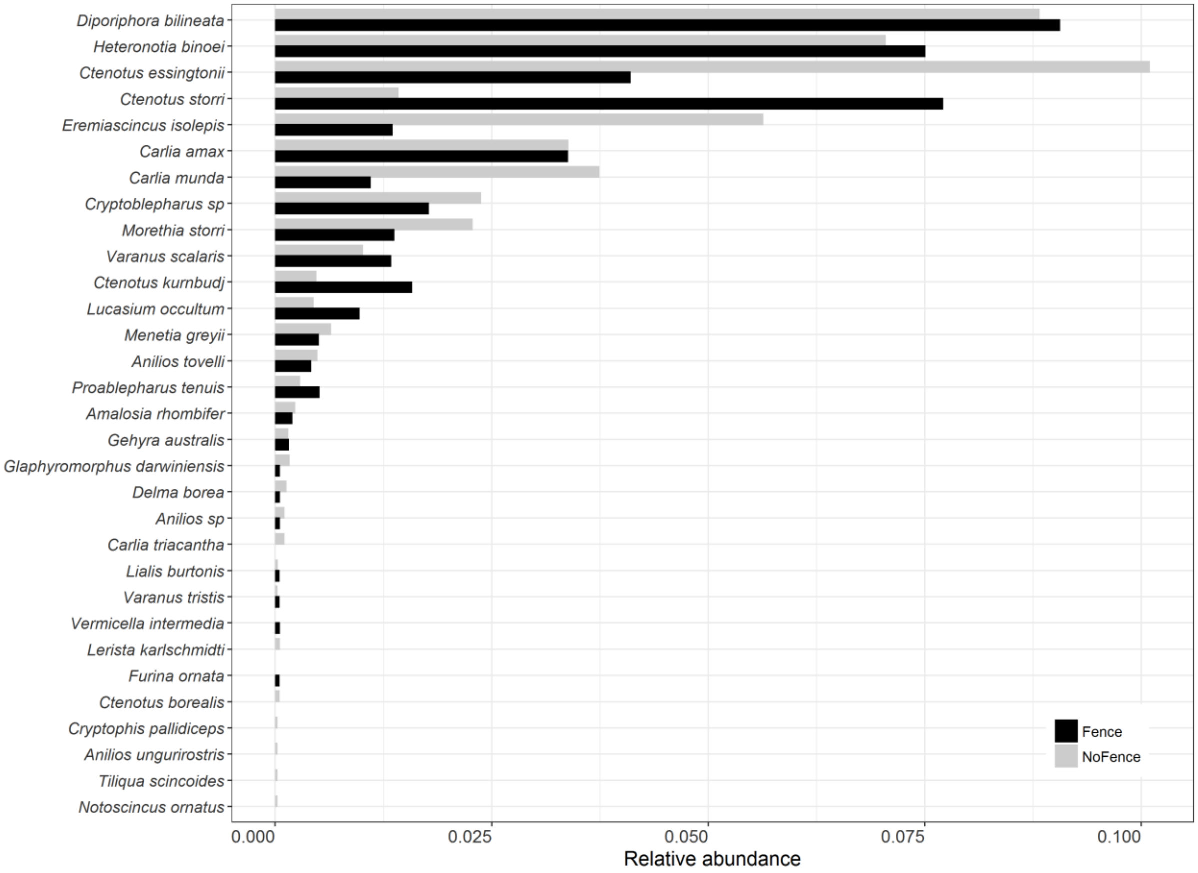

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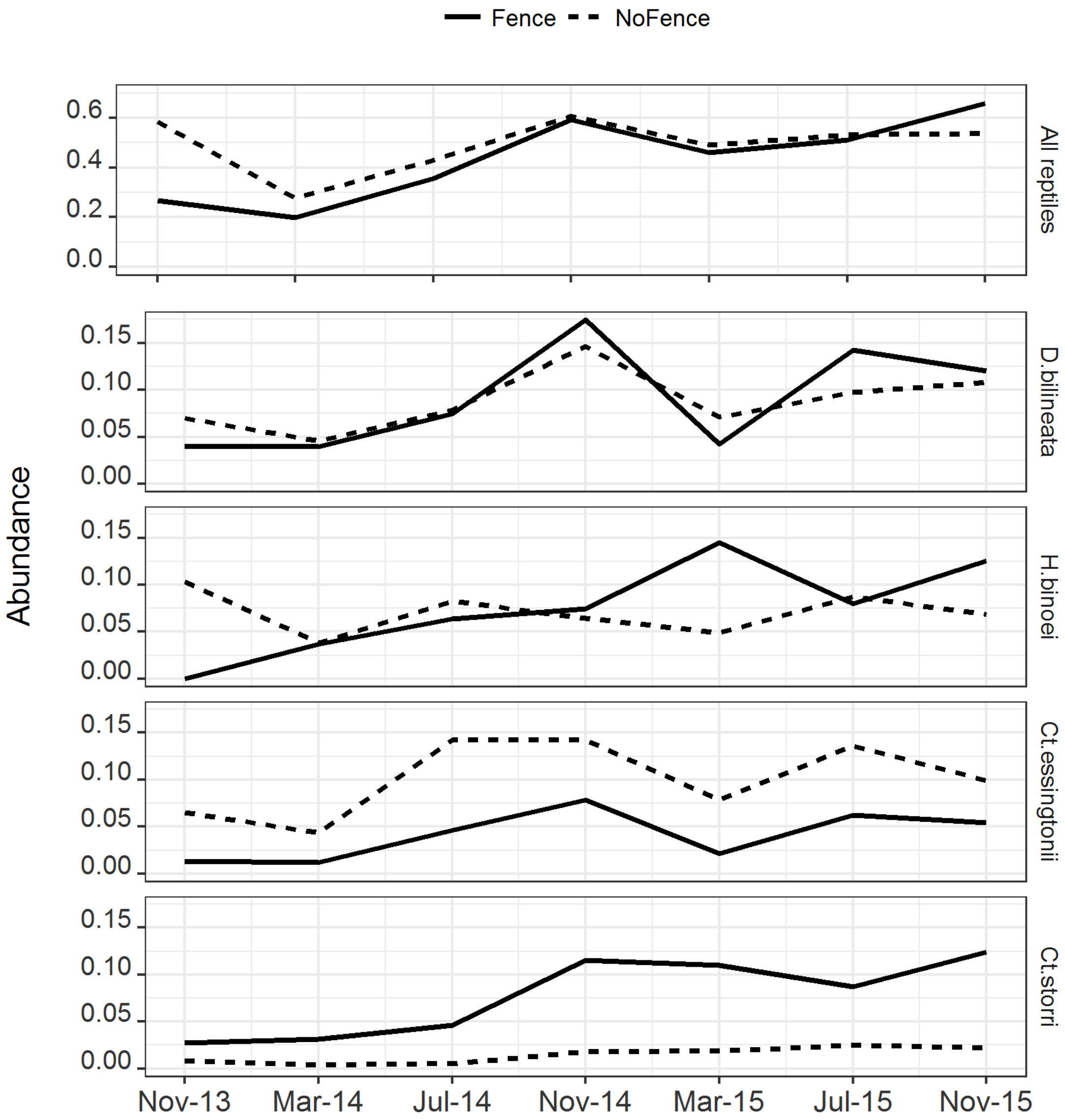

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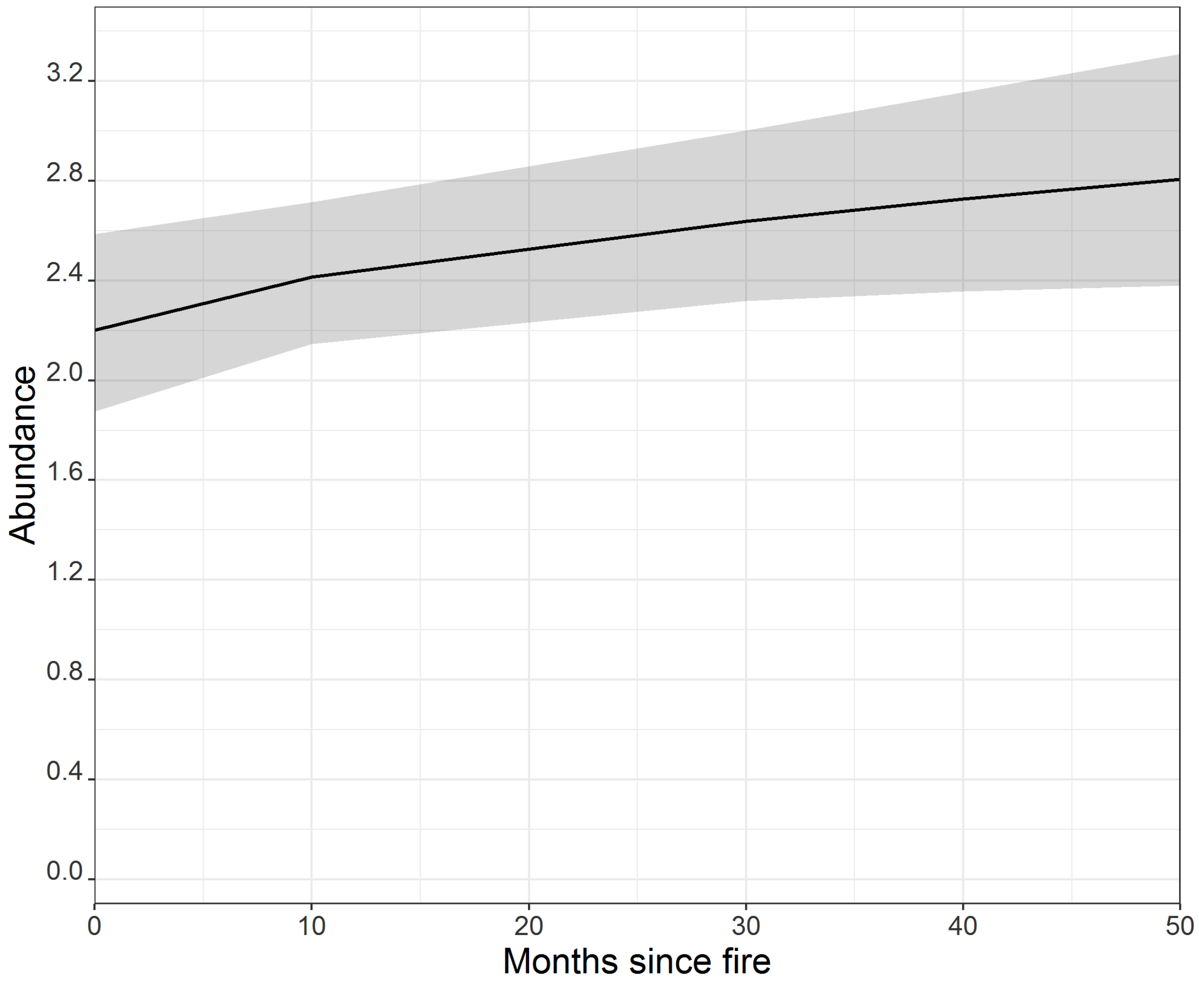

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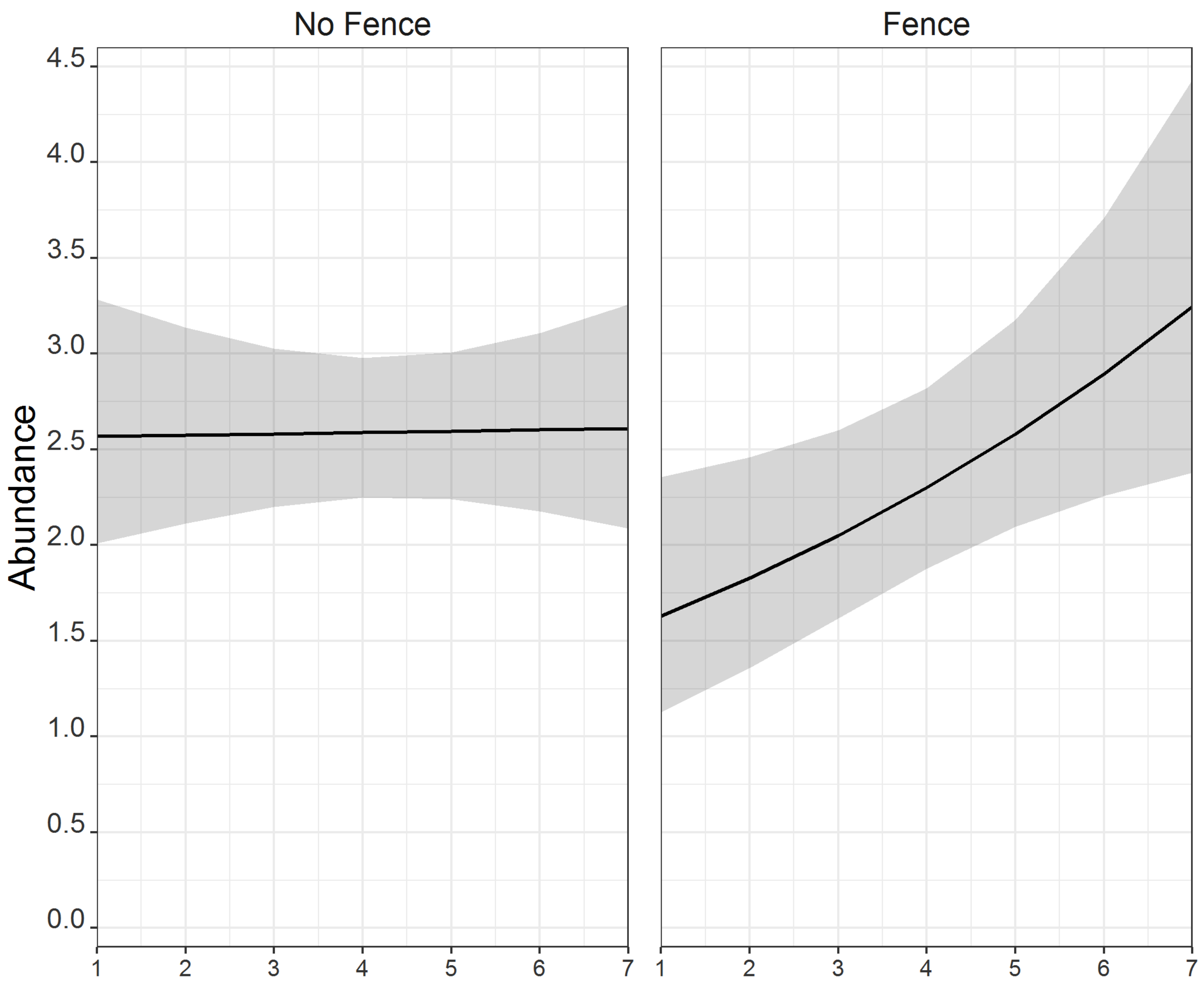

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