



Traits influence reptile responses to fire in a fragmented agricultural landscape

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Received: 7 July 2021 / Accepted: 6 February 2022 / Published online: 19 July 2022
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Abstract

Context Habitat loss and fragmentation can interact with other threats, including altered fire regimes, and responses to these effects can be mediated by functional traits.

Objectives To determine how richness and abundance of reptile trait groups respond to habitat fragmentation, patch isolation and fire.

Methods We surveyed reptiles in 30 sites over 3 years. Sites in remnant patches in farmland were adjacent to a conservation park with either recently burnt or long-unburnt habitat. The remnant patches were stratified by distance from the reserve. Sites were spatially paired, and we experimentally burnt one of each pair in farmland. Trait groups included size, reproduction, habitat position, diet, and activity period.

Results None of the trait groups benefited from experimental burns, while the burns reduced

abundance of viviparous, small, and above-ground species. Species richness was lower in isolated sites than in sites close to the conservation park, while generalist trait groups appeared unaffected by patch isolation. Large-sized reptiles had higher abundance in remnants. There was not more rapid colonisation of burnt sites near recently burnt conservation park. Instead, low initial abundance may have been caused by fire in combination with drought, with high rainfall during the study allowing recovery and spill-over into adjacent remnants.

Conclusions Landscape structure appears to interact with natural fires, restoration burns and longer-term climatic trends to influence the abundance and distribution of reptiles. Traits mediate responses, enabling us to formulate a set of testable mechanistic hypotheses, which illustrates a pathway to generalisation and prediction.

Keywords Body size · Fire · Functional traits · Habitat loss and fragmentation · Oviparous · Patch isolation

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01417-9>.

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Introduction

Habitat loss and fragmentation are major drivers of biodiversity loss, and rising demand for resources along with growing human populations will see habitat loss increase in many parts of the world (Williams et al. 2021a). The detrimental impacts of habitat loss

and fragmentation are partly due to loss of habitat area but also ecosystem decay (Haddad et al. 2015; Chase et al. 2020). As remnant vegetation becomes smaller and more isolated, the quality of habitat can degrade through edge effects, including altered microclimates and spill-over of farm-adapted species (Driscoll et al. 2013), and disturbances, such as livestock grazing and inappropriate fire regimes (Ewers and Didham 2006). When acting concurrently, these additional threatening processes can modify the effects of habitat loss and fragmentation (Geary et al. 2019).

Altered fire regimes, for example, can act with habitat loss and fragmentation to modify the impacts that either would have alone (Driscoll et al. 2021). Their combined effects can be detrimental, with fire causing local extinctions and fragmentation preventing populations from re-establishing (Alstad and Damshen 2016), or their combined effects can exceed an optimal intermediate level of disturbance (Scroggie et al. 2019). Conversely, fire suppression can drive fragmentation and addition of fire can restore connectivity for species that use more open habitats (Neuwald and Templeton 2013). However, successful restoration of connectivity with fire can depend on proximity to source populations, with patches close to sources receiving more immigrants than isolated sites (MacArthur and Wilson 1967; Hanski 1998; Leibold et al. 2004). Colonisation of unoccupied patches can also depend on the similarity of successional stage between patches and potential sources, because species often have strong affiliations with particular successional stages of vegetation recovery (Smith et al. 2013). However, knowledge of such spill-over effects is limited (Matthews 2021).

An important approach to generate transferable knowledge has been to use traits to identify groups of species that are vulnerable to the effects of habitat disturbance (Keinath et al. 2017). For reptiles—a group threatened by habitat loss, fragmentation and modification (Keinath et al. 2017; Doherty et al. 2020), particularly agriculture (Chapple et al. 2021; Wong et al. 2021)—a range of traits have proven useful in discriminating responses, including body size, reproduction, diet, habitat position and activity period (Watling and Donnelly 2007; Santos and Cheylan 2013; Carvajal-Cogollo and Urbina-Cardona 2015; Bohm et al. 2016; Neilly et al. 2018; Val et al. 2019; Chergui et al. 2020; Williams et al. 2021b). While

substantial research effort has been directed towards understanding the role of traits in explaining reptile responses to disturbance, consistent trends have not yet emerged. More cases describing the circumstances in which particular traits influence responses to fire, habitat loss and fragmentation are needed to help develop contingent theory (Driscoll and Lindenmayer 2012).

Parts of the semi-arid mallee woodlands of southern Australia have been extensively cleared for agriculture, leaving linear remnants and small patches that experience fire suppression (Driscoll and Henderson 2008; Williams et al. 2012). Adjacent parts consist of large tracts of mallee in nature reserves that have natural fire return intervals of decades to centuries, depending on rainfall (Gibson et al. 2015). The reptile fauna is rich, and many species have strong responses to both fire and habitat fragmentation (Driscoll 2004; Nimmo et al. 2012; Smith et al. 2013). With this combination of intact woodlands adjacent to fire-suppressed remnant patches, mallee landscapes are ideal for examining how traits of reptiles influence their response to the combination of habitat fragmentation and experimental fire added as a potential restoration tool.

Our specific aims were to:

- (1) Investigate how the addition of fire to remnant vegetation affects the abundance and richness of different reptile trait groups.
- (2) Quantify the effects of patch isolation on richness and abundance of reptile trait groups.
- (3) Determine the overall effects of habitat conversion to farmland on reptiles in remnant vegetation by comparing reserves with remnants.
- (4) Determine how the effects of fire in remnants are moderated by potential source populations in adjacent reserves, using reserves at different stages of post-fire succession.

Given that reptile trait groups show diverse responses to fire, and research has not always included traits we have available, it is difficult to make predictions about responses to the addition of fire to remnant vegetation (aim 1). However, with predicted detrimental impacts of an agricultural matrix on remnants (Driscoll et al. 2013), small patch size (Doherty et al. 2020), and the likely limited dispersal of reptiles in our study (Williams

et al. 2012; Driscoll et al. 2012b), we expected that richness and abundance of most trait groups would be lowest in the most isolated remnants (aim 2) and lower in the remnant vegetation compared with the conservation park (aim 3). Possible exceptions would be traits that confer some advantage in disturbed landscapes, such as generalist habits (Watling and Donnelly 2007; Bohm et al. 2016). We expected that experimentally burnt patches close to the recently burnt conservation park would gather colonists faster than recently burnt patches adjacent to long unburnt mallee (aim 4) (Gentry and Vierling 2007).

The impacts of habitat fragmentation and loss are global and worsening as they interact with other threats including climate change (Segan et al. 2016), invasive or irruptive species (Geary et al. 2019) and altered fire regimes (Driscoll et al. 2021). Understanding how these interactions affect biodiversity depends on knowledge of landscape processes, including the effects of patch isolation, patch condition and sources of colonists. Our study, a combination of natural and manipulative experiment in a large-scale field setting, aims to improve

knowledge of the ecology of adding fire to fragmented landscapes.

Methods

Study area

Our study was conducted in Pinkawillinie Conservation Park (33° 05' 41.05" S, 135° 59' 57.75" E) and remnant native vegetation on linear sand dunes in the adjacent farmland in the northern Eyre Peninsula, South Australia (Fig. 1). The region has a semi-arid climate, with a mean annual rainfall of 265 mm. The low topographic relief comprises shallow soils that are mainly siliceous and calcareous sands (Blackburn and Wright 1989). The vegetation consists of mallee woodlands dominated by multi-stemmed eucalypts (predominantly *Eucalyptus costata* and *E. socialis*), often with shrubs (*Melaleuca uncinata*) and spinifex (*Triodia irritans*) (Robinson and Heard 1985). Remnants in farmland are subject to disturbances associated with cropping (weeds, pesticides, fertiliser) and livestock grazing, reducing shrub cover and plant species richness (Schutz and Driscoll 2008; Driscoll

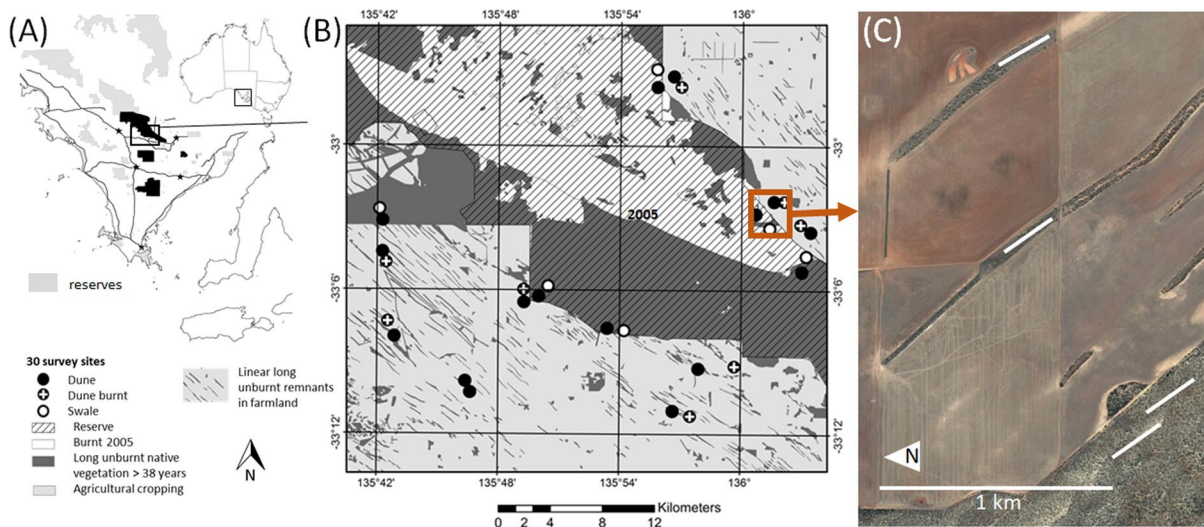


Fig. 1 Study area showing **A** the study region on the semi-arid Eyre Peninsula in southern Australia, **B** the layout of sites in Pinkawillinie Conservation Park and **C** the layout of transects in one of the northern blocks. The light grey shading within **B** indicates the recently burnt woodland (i.e. burnt in 2005); the dark-shaded area within the reserve border is long unburnt

woodland. Reptiles were surveyed along a total of 30 transect sites that were paired and established in dunes and swales in the reserve and in remnant dunes in the cropping matrix (**C**). Surveys took place in 2010 before experimental burns and in the subsequent 2 years

et al. 2012b), but there are no fires recorded in recent history at these sites. A bushfire burnt the northern section of the park in 2005, 5 years before our surveys began (Fig. 1).

Survey design

Our survey design consisted of three blocks in the south and three in the north of the study area (Fig. 1). Each southern block included six sites; a dune and swale (inter-dune) site within the conservation park in an area that had no fire records within the past 38 years, two dunes in farmland close to the conservation park (0.05–2.7 km), and two dunes far from the conservation park in farmland (5.5–8.8 km, details in Online Resource 1 in supporting information). Each northern block included a dune and swale site in the conservation park in an area burnt 5 years previously, and two dune sites close to the conservation park in farmland (0.18–1.6 km). All dune-top remnants embedded in farmland were long-unburnt. Patch area did not differ among treatments (ANOVA, with patch area of sites embedded in farmland as response, and a six-level factor delimiting each treatment; $F_{5,12} = 1.26$, $P = 0.34$).

One of the two dunes at each level of isolation (near, far) in each block was selected by landholders

for an experimental burn, with one exception where the landholder did not give permission to burn a far site (Fig. 1). After surveys in early 2010, northern sites were burnt on 26th March 2010 and southern sites the next day. Fires were set under mild conditions with winds < 10 km/h, humidity 40–80%, and with low fuel loads (~2 tonnes/ha). The fires rarely entered the tree canopy and often did not carry unassisted across the ground due to an absence of fuel (Fig. 2). The fires were therefore atypical of natural fires in mallee ecosystems which tend to be large and consume the entire canopy. Dunes within conservation parks were not burnt due to risks of fire escaping into the park.

We surveyed each site for two 14-day trapping sessions (i.e., 28 nights total) in each of three consecutive summers (2010, 2011 and 2012). We sampled dunes in the conservation park and adjacent farmland, but swales were only in the reserve. All swale habitat was cleared for cropping in farmland and few reptiles use cleared land (Driscoll 2004; Schutz and Driscoll 2008). We sampled swales to understand the pool of nearby species that could potentially colonise dunes in farmland.

At each of the 30 sites, we surveyed reptiles using ten 20 L pitfall traps spaced 25 m apart, each with a 30 cm high × 10 m long, plastic drift fence, placed at

Fig. 2 Planned fires in dune-top linear remnants burnt most of the ground cover and rarely burnt the canopy. Photo credits: Joe Tilley, JL (top, right)



alternate right angles. We also placed a 15 cm long half PVC pipe in the bottom of each bucket with a 15×20 cm wood block to act as a shelter from heat and that could float in case of rain. We uniquely marked trapped animals using implanted elastomer so that we could omit recaptures from the counts. We released marked animals at the point of capture the following day. Trapped individuals were identified to species, except for *Pogona* species, which have unresolved taxonomy in our study area (Driscoll and Henderson 2008).

Traits

We used published literature and personal observations to assign traits relevant to reptile fire responses (Smith et al. 2013; Meiri 2018) to each species. These traits included body size (small—< 66 mm snout-vent length; medium—66–140 mm; large—> 190 mm), reproduction (oviparous, viviparous), habitat-position (above-ground—semi-arboreal or living on the ground or in leaf litter; below-ground—species that use burrows or are fossorial), diet (carnivorous; insectivorous; omnivorous), and activity period (diurnal; nocturnal (includes crepuscular); both day and night active) (Online Resource 2). We limited traits to those for which we had data for all species. We calculated species richness and total abundance for each trait category to use as response variables.

Analysis

We combined data from the two trapping sessions within each year. We used the secondary candidate set strategy to identify the most plausible models (Morin et al. 2020), based on generalised linear and generalised linear mixed models (Bolker et al. 2009). To identify random effects models to carry through to the second phase of analysis, we fitted all additive and nested combinations of site, pair and block to each response variable and retained models within six Akaike's Information Criterion for small samples (AICc) of the best model (Burnham and Anderson 2002).

Fixed effects in the models included combinations of variables that delimited our study design (Fig. 1) plus appropriate two and three-way interactions. We included topographic position (dune vs swale) in our analysis to account for that source of variation, rather

than to explore its specific effects. Main effects were: Region (South—where the conservation park was long unburnt, North—conservation park recently burnt); Tenure (Park, Farm); Topographic Position (Dune, Swale); Isolation (Close, Far); Burn (Unburnt, Burnt); Year1 (2010 before burn treatments, 2011–2012 after burns implemented), and; Year (2010, 2011, 2012, a variable fitted as a more detailed alternative to Year1). Interactions included: Tenure:Region; Region:Burn; Year1:Burn; Year1:Far; Year1:Region; Year1:Tenure; Year1:Region:Burn; Year1:Region:Tenure. We included models with all possible combinations of the interactions. Models including Year1 were repeated but with Year instead. Although we intended to examine Year:Far:Burn interactions, we did not because one of three planned far-burnt sites was not burnt. We did not use Year1 and Year in the same models (variables we refer to as 'time') and when both Year1 and Year (or interactions) were among the best models, we present results for Year to avoid repetition. We retained models with $\Delta AICc \leq 6$ for the second phase of analysis.

In the second phase of analysis, we explored all possible combinations of the best random effects models and the best fixed effects models in mixed-effects models. We ranked these using AICc, then averaged estimates over models with $\Delta AICc \leq 2$. We plotted results for variables with $P \leq 0.05$.

To avoid over-fitting, we limited the models fitted to each response to those where the number of parameters in the model was less than one third of the number of non-zero response values. This resulted in the 30 most complex models being dropped for viviparous reptiles, and the three most complex models being dropped for carnivorous reptiles. By only interpreting results with $P < 0.05$, the set of parameters excluded from interpretation included those that could be classified as uninformative (Leroux 2019). We converted responses with five or fewer values > 2 or with < 10 unique values to presence/absence data and analysed assuming a binomial distribution of errors with a logit link function (only carnivorous reptile abundance met this criteria). We analysed all other responses assuming Poisson distribution of errors with a log-link function. We assessed over-dispersion using a Pearson Chi-squared test of Pearson residuals divided by residual degrees of freedom (Maindonald and Braun 2010). No models had significant evidence of over-dispersion. We conducted

analyses in R (R Core Team 2021) using libraries lme4 (glmer) (Bates et al. 2015); bbmle (AICcTab) (Bolker and R Development Core Team 2020), rsq (rsq) (Zhang 2021), effects (effect), car (Anova) (Fox and Weisberg 2019), and MuMin (model.avg, AICc) (Barton 2020).

The package MuMin has a predict function that does not average over levels of categorical variables, and therefore requires arbitrary choices about which level of categorical variables to include in predictions for plotting results. Instead, we use the effects package to obtain predicted values and confidence limits from the best model in which a particular variable occurred. The variables plotted were nevertheless limited to those with $P < 0.05$ based on model averaging. The estimates were in the same direction and within 10% of one another (mean ratio of model-averaged vs best model estimates = 0.99, SD = 0.07), with five exceptions (Online Resource 3).

Results

Overall, we recorded 2200 reptiles from 42 species in seven families: geckoes (822, 3 species); skinks (637 individuals, 21 species); dragons (512 individuals, 6 species); blind snakes (111 individuals, 2 species);

elapid snakes (71 individuals, 5 species); goannas (33 individuals, 1 species) and legless lizards (14 individuals, 4 species). In 2010, 2011 and 2012, we recorded 685, 707 and 808 reptiles respectively.

Aim 1: fire-time interactions

Four reptile response variables had fire-time interactions, representing effects of our experimental burns in remnant patches (see Online Resource 4 for ranked models, and Online Resource 5 for model averaged estimates). Abundance of viviparous species declined after fire (Fig. 3A). The abundance of small reptiles and those that live on or above the ground showed a substantial increase over time in unburnt sites, but this trend was not observed at burnt sites (Fig. 3B, C). There was weak evidence that abundance was beginning to recover by the 3rd year (Fig. 3B, C). Nocturnal reptiles had very low abundance on sites planned for burning in 2010 in the northern blocks, and abundance increased on those sites after they were burnt (Fig. 3D).

Aim 2: patch isolation

On far sites, there were fewer species overall and fewer species of three trait groups (small,

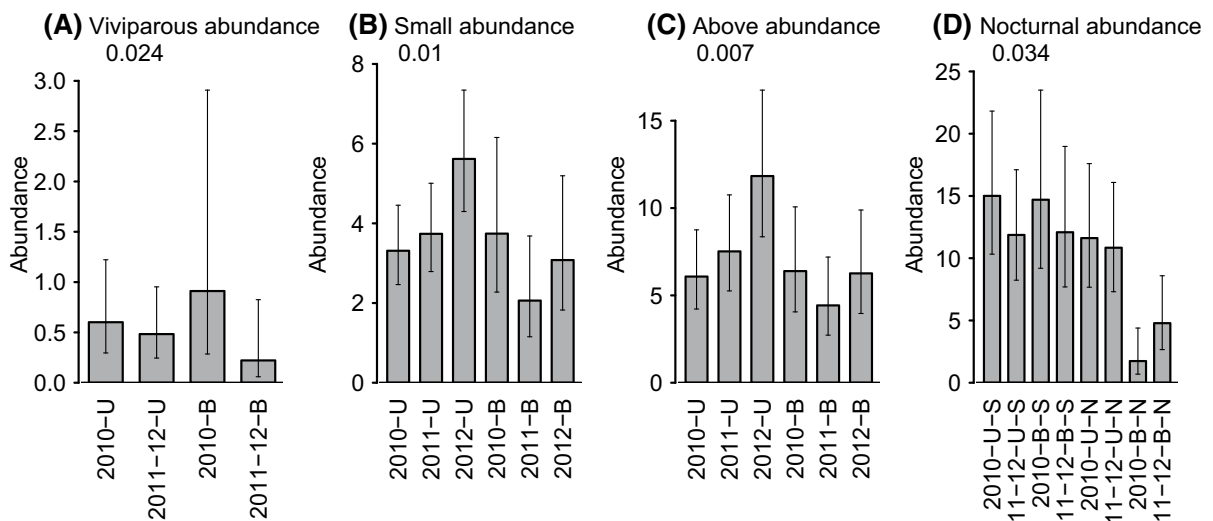


Fig. 3 Predicted mean abundance of trait groups for which an interaction of burn and year was in the best model. Headers for each panel indicate the dependent variable and P values based on model averaged estimates. Error bars indicate 95%

confidence intervals. *U* unburnt, *B* burnt, *SS* South, *NN* North, *11–12* 2011–2012. Experimental burns took place after the 2010 surveys

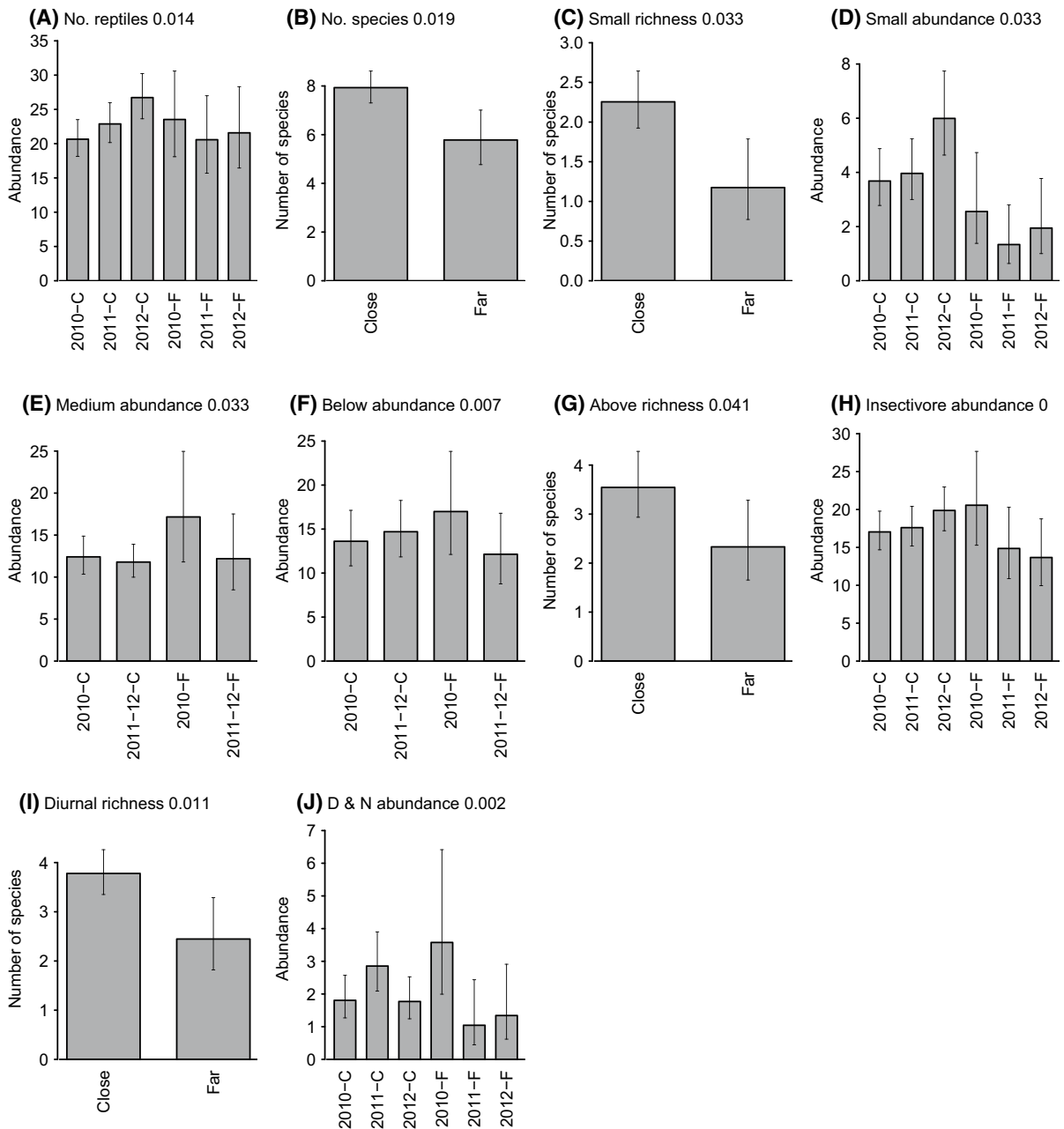


Fig. 4 Predicted mean abundance and mean species richness of trait groups for which patch isolation (close vs far) was in the best model. Headers for each panel indicate the depend-

ent variable and P values. Error bars indicate 95% confidence intervals. *D & N* reptiles active in both day and night

above-ground and diurnal; Fig. 4B, C, G, I). Increasing trends in abundance of all reptiles (Fig. 4A) and small species (Fig. 4D) in close sites contrasted with abundance in far sites which did not show increases. Four other trait groups showed

patterns of decline in far sites over time (medium, below-ground, insectivores, day and night active, Fig. 4E, F, H, J), but with high initial abundance in far sites and weak or fluctuating changes over time in close sites.

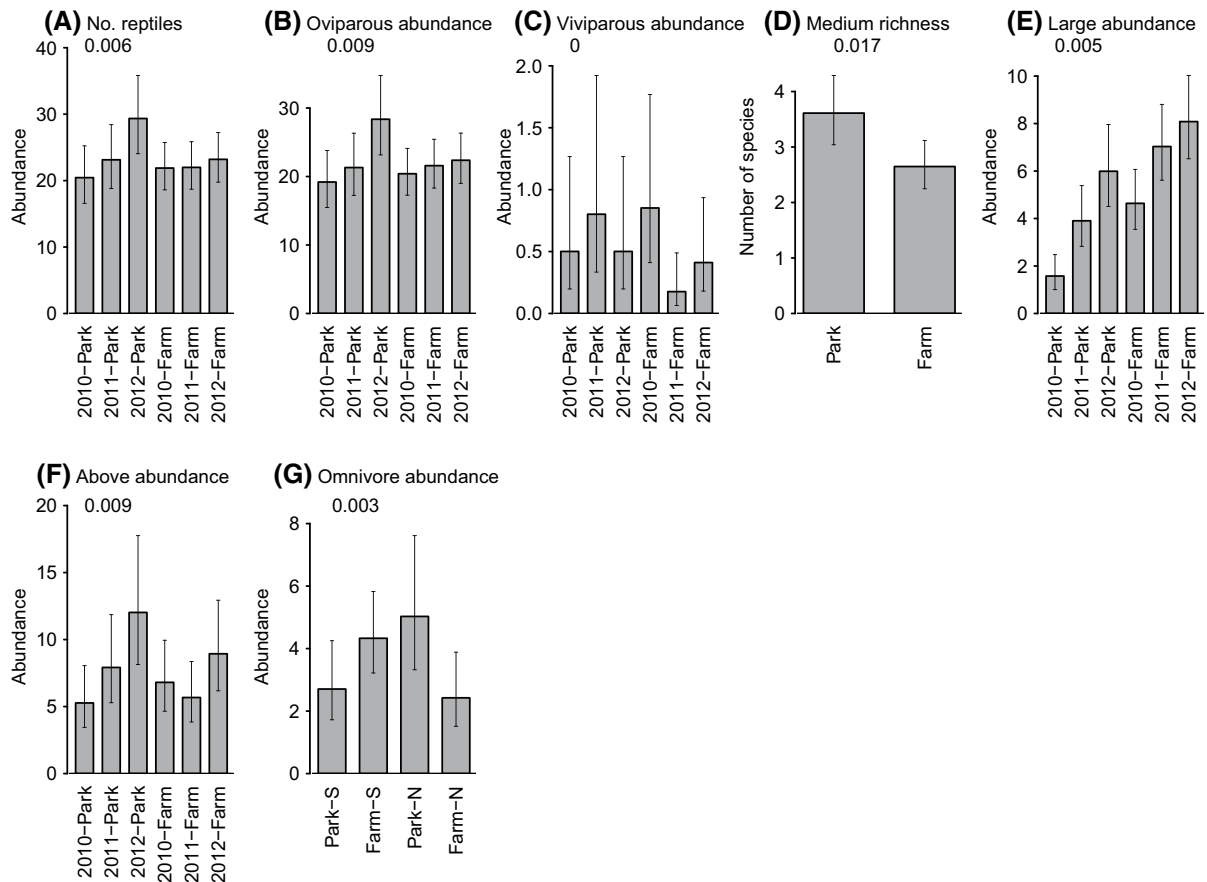


Fig. 5 Predicted mean abundance and mean species richness of trait groups for which tenure (conservation park vs farm) was in the best model, or in interaction with year or region

(north, south). Headers for each panel indicate the dependent variable and P values. Error bars indicate 95% confidence intervals. *SS*South, *NN*North

Aim 3: habitat conversion; conservation park vs farms

Abundance of all reptiles (Fig. 5A), oviparous and on/above-ground reptiles (Fig. 5B, F) increased over time in the conservation park but showed weaker responses in farm remnants. Abundance of viviparous species was higher in the park than in farmland in 2011 due to a marked drop in numbers on farmland and high average numbers in the park (Fig. 5C). There were fewer species of medium-sized reptiles (Fig. 5D) in farm remnants. Large species had higher abundance in farm remnants compared with the conservation park, with increasing numbers over time (Fig. 5E). Omnivorous reptiles had lower abundance in farms than parks, but only in the northern region, with the opposite pattern in the south (Fig. 5G).

Aim 4: proximity to recently burnt or long unburnt conservation park

Abundance in the northern region tended to be lower in the 1st year than in the south (except for diurnal species), then increased over time, in some cases becoming more abundant than in the south. This general trend was seen for total number of reptiles and oviparous, large, below, on or above, omnivorous and diurnal reptiles (Fig. 6A, B, E–I). Similar trends were shown by medium and day and night active species, but the latter had highest abundance in 2011, and both showed declines in the south (Fig. 6D, J). Small reptiles were consistently less abundant in the north (Fig. 6C).

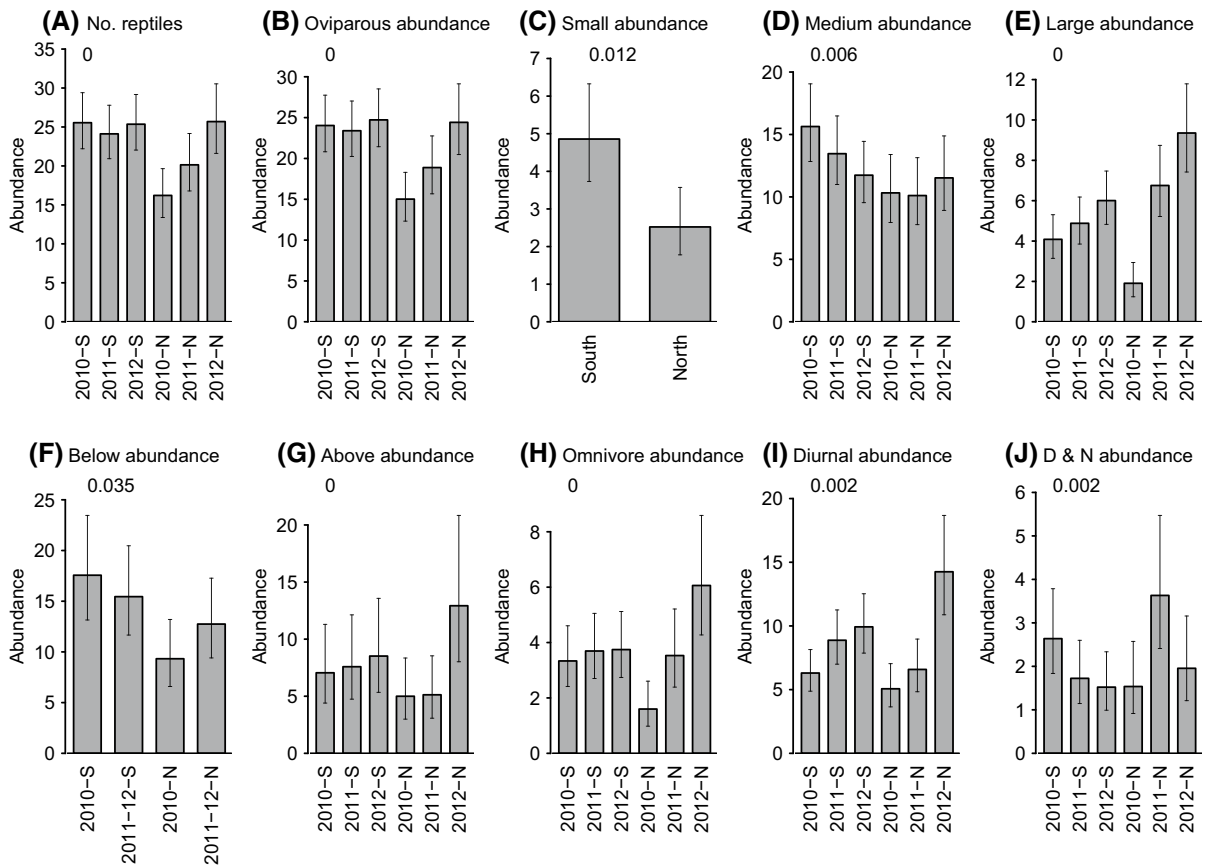


Fig. 6 Predicted mean abundance of trait groups for which region (North (N) vs South (S)) was in the best model, or in interaction with year. Headers for each panel indicate the dependent variable and P values. Error bars indicate 95% confidence intervals

Main effects of burn, time, and topographic position

We did not expect to see main effects of burn (without interaction with time) in our results because the burns took place after the 1st year of data were collected. These main effects indicate our burnt sites were different throughout the study, including before the burn treatment was implemented. Burnt sites had fewer species of small, above-ground, insectivorous and diurnal species. Burn sites also had lower abundance of large reptiles, and in the north burnt sites, lower abundance of all reptiles, oviparous, medium, below ground, and insectivorous species (Online Resource 6).

Over the 3 years of the study, there was an increase in reptile species richness, richness of nine trait groups (oviparous, small, large, below-ground, above-ground, insectivorous, carnivorous, diurnal,

and nocturnal) and occurrence of carnivores (Online Resource 7). Four trait groups responded to topographic position, with dunes supporting higher abundance of medium-sized, below-ground, and nocturnal reptiles but fewer large-bodied reptiles than in swales (Online Resource 8).

Discussion

Our study confirms the strong negative effects that habitat loss, fragmentation and patch isolation have on reptiles (Keinath et al. 2017). By examining traits, we can provide some guidance about reptiles that may be most vulnerable or resilient to habitat modification, as well as insight into the possible mechanisms for these responses. Experimental fires in general were not beneficial within the timeframe of our study,

and there were some detrimental effects. However, in comparing the southern region that had long-unburnt habitat with the northern region that had recently burnt habitat, we reveal patterns that suggest fire in reserves could have landscape-scale effects into the nearby farmland remnants.

Fire

Fire in remnant vegetation was associated with declines in viviparous species, and reductions in small and above-ground species at a time when these groups were increasing on unburnt sites. That species living on or above ground, rather than those living underground, were sensitive to fire is expected: species living in the strata of the environment that are disturbed should be most sensitive to the disturbance (Driscoll and Weir 2005; Neilly et al. 2018). Given the canopy did not burn in our experimental fires, the observed impact on above-ground species may be smaller than would occur in a wildfire. Body size rarely affects reptile responses to disturbance (Wang et al. 2009; Martin and Murray 2011; Doherty et al. 2020; Hu et al. 2020). However, small species can be vulnerable to extinction if they experience rapid drops in population growth rates (Williams et al. 2021b), potentially explaining reduced abundance after fire in small but not larger species. Finally, although oviparous reptiles are expected to be more vulnerable to disturbance because incubation temperatures cannot be controlled and nest sites can be lost (Doherty et al. 2020), it was viviparous species that declined after our experimental burns. We suggest that some of the oviparous species had eggs below ground at the time of our fires (e.g. Smith et al. 2012), reducing the impact of fire on reproduction. Further, 65% of oviparous individuals were burrowers or fossorial whereas 47% of viviparous individuals were, meaning more viviparous individuals may have been directly exposed to fire.

Low abundance of nocturnal reptiles before experimental burning suggests that factors other than fire dominated abundance of these groups, driving low numbers in the north in the 1st year. However, we expected that recovery after fire in the north would be aided by proximity to recently burnt habitat. If this hypothesis was correct, we would expect species that increased in abundance on burnt remnants in the north to also have low abundance on unburnt

remnants, and high source populations in the reserve in the north. However, there were no data for individual species that were consistent with this expectation (data not shown), so this colonisation hypothesis is unlikely. We offer a tentative explanation in the final section of this discussion.

Most trait groups in our study did not respond to experimental burning. These muted fire responses could be caused by variation among the species within trait groups (Santos et al. 2014). Of the 42 species we trapped, 16 species have a published fire response (Driscoll and Henderson 2008; Nimmo et al. 2012; Driscoll et al. 2012a; Smith et al. 2013). Most of our trait groups included both early and late successional species (e.g. insectivores had five early and eight late successional species; diurnal had five early and four late, above-ground had two early and five late). By taking a focus on single trait groups, fire responses at the trait level could be obscured because species with the same traits nevertheless have different fire responses. In future, considering interactions among traits or trait combinations could be a more insightful approach to predicting fire responses. However, large datasets with many species are required, making that a challenging approach (Driscoll et al. 2020).

Sites that were planned for burning had differences from unburnt patches before we burnt them. This was most likely related to initial site selection where farmers gave permission to burn one of two remnants in a non-random way, often selecting the most degraded of two remnants for burning. Our results for burning by year interactions therefore have the caveat that they represent responses of reptiles on degraded remnants. Further work is needed to understand if reptiles show a different response if remnants in good condition are burnt.

Patch isolation

The most isolated sites had lower species richness, lower richness for three trait groups (diurnal, small, above-ground) and lower abundance of small species. Reduced species richness in more isolated sites is predicted by island biogeography theory (MacArthur and Wilson 1967), metacommunity theories that invoke dispersal limitation (Leibold et al. 2004), and metapopulation theory applied to multiple species (Driscoll 2008). Small populations in remnant patches have a

substantial risk of extinction and where dispersal is limited so that recolonization is prevented, species can be permanently lost from the landscape (Hanski 1998). In our study system, this process was previously illustrated by the knob tailed gecko *Nephrurus stellatus*, which had high occurrence rates in patches within 300 m of occupied sites but very low occurrence in patches further than 700 m from occupied sites (Driscoll et al. 2012b). Further, distance-limited spill-over (Leibold et al. 2004; Lucey et al. 2014) from the conservation park could explain increasing abundance of small reptiles in close sites, but not far sites.

For the trait groups without significant effects of patch isolation on richness, we further examined average species richness in close and far sites. Almost all reptile trait groups had substantially lower average richness in far sites compared with close sites (Online Resource 9a). We suggest the lack of a significant effect in these trait groups could be due to limited statistical power. However, species that were omnivorous, medium in size or active both day and night had substantially smaller mean differences than other groups, so these groups may be more robust to patch isolation. Omnivores and species that can be active day or night are more flexible in their life strategies than other trait groups (Santos et al. 2014), potentially providing advantages in more isolated sites. Generalists typically do better in disturbed sites and have lower risk of extinction than specialist species (Bohm et al. 2016; Palmeirim et al. 2017a). One potential explanation for minimal decline in richness of medium-sized reptiles in isolated sites is predator release. Lion et al (2016) suggested the absence of key avian predators from small Atlantic Forest remnants may have contributed to higher reptile richness. In our study, predator release potentially counterbalances the otherwise negative effects of isolation.

Predator release could also explain why abundance of medium, below-ground, insectivorous and reptiles active in day and night had high abundance in far sites in the 1st year, then declined. The importance of predation in community organisation is expected to increase as resources increase, while the role of competition should decrease (Bohannon and Lenski 2000; Letnic et al. 2013). Rainfall, and thus resources, were very low prior to our study during the millennial drought (average rainfall 2002–2008 210 mm (range 174–251 mm), Buckleboo station, Australian Bureau

of Meteorology). However, in 2009, 2010 and 2011, rainfall at Buckleboo was 48%, 90% and 71% higher respectively than the drought average. With high rainfall after a period of drought, predation pressure may have increased in isolated sites over time. This hypothesis raises the suggestion that predators expand outwards from the reserve and close sites in high rainfall years, altering community composition in isolated sites.

Although we could not test for an interaction of burn with isolation, average numbers (Online Resource 9b) suggest that the burn in far sites did not cause substantial declines in medium, below-ground and day–night active reptiles. However, the low numbers of insectivores in far sites in 2011 and 2012 could be related to an interaction of burn and isolation, an alternative to the predator release hypothesis. In insectivores, the change over time was small on close sites, regardless of burn treatment, but on far sites, declines were twice as large on burnt (48% decline) compared with unburnt sites (25% decline, Online Resource 9b). Possibly insects were less abundant immediately after the fires in far sites, although, 4 years after fire, insect numbers can be as high or higher than in unburnt, unfragmented mallee (Teasdale et al. 2013).

Habitat conversion

Our comparison of conservation parks and farms highlight the overall effect of landscape conversion from natural vegetation to agriculture. Remnants in farmland experience a range of different conditions compared with conservation parks. Hansen et al. (2019) reported elevated attacks on reptile models by mammals and birds along remnant edges in Australian woodlands, while other studies have found higher predation risk in open areas (Bateman et al. 2017). Mallee remnants in farmland have more weeds (Davies et al. 2013), less native vegetation cover (Driscoll 2004; Schutz and Driscoll 2008), foundation plant species are less common (Bell et al. 2021) and are likely to experience a range of abiotic edge effects (Driscoll et al. 2013). These environmental differences suggest possible links with traits, enabling formulation of testable hypotheses. For example, these changes could make species living on or above ground more vulnerable to decline, rather than those living under-ground which could retreat to avoid

predators and inclement environmental conditions (Bruton et al. 2014).

Abundance in farmland frequently varied by year, implying more complex dynamics than attributable to correlates of land-conversion alone. Viviparous reptiles declined in the 2nd year on farms but rebounded in the 3rd year. In our parallel study on small mammals, house mice (*Mus musculus*) were 30% less abundant in parks than on farms and had very low abundance in 2011 (unpublished data). At the same time, the native predator *Ningaui yvonneae* was most abundant in 2011. Both species can kill reptiles. Temporal changes in the predator fauna, responding to changing resources with post-drought rainfall, could explain declines. Viviparous reptiles could be more vulnerable to the altered predation risks in 2011 than oviparous reptiles because a lower proportion live underground, and eggs of oviparous species may not be as vulnerable to predation by the relevant predator.

Only large species appeared to do better in the farmland. In some respects this is surprising; large species may be at higher risk of extinction due to smaller population sizes (Cardillo and Bromham 2001; Bohm et al. 2016) and other empirical research and meta-analyses have not found an effect of reptile body size on response to disturbance (Wang et al. 2009; Martin and Murray 2011; Doherty et al. 2020; Hu et al. 2020). However, a recent analysis of extinction-monitoring data suggests small species are more vulnerable to extinction, partly because they are prone to high variability in population growth rates (Williams et al. 2021b). Further, Palmeirim et al. (2017b) found that the lizards remaining on small, isolated islands in a hydro-electric dam in Brazil were large generalist species, which had higher dispersal and could eat a wider size-range of prey than small species. This could help explain the bias towards farmland for the large generalist agamid *Pogona* sp. (average abundance 10.1/site in farms, 8.5/site in parks), along with its ability to climb trees for refuge (Doherty et al. 2019). However, other large species commonly found on remnants in farmland included fossorial insectivorous snakes (*Simoselaps bertholdi*: 1.7/site farm, 0.3 park; *Ramphotyphlops bituberculatus*: 3.7 farm, 2.2 park) and a fossorial lizard-eating snake (*Parasuta spectabilis*: 0.7 farm, 0.4 park), all of which are nocturnal. This suggests a range of mechanisms could contribute to the success of large species, including combinations of traits that afford protection

in narrow remnants in farmland such as burrowing and nocturnal activity. Further, the success of large species, including predators like snakes, may contribute to lower species richness of medium-sized species in farmland.

The response of omnivores to habitat conversion depended on region, which is likely related to fire responses of the dominant omnivore species. Of the six omnivore species, 97% of records were for two species, both of which are early to mid-successional species (*Pogona* sp. and *Liopholis inornata*, Smith et al. 2013). This explains lower abundance in the long unburnt park in the south compared with the recently burnt park in the north, although high abundance on farm remnants in the south remains unexplained. Oviparous species did not increase in 2012 on farms but did in the conservation park, a surprising result given they appeared to be more robust to fires in remnants than viviparous species. Reptile vulnerability to disturbance can depend on the timing of egg laying relative to the timing of disturbance (Pike and Stiner 2007). Possibly eggs were vulnerable to disturbances at times other than when the fire took place, or to other disturbances, such as livestock trampling.

Proximity to recently burnt or long unburnt conservation park

Low initial abundance in the north in 2010 followed by substantial increases could be explained by an interaction of fire, dispersal, and drought. The conservation park in the north was burnt in a wildfire in 2005 during the millennial drought. We suggest that slow recovery from fire during the dry years and the coincidence of our surveys with higher rainfall could account for growing numbers in the North. Our general observation of increasing abundance over the 3 years for many trait groups (Online Resource 7) likely also relates to high rainfall after the drought, similar to boom and bust patterns seen in desert mammals (Bennison et al. 2018). With evidence that the distance to conservation parks can affect some of the reptiles in our study region (this study and Williams et al. 2012), it is plausible that the combined fire and drought had spill-over effects on the adjacent remnants. We suggest that when abundance was reduced in the reserve due to fire and maintained at low levels during the drought, abundance and richness in adjacent remnants declined due to reduced immigration

from the reserve. This spill-over part of the hypothesis is needed because we did not detect any significant three-way interactions of year, tenure, and region, which implies that both the remnants and reserves in the north followed similar trajectories. We emphasise this is a hypothesis for testing and acknowledge that our design does not allow us to exclude unknown and unobserved confounding factors between the north and south such as historical disturbance legacies (Gonzalez-Trujillo et al. 2021).

Combining this fire-dispersal-drought hypothesis with the acknowledgement that burnt sites were generally those in worst ecological condition enables a potential explanation for the region-year-burn interaction shown by nocturnal reptiles (Fig. 3D). It is plausible that it took the combined effects of reduced immigration from reserves due to fire and drought, and reduced patch-level success in the degraded sites to reduce abundance of nocturnal reptiles on sites selected for burning in the north.

Conclusion

Habitat loss and fragmentation are severe threats to biodiversity, and the threat escalates as intensifying land use increases the contrast between matrix and remnant (Chase et al. 2020). Our findings are consistent with this global trend; at least half of our reptile trait groups were less abundant or had fewer species in fragmented landscapes and in more isolated sites. The exceptions included trait groups with flexible life histories (omnivores and reptiles active day and night) suggesting that generalist species are most adept at surviving in isolated remnants in highly modified landscapes. Conversely, more specialised species are most vulnerable to decline (Watling and Donnelly 2007; Bohm et al. 2016).

Reptile declines globally have been associated with a broad range of traits including: small body size, large body size, habitat specialisation, ovipary, being diurnal; narrow trophic range; vertebrate prey; small geographic range; small clutch size, low population density; weak dispersal and low heat tolerance (Driscoll 2004; Watling and Donnelly 2007; Wang et al. 2009; Carvajal-Cogollo and Urbina-Cardona 2015; Bohm et al. 2016; Todd et al. 2017; Palmeirim et al. 2017a; Nowakowski et al. 2018; Doherty et al. 2020; Hu et al. 2020; Williams et al. 2021b). With this range of traits and responses, the approach we and most other studies take, correlating abundance or richness with disturbance, are revealed as useful first steps. However, these relationships are destined to remain speculative until mechanisms of vulnerability can be identified, such as by using more detailed demographic, behavioural and experimental research (e.g. Ferreira et al. 2016; Alvarez-Ruiz et al. 2021), including exploring effects of multiple correlated traits. To this end, we have summarised the hypotheses raised in our study to explain links between traits and landscape features as a guide to future research that can move beyond correlation and develop a mechanistic understanding (Table 1).

Our multifaceted survey design over multiple years suggests an equally multifaceted sequence of effects that influence reptile communities and highlights the role of non-stationary phenomena in driving spatial and temporal variation in ecological responses (Rolinson et al. 2021). We have suggested that the relatively static aspects of the landscape; habitat loss, fragmentation, and patch isolation, interact with natural fires, restoration burns and longer-term climatic trends. Reptile responses to these common landscape structures and disturbances can be mediated by traits, and detecting these relationships provide both a means of generalising the response and a testable guide to potential mechanisms.

Table 1 Summary of responses for trait groups to four landscape features: (1) experimental fire in remnants; (2) isolated remnants; (3) remnants in farms compared with conservation parks; (4) landscapes with recent bushfire in the conservation park compared with landscapes with long-unburnt conservation park (early TSF park)

Trait	Trait group	1. Fire added	2. Isolated remnants	3. Habitat conversion	4. Early TSF park	Hypotheses (related to the four numbered landscape features, i.e. 1 = hypothesis to explain response to fire added)
Habitat position	On or above ground	Decline abundance	Decline richness	Lower abundance over time	Low initial abundance then increase	<ol style="list-style-type: none"> 1. Fire damages the part of the habitat they live in 2. Metapopulation dynamics: extinction exceeds recolonisation 3. Less buffered from environmental correlates of land-clearing 4. Fire reduced abundance in park, low numbers maintained by drought, increase with high rainfall, spill-over to remnants
	Underground		Decline from high numbers		Low initial abundance then increase	<ol style="list-style-type: none"> 2. Low predation in drought years, predators expand to isolated sites in high rainfall years, reducing abundance 4. As for On or above-ground

Table 1 (continued)

Trait	Trait group	1. Fire added	2. Isolated remnants	3. Habitat conversion	4. Early TSF park	Hypotheses (related to the four numbered landscape features, i.e. 1 = hypothesis to explain response to fire added)
Reproduction	Oviparous			Lower abundance over time	Low initial abundance then increase	<ol style="list-style-type: none"> 3. In remnants, eggs vulnerable to disturbance or thermal risks unrelated to fire 4. As for On or above-ground
	Viviparous	Decline abundance		Lower abundance in 2011		<ol style="list-style-type: none"> 1. More sensitive to fire disturbance without underground eggs, and > half of individuals live above-ground 3. Increase in predation risk in 2011, possibly small mammalian predators, linked to changes in post-drought resources
Activity period	Nocturnal	Increase abundance in N				<ol style="list-style-type: none"> 1. Interaction of fire, dispersal, drought, and initial condition of burnt sites
	Diurnal		Decline richness		Low initial abundance then increase	<ol style="list-style-type: none"> 2. As for On or above-ground 4. As for On or above-ground
	Both		No decline richness* Decline from high numbers		Low initial abundance then increase in 2011	<ol style="list-style-type: none"> 2. Flexibility by being generalist 2. As for underground 4. Similar to On or above-ground, but with some additional mechanism reducing numbers in 2012

Table 1 (continued)

Trait	Trait group	1. Fire added	2. Isolated remnants	3. Habitat conversion	4. Early TSF park	Hypotheses (related to the four numbered landscape features, i.e. 1 = hypothesis to explain response to fire added)
Size	Small	Decline abundance	Decline richness No abundance increase		Low abundance	<ol style="list-style-type: none"> 1. High risk of large fluctuations in population size 2. As for On or above-ground 2. Distance-limited spill-over 4. Similar to On or above-ground, but with some additional mechanism preventing increase over time
	Medium		No decline richness* Decline from high numbers	Decline richness	Low initial abundance	<ol style="list-style-type: none"> 2. Predator release in most isolated sites countering isolation 2. As for underground 3. High predation of medium-sized reptiles by larger species in farmland 4. Similar to On or above-ground, but with some additional mechanism applying downwards pressure on abundance
	Large			Higher abundance	Low initial abundance then increase	<ol style="list-style-type: none"> 3. Generalist feeding habits, more stable population demography than small species, fossorial and nocturnal, conferring protection from disturbance, diurnal predators and edge effects 4. As for On or above-ground
Food	Insectivore		Decline from high numbers			<ol style="list-style-type: none"> 2. Interaction of fire and patch isolation

Table 1 (continued)

Trait	1. Fire added	2. Isolated remnants	3. Habitat conversion	4. Early TSF park	Hypotheses (related to the four numbered landscape features, i.e. 1 = hypothesis to explain response to fire added)
Carnivore					Rare and with no significant effects most likely due to limited data
Omnivore		No decline richness*	Abundance lower N + higher S	Low initial abundance then increase	2. Flexibility by being generalist 3. Early successional species responding to time since fire 4. As for On or above-ground

Hypotheses raised to explain responses are listed except the hypothesis that trait groups that did not respond to burning were attributable to having both early and late successional species within the group. Blank spaces in the four landscape-feature columns indicate no significant effects

*These taxa had no significant effect of isolation and mean values suggested no substantive difference

Acknowledgements We thank the many volunteers who assisted with field work, particularly Kevin Mayes. We thank Joe Tilley from the South Australian Department of Environment and Natural Resources for implementing the burns. Sam Banks and Saul Cunningham provided valuable feedback on an earlier draft and Wade Blanchard provided statistical advice. Thanks to the landholders for access to properties and accommodation.

Author contributions JL: conception, field work, data preparation, contributions to manuscript preparation. CS: critical revisions of manuscript. DD: conception, analysis, re-analysis, writing, corresponding.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Australian Research Council LP0667796.

Data availability Data available from DRO <http://dro.deakin.edu.au>.

Code availability Not relevant.

Declarations

Conflict of interest Not relevant.

Ethical approval Scientific permit K25737-1 and animal ethics permits 26/2009-M1 (Government of South Australia) and S.RE.09.09 (Australian National University).

Consent to participate Not relevant.

Consent for publication Not relevant.

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