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Effects of time since fire on frog occurrence are altered by isolation, vegetation and fire frequency gradients

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Abstract

Aim: To quantify how frogs in terrestrial environments respond to recurrent fire, and to what extent this is mediated by isolation from breeding sites or vegetation structure.

Location: Jervis Bay, south-eastern Australia.

Methods: We used data from 8 years of pitfall trapping, collected via a random stratified design, to quantify frog occurrence at 110 locations. We then used an information theoretic approach to compare 13 logistic generalized linear mixed models, each of which related frog occurrence to a distinct combination of additive and interactive effects of fire, vegetation structure and proximity to known breeding sites.

Results: For all four species, the effect of one or more fire variables on frog occurrence depended on both the density of breeding sites in the surrounding area, or on the vegetation structure at the trap locality. A classic "fire averse" response of initial declines followed by post-fire recovery did occur, but only in frequently burned, low-quality terrestrial habitats (i.e., heath vegetation for *Uperoleia tyleri*, or locations with few available breeding sites for the remaining species), or in some cases, when suitable habitats were infrequently burned. However, a "fire-dependent" result of negative effects of time since fire was also evident for some species and contexts.

Main conclusions: The effect of fire on frog occurrence can be mediated by environment. Therefore, a single species could be identified as either "fire dependent" or "fire averse" depending on the combination of isolation, vegetation types and fire histories in the study region. Failure to account for the context specificity of fire response curves could lead to incomplete conclusions regarding the effect of time since fire—or the cumulative impacts of multiple fires—on faunal assemblages.

KEYWORDS
amphibians, disturbance, fire regime, pyrodiversity

1 | INTRODUCTION

Fire is a globally significant form of ecological disturbance (Bowman et al., 2009), and the frequency, intensity and spatial distribution of wildfire are expected to shift in coming years (Barbero et al., 2015; Moritz et al., 2012). However, scientists' capacity to predict the

impacts of altered fire regimes on ecosystems is constrained by the variety of effects that fire can have on plant and animal populations. For example, different animal taxa often show variable—or even opposite—responses to time since fire (Barton et al., 2014; Driscoll & Henderson, 2008; Smith et al., 2013; Watson et al., 2012). Further, while time elapsed since the last fire in an environment is a strong

predictor of species abundance in many instances (Haslem et al., 2016; Kelly et al., 2011), some species also respond to other aspects of the fire regime, such as the frequency of past fires (Lindenmayer et al., 2008a; Lindenmayer, Blanchard, et al., 2016). Finally, the effects of fire on biota can vary markedly between locations with distinct vegetation, climate or topography (Nimmo et al., 2014). Given this enormous diversity of fire responses, a critical question for ecology is whether the effects of fire on faunal populations are too idiosyncratic to be reliably predicted, or conversely, whether there are unifying principles that drive the diversity of fire responses observed in nature (Kelly & Brotons, 2017; Pulsford et al., 2016; Shackelford et al., 2017).

One potential explanation for the large diversity of animal responses to fire is that species response trajectories could be mediated by other variables. For example, the habitat accommodation model (Fox, 1982) argues that responses to time since fire are mediated by changes in habitat suitability between seral stages (Swan et al., 2015). Similarly, the effect of fire on biota can be altered by the presence of specific functional groups, such as grazers (Foster et al., 2015) or carnivores (Doherty et al., 2015). Finally, succession trajectories can vary depending on the history of fire events at that location prior to the most recent fire (Haslem et al., 2016). Consequently, interactions among different components of the ecosystem, or of the fire regime, are known to alter patterns of ecological succession; but the strength and nature of these interactions have yet to be studied for many taxa and ecosystems (Driscoll et al., 2010).

In this paper, we use data from an 8-year study of the terrestrial distributions of frogs to answer the question "Does the post-fire trajectory in frog occurrence vary depending on environmental context?" We investigated this question by fitting logistic mixed models to frog capture data, and testing for interactive effects of time since fire with vegetation structure, the number of previous fires and the density of nearby breeding sites for each species. Amphibians are an important target for investigation because they are under-represented in fire ecology research relative to other vertebrate classes (Pastro et al., 2014), are highly susceptible to disturbance impacts during the terrestrial stages of their life cycle (Harper et al., 2008) and are among the most abundant terrestrial vertebrates in some ecosystems (Burton & Likens, 1975). Frogs are also the most geographically widespread order of amphibians (Duellman, 1999), but the vast majority of frog research focusses on aquatic breeding habitats, leaving considerable gaps in knowledge of their terrestrial habitat use and responses to disturbance (see Hossack et al., 2013a, 2013b). Consequently, our study has the combined benefits of providing an empirical assessment of a body of ecological theory from which amphibians have been largely absent, and of generating new insights into the habitat requirements of species from a globally threatened vertebrate order (Alroy, 2015).

Although our research question is conceptually well supported in the fire ecology literature (see Driscoll et al., 2010; Foster et al., 2015; Haslem et al., 2016), few previous studies have investigated the context dependence of fire effects in frogs, meaning that it was difficult to predict exactly what effects we might expect to observe during our study. Previous research in forest ecosystems characterized by long interfire intervals showed generally negative associations between frog occurrence and time since fire (Hossack et al., 2013a), a finding almost exactly opposite to those of Schurbon and Fauth (2003), who found positive frog responses to time since fire in a long-leaf pine ecosystem subject to frequent fire. Taken together, these studies suggest that frog responses to a fire may be shaped by either the frequency of fire in the ecosystem, or vegetation structure, or both. However, frog breeding sites can act as refugia from fire (Pilliod et al., 2003), meaning that isolation from breeding sites may further influence frog responses to fire (see also Shackelford et al., 2017). Perhaps reflecting this complexity, we are unaware of research that investigates the effect of the interaction between these variables (isolation, time since fire, fire frequency and vegetation structure) on frogs in a single ecosystem. Our study region provides an ideal context to investigate this knowledge gap because it is characterized by a complex combination of vegetation types and fire mosaics (Lindenmayer, Blanchard, et al., 2016), and because previous work has identified diverse amphibian responses to fire in aquatic breeding habitats (Westgate et al., 2012a).

2 | METHODS

2.1 | Study area and data collection

Our study area was Booderee National Park, on the south-east coast of Australia (Figure 1). This area contains a variety of aquatic habitat types used by frogs, including creeks, pools and lakes (Roe & Georges, 2007), as well as a range of vegetation types and fire histories (Barton et al., 2014; Lindenmayer, Candy, et al., 2016). Booderee National Park supports at least 12 frog species (Westgate et al., 2012a), including specialists that require breeding habitats in specific vegetation types (i.e., forests or heaths; Penman & Brassil, 2010). The frog species that we study (members of the families Myobatrachidae and Limnodynastidae; Cogger, 2014) require open water for breeding, but differ in the extent and nature of their terrestrial habitat use. Several are obligate wetland-dependent species that display migratory movements (e.g., *Limnodynastes* spp. and *Uperoleia tyleri*; Westgate et al., 2012b), while others are predominantly terrestrial species that
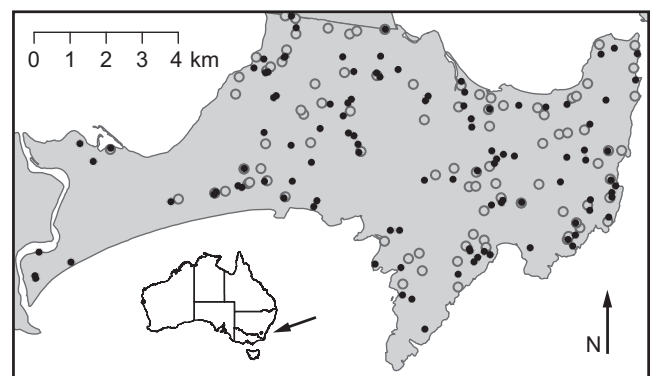

FIGURE 1 Map of the study area. Filled circles show pitfall trap locations, while open circles show sites investigated for calling male frogs via aural survey. Inset shows location of the study region on a map of Australia

utilize ephemeral water bodies for breeding (*Pseudophryne bibronii* and *Heleioporus australiacus*; Penman & Brassil, 2010). Finally, *Crinia signifera* is a generalist species that breeds in any available water source (Lauck, 2005).

We quantified frog occurrence in terrestrial areas using pitfall traps, which we established at locations selected using a stratified random approach. First, we stratified the landscape according to vegetation type (following classifications in Taws, 1997) and by fire history. After removing from consideration any patches that were not large enough to contain a 100-m transect, we randomly selected 110 sites that represented each of 10 vegetation and four fire history classes. Each trap site consisted of three 20-m drift fences, 20 m apart, with a 300-mm-diameter bucket at each end.

We ran our first trapping session in May and June 2003, which was followed in December 2003 by a large wildfire that burned approximately 50% of the park (Lindenmayer et al., 2008b). We evaluated the effects of this fire on fauna by running a second trapping session between February and April 2004, and again every Spring or Summer (October–February) from November 2004 to February 2010. Our dataset also includes a small number of observations from incidental trapping events that occurred outside of these months (16 observations in March, five in August, five in September). Each trapping session involved opening all traps ($n = 6–7$) at each site for 3–4 consecutive nights. We attempted to survey all sites in each trapping period (i.e., once per year) and accomplished this goal for 52 sites (47%), while a further 54 sites were surveyed in five or more years (totalling 96% of sites). For this analysis, we grouped data from all consecutive nights at a single location as our units of observation ($n = 944$). Using this measure, each site was visited an average of 8.6 times (range = 2–12), corresponding to a mean survey effort of 156 trap nights per site (8.6 visits by three nights with six traps). The average interval between visits to a single site was 308 days, although the same site was resurveyed within 60 days on 45 occasions (i.e., 5% of all surveys).

2.2 | Predictor variables

We calculated two aspects of the fire regime—the time since the most recent fire, and the number of fires at each location known to have occurred prior to that fire—by comparing the dates of pitfall trap surveys at each site against the dates of all fires recorded at that site. The earliest fire recorded in our spatially explicit fire dataset occurred on 3 November 1957, giving us a known chronosequence of 46 years of fire records prior to the start of our study. Sites had been burned between zero and six times each by the conclusion of our study (mean = 2.4 fires/site) as the result of 66 separate fires that affected our study sites between 1957 and 2010 (mean = 1.2 fires/year). The median area burned by each fire was relatively small (100.8 ha), but four fires were unusually large, with fires >1,000 ha occurring in 1962, twice in 1972 and in 2003.

While our fire history dataset is unusually complete, there are two caveats to the conclusions that we draw from it. First, these data fail to capture variability in the severity of fire within each boundary

(Lindenmayer et al., 2008a), meaning that our count of the number of fires at each site can only be approximate. Second, our two fire variables are confounded, because not all potential combinations of times since fire and number of fires were present in our dataset (Fig. S1). For example, the only sites to experience one fire in the whole dataset burned in the large wildfire at the beginning of our study (i.e., in 2003), meaning that the maximum time since fire for sites in this category was 7 years. Conversely, there were no sites in our dataset that had been burned 4–5 times previously (i.e., 5–6 times total), and which had a maximum time since fire of >10 years. These considerations limit our capacity to extrapolate any results to locations where fires occur significantly more reliably and frequently than those in our study region (i.e., consistently more than once per decade). We log-transformed both fire variables prior to analysis, so as to reduce the influence of high-value outliers on the resulting coefficient estimates.

Because fire regimes can vary between vegetation types (Fig. S1), we collected data on vegetation structural attributes at each site. At two locations along each transect (20–40 and 60–80 m), we calculated the proportion of understorey (<2 m) and overstorey (>10 m) vegetation on four occasions during our study. We then used these data to calculate a single variable that described the major axis of vegetation structure in our study system. This variable was the mean percentage cover of overstorey vegetation, minus the mean percentage cover of understorey vegetation at each site. Therefore, our vegetation structural covariate measured the gradient between dense, low-growing heath (negative values) and tall forest with low understorey cover (positive values), a gradient that has been shown to influence the fire responses of other vertebrate taxa in our study region (Barton et al., 2014).

Although we were primarily interested in the effects of fire and vegetation on frog populations, our capacity to model these effects was dependent on a method for controlling for the fact that the probability of capturing frogs decreases rapidly with increasing distance from water (Westgate et al., 2012b). To account for this effect, we calculated the density of known breeding sites in the vicinity of each trap location (Baddeley & Turner, 2005). Density is a useful measure because traps that are equidistant from many potential breeding sites might be expected to capture more frogs than a trap that same distance from only one breeding site, a subtlety not captured using straight-line distance to investigate proximity of pitfall locations to breeding sites (although the two measures are highly correlated; Fig. S1). We calculated breeding site density from a dataset of 1108 surveys at 119 potential frog breeding sites conducted in 2007/08. To collect this dataset, one of us (MW) identified and surveyed each potential breeding site on ≥8 occasions, spread as evenly as possible between spring, summer and autumn to account for variation in breeding period of each species. Surveys consisted of 5-min aural surveys for calling males after sunset, a method known to have high detection rates when species are present (Scheele et al., 2014). This dataset provides the best available census of frog breeding sites in our study region for the period during which our trapping dataset was collected.

2.3 | Statistical analysis

Our dataset comprised repeat visits to 110 pitfall trap sites. Our units of analysis were site-level trap sessions (each consisting of 3–4 consecutive trap nights with all pitfall traps open, $n = 944$), while our response variable was the proportion of those nights in which each species was observed, which we refer to as frog "occurrence." This design is commonly analysed using occupancy modelling (MacKenzie et al., 2002), but this was not possible in our case because our detection rates were too low for occupancy models to provide reliable estimates of detection and occupancy parameters (Welsh et al., 2013). Consequently, we used binomial generalized linear mixed models (Bates et al., 2014) to investigate variation in species occurrence in relation to our predictor variables. We used mixed models to account for non-independence resulting from repeat visits to each survey location, via inclusion of a site-level random effect (see Westgate et al., 2015 for an example of this approach).

We used an information theoretic approach (Burnham & Anderson, 2002) to compare models that tested distinct hypotheses, namely that fire had either no effect (set 1), additive effects (set 2) or interactive effects (set 3) with proximity to breeding sites or vegetation structure. Our first model set ($n = 4$) contained no effects of fire, including only additive effects of breeding site density and/or vegetation structure, as well as a null model with no covariates. Our second set contained the same combination of additive effects as the first set, but also included effects of fire variables. Specifically, every model in this set ($n = 4$) included an interaction between the number of previous fires at a location, and the time since the last fire at that location. We included interactions between our two fire variables—rather than testing for their additive or individual effects—because these terms are inherently non-independent. For example, the effect of two previous fires on an ecosystem will depend on how long the system has since had to recover, while the rate of recovery from a single fire could differ between locations that have been frequently versus rarely burnt. Our third model set ($n = 5$) allowed three- or four-way interactions between our two fire variables and either or both of breeding site density and vegetation structure. This set tested the hypothesis that the effect of fire on frog occurrence is mediated by other environmental gradients. This gave us a candidate set of 13 models, which we calculated for each of the four species that were sufficiently common in our dataset to analyse, and compared those models using AICc. All variables were scaled to a mean of zero and a standard deviation of one prior to modelling.

Because some of our models of fire effects on frog occurrence included non-independent terms describing different aspects of the fire regime, they were inherently less parsimonious than if we had neglected the need for interactions among fire regime components. Therefore, we plotted the best model as identified using AICc, but did not anticipate all variables in this "best" model to display high explanatory power. We plotted expected values of frog occurrence in relation to fixed effects only for the top-ranked model (i.e., lowest AICc), but treated all models within two AICc as "competitive", that is as having potential explanatory power. Because AICc will select a "best" model even where that model provides poor fit to the data, we also assessed fit of the final model using both the area under the ROC curve (Fig. S2), and pseudo-R^2 as described by Jaeger et al. (2016). We chose this latter method over the more established approach of Nakagawa and Schielzeth (2013) because (1) it provides "semipartial" R^2 values for each fixed effect (as well as for the whole model), and (2) it does not require comparison models with additional random effects (which did not converge for our dataset).

Using high survey effort (110 sites surveyed for 8 years) to offset the low capture rates that are common when investigating frog populations at large distances from aquatic breeding habitat (see Westgate et al., 2012b), our analysis has high statistical power to detect the effects of fire, and to distinguish them from other landscape-ecological effects. However, our modelling approach was impossible to apply to sites with no recorded history of fire, and so we investigated these observations separately using generalized linear models (GLMs; McCullagh & Nelder, 1989). Low numbers of observations at unburnt sites ($n = 92$ observations from 13 sites) meant that we were unable to control for site-level predictors, and so for these data, we estimated mean occurrence using the intercept of a binomial GLM with no predictor covariates and no random effects.

3 | RESULTS

We surveyed frogs at 110 sites on 944 occasions over 8 years (17,590 trap nights in total), leading to captures of individuals from seven species of ground-dwelling frogs (Table 1). Detection rates were low, averaging a 41% probability of capturing any frogs in a three-night trapping window, or 5% per trap per night. We captured one or more species in 101 of our 110 study sites (92%). *Limnodynastes peronii* was by far the most abundant species in our dataset, largely as the result of a single trapping event in 2006 that captured large numbers of dispersing metamorphs near water. This species was ranked second as measured by the number of occasions on which it was observed (behind *C. signifera*) and was third ranked in terms of observed site occupancy (behind *C. signifera* and *P. bibronii*).

We modelled the occurrence of four species in terrestrial locations: *C. signifera*, *L. peronii*, *P. bibronii* and *U. tyleri*. Comparison of model fit by AICc (Table 2) showed that models that excluded fire effects were not competitive, with the exception that the null model was within 2 AICc of the best model for *L. peronii*. For the remaining species, model selection was straightforward and identified models that included mediation of fire effects by breeding site density (*C. signifera* and *P. bibronii*) or vegetation structure (*U. tyleri*). Model pseudo-R^2 was relatively high, ranging from 0.59 (*C. signifera*) to 0.80 for *U. tyleri* (Table S1; see Fig. S2 for ROC curves).

Breeding site density was included in the final model for all species. The effect of this variable was consistently positive, with all species being significantly more likely to occur when the trap locality was close

to one or more breeding sites where that species had been observed, although this effect was only statistically significant for *C. signifera* (coefficient = 0.35, *SE* = 0.13, *p* = .007) and *U. tyleri* (coefficient = 0.92, *SE* = 0.17, *p* < .001). Conversely, only two species showed responses to vegetation structure (Table S1), and then in opposite directions; *C. signifera* was more likely to be captured in sites with high ground cover (−0.65, *SE* = 0.14, *p* < .001), while *U. tyleri* was moderately more likely to be observed in areas with high canopy cover (0.27, *SE* = 0.16, *p* = .09).

Treated independently, our fire variables explained little variance in occurrence of most frog species (Table S1). The only statistically significant effect of either fire variable (from eight terms fit to four

TABLE 1 Counts of the number of individuals, observations and occupied sites for each species

Species	Individuals	Observations	Sites
*Crinia signifera**	432	249	76
*Limnodynastes peronii**	1,597	193	58
*Pseudophryne bibronii**	236	161	59
*Uperoleia tyleri**	248	153	54
Paracrinia haswelli	60	37	26
Limnodynastes dumerilii	29	17	10
Heleioporus australiacus	17	14	12
Total	2,619	2,874	110

Species are ranked by decreasing number of observations. Total row gives the sum of all individuals, but the maximum possible number of observations and sites. Observations count the number of times each species was recorded at a site per night, but the total survey effort was 17,800 trap nights as each site contained multiple traps.
*Denotes species that occurred sufficiently often to allow statistical analysis.

species) was that *U. tyleri* was observed less often in locations that had been unburned for long periods of time (−0.24, *SE* = 0.12, *p* = .04). However, interactions between variables were highly influential. The effect of time since fire on frog occurrence varied markedly depending on the number of previous fires and either vegetation structure (for *U. tyleri*) or breeding site density (all other species; Figure 2). For example, the effect of time since fire on occurrence of *C. signifera* was marginally lower in locations surrounded by large numbers of potential breeding sites and was significantly higher (0.23, *SE* = 0.11, *p* = .04) at high fire frequencies (Figure 2a). More surprising was that the effect of time since fire on *P. bibronii* occurrence declined with breeding site density when fires were frequent, but increased when fires were rare (Figure 2c; −0.4, *SE* = 0.18, *p* = .03). A similar trend was observed for *L. peronii* (although not statistically significant; Figure 2b), while for *U. tyleri* the effect of time since fire increased with fire frequency (0.26, *SE* = 0.12, *p* = .035) but decreased as vegetation structure became more forest-like (−0.4, *SE* = 0.14, *p* = .004; Figure 2d). This shows that the effect of previous fire on frog occurrence is highly conditional on the ecological context in which those fires occurred.

Despite containing similar terms, models for different species made markedly different predictions about the probability of observing frogs with increasing time since fire (Figure 3). It is common in fire ecology studies to expect population recovery (i.e., increasing occurrence) with increasing time since fire, and this pattern was evident in locations with low density of potential breeding sites and high fire frequency for both *C. signifera* (Figure 3a) and *P. bibronii* (Figure 3c). However, the opposite pattern of post-fire peaks in occurrence followed by declines was also present, namely for *C. signifera* in locations characterized by high breeding site density (Figure 3e), and in frequently burned forests for *U. tyleri* (Figure 3h). Finally, frequent burning was associated with lower occurrence of *C. signifera* where

TABLE 2 Difference in AICc values from the "best" model, for each species and combination of terms

Description	Model	Predictors	Crinia signifera	Limnodynastes peronii	Pseudophryne bibronii	Uperoleia tyleri
No fire effects	1		25.30	**1.46**	12.37	42.37
	2	A	21.85	3.22	12.68	7.77
	3	B	7.39	3.39	13.54	39.56
	4	A + B	2.34	5.19	13.68	5.57
Effects of fire in addition to breeding site density or vegetation structure	5	C × D	26.63	**1.46**	8.90	35.12
	6	A + C × D	21.95	2.72	8.58	6.22
	7	B + C × D	9.95	3.10	9.34	31.57
	8	A + B + C × D	3.74	4.47	8.75	3.32
Effects of fire are mediated by breeding site density and/or vegetation structure	9	A × C × D	21.70	**_0.00_**	**_0.00_**	9.33
	10	B × C × D	11.91	8.48	15.01	30.84
	11	A × C × D + B	**_0.00_**	2.02	**0.68**	6.75
	12	B × C × D + A	5.02	10.01	14.43	**_0.00_**
	13	A × B × C × D	**1.00**	10.04	12.68	9.68

Key to formulae: A = breeding site density; B = vegetation structure; C = time since last fire; D = number of previous fires. Models with AICc ≤2 shown in bold, with selected model underlined (and drawn in Figure 3).
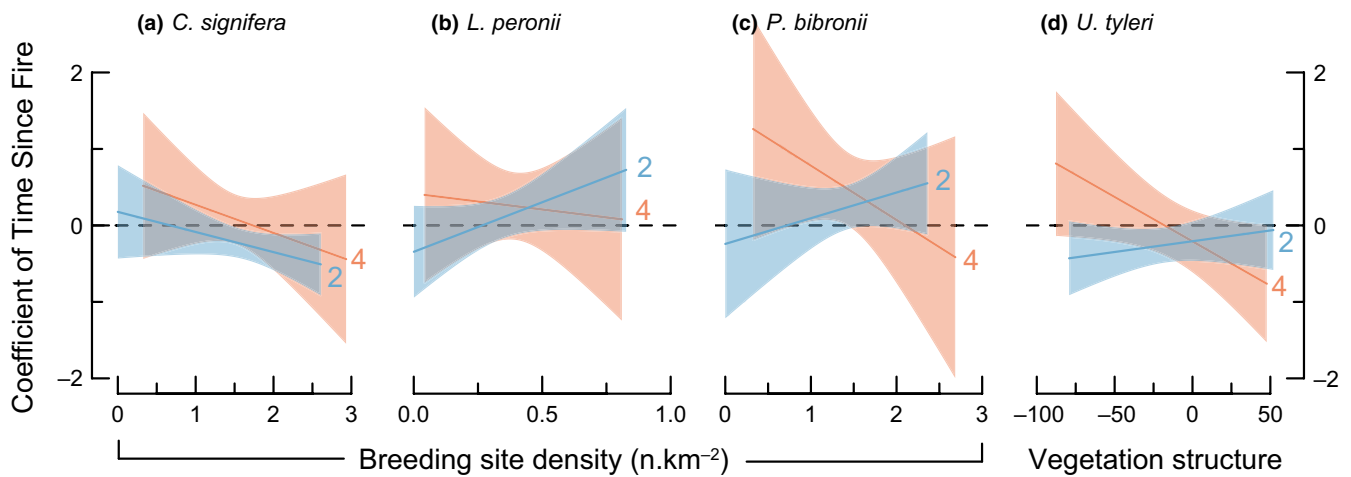
FIGURE 2 Difference in coefficient of time since fire with change in breeding site density (a–c) or vegetation structure (d), showing the effect of the number of previous fires (either 2 or 4, shown by lines). Shaded regions show 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]
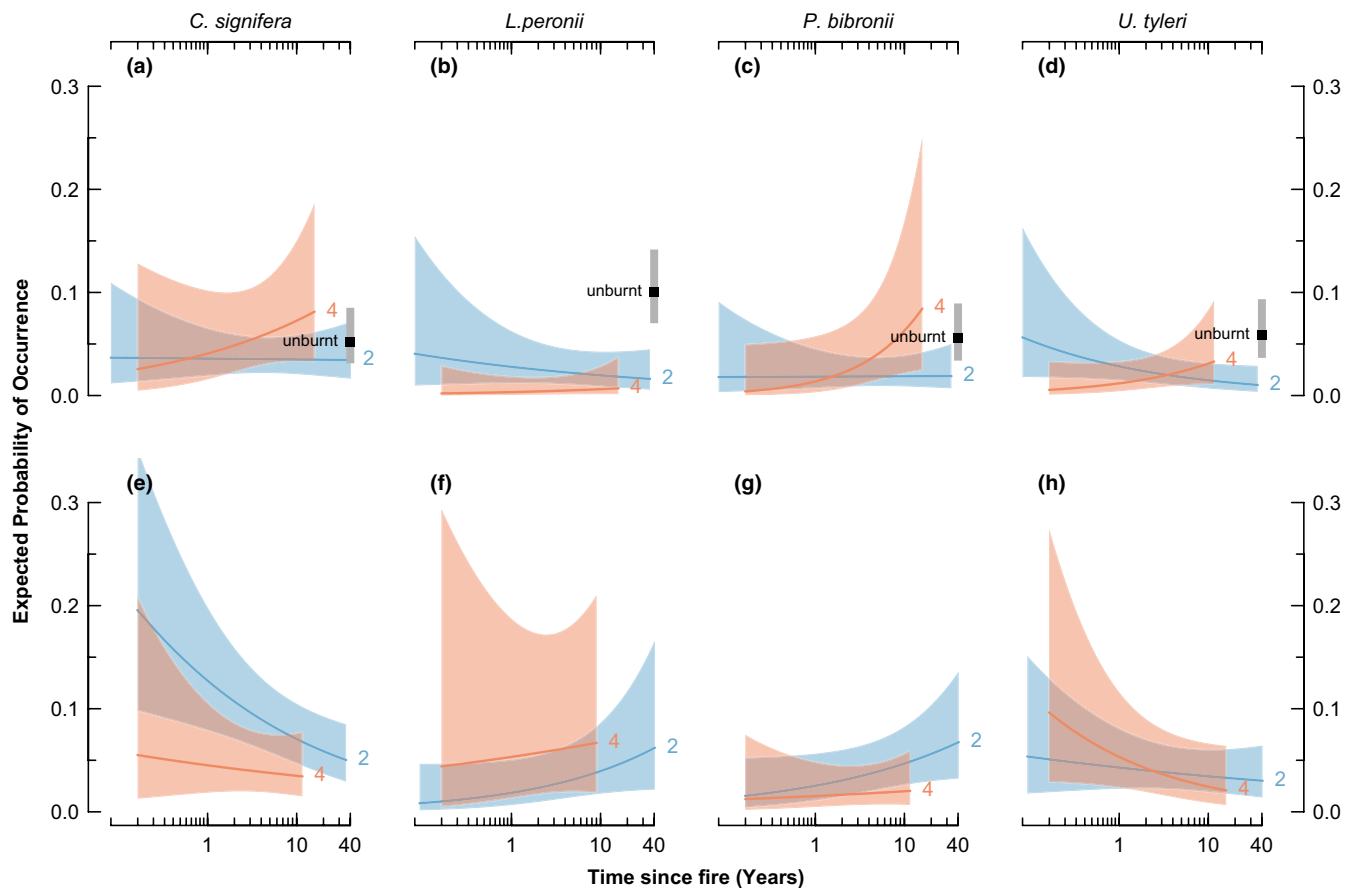

FIGURE 3 Expected occurrence of each frog species in relation to time since last fire (years, log scale) and species (columns). Plotted lines show expected occurrence as a function of the number of previous fires, with shaded regions showing 95% confidence intervals. Rows represent 10% (top row) and 90% (bottom row) quantiles of the second interacting variable, which was breeding site density in all cases except *Uperoleia tyleri*, for which it was vegetation structure. [Colour figure can be viewed at wileyonlinelibrary.com]

breeding site density was high (Figure 3e), but high occurrence in more isolated locations (−0.45, *SE* = 0.16, *p* = .003; Figure 3a). Strong interactions between breeding site density and the number of previous

fires were also evident for *P. bibronii* (−0.51, *SE* = 0.22, *p* = .02) and *L. peronii*; but the direction of this effect was reversed in the latter case (0.68, *SE* = 0.26, *p* = .008).

4 | DISCUSSION

Terrestrial environments are an important, but often unstudied, component of the environmental niche of most amphibian species (Grant et al., 2010; Harper et al., 2008). Consequently, fundamental questions regarding the determinants and dynamics of frog assemblages in terrestrial environments often remain unanswered. In this study, we investigated one such question, namely: Does the post-fire trajectory in frog occurrence vary depending on environmental context? We found that the effect of a single fire on frog occurrence can be profoundly altered—even reversed—depending on fire history or degree of isolation of the survey location. These findings of conditional effects of fire on frog occurrence were broadly consistent across all four species for which data were available.

A critical implication of context-dependent fire response curves is that a single species could be classified as either an early or late successional specialist depending on the attributes of the study environment, undermining the usefulness of those terms for ecological prediction and management. This makes sense when we consider that time since fire is typically used as a surrogate for a number of biotic processes that vary between seral stages, rather than reflecting a single process such as population recovery from mortality (Swan et al., 2015). The contrasting view—that fire response curves are a trait-mediated biological attribute of each species (which is common in plants, for example; see Keeley et al., 2005)—seems less applicable, as this would require that locations separated by short distances (<1 km in this study) with different fire histories should sustain populations of the same species but with opposing life history strategies. Consequently, attempts to transfer the long-established but predominantly plant-focused concept of fixed functional responses to disturbance (Lavorel & Garnier, 2002) to animal population dynamics are unlikely to be consistently successful, a finding also supported by previous studies (Driscoll & Henderson, 2008; Nimmo et al., 2014; Watson et al., 2012). As with all surrogates, therefore, we suggest that careful testing is needed before assuming that observed fire response curves will apply in novel contexts or ecosystems (Lindenmayer et al., 2015).

We also found a complex relationship between fire regimes, water availability, and the capacity of frogs to persist given both attributes. Interactions between breeding site density and fire were selected for all four species (Table 2), leading to complex patterns of expected occurrence (Figure 3). For example, occurrence of *C. signifera* increased with time since fire in isolated locations that had been burned on three or more occasions (Figure 3a), whereas locations close to breeding sites progressively lost this species under the same conditions (Figure 3e). Similarly, *U. tyleri* was common immediately after fire near breeding sites but declined over time, while away from breeding sites this species was rare after fire but gradually became more common (Figure 3d,h). These complex effects most likely reflect a combination of mortality and shifts in habitat suitability and dispersal in the post-fire environment. That is, we should expect interactions between isolation (from breeding sites) and fire because frog breeding sites act as partial refugia from fire (Pilliod et al., 2003), while colonization of burnt areas by frogs depends on dispersal from those refugia. However, frequent fire may also increase landscape permeability to frog movement (Hossack

et al., 2013b; Zeigler & Fagan, 2014), potentially offsetting decreased occurrence resulting from mortality. Consequently, a key benefit of our approach is to investigate the strength and directions of these forms of interaction among key ecological predictors of faunal occurrence.

Our results are consistent with the observation that fire effects can be modified by isolation (Shackelford et al., 2017) or by other forms of disturbance (such as grazing; Foster et al., 2015). For example, every species showed at least one statistically significant interaction between the number of previous fires and one or more other terms (Table S1). Interactions of this kind may explain why previous studies have found apparently inconsistent effects of the time since fire on frog populations and assemblages (e.g., longleaf pines; see Means et al., 2004; Schurbon & Fauth, 2004). More importantly, however, our results support the growing body of work showing that the effects on fauna of fire versus alternative aspects of habitat suitability are not interpretable in isolation (Kelly & Brotons, 2017). This suggests that the impact of a set of fire management practices on a single species may differ strongly between ecosystems.

From a management perspective, these results show that our study species can persist across a wider range of fire regimes than previously expected. The association between time since fire and frog occurrence was generally weak, and even where some effects were present, strong positive responses to time since fire (indicating that fire is a damaging process) were typically offset by weak or negative responses in a different part of the system (Figure 3). While trapping within the area of the 2003 fire *c.* 60 days after burning, for example, we found individuals from all species except *P. bibronii* in locations that had been burned on four previous occasions. These results suggest a high degree of resilience to burning of terrestrial habitats in the frog species that we studied, a finding that mirrors previous research into amphibian responses to fire (Hossack & Corn, 2007) and other disturbances (e.g., logging; Spear et al., 2012). However, there were examples where high fire frequency was associated with lower occurrence of frog species, and in each case, these overlapped with preferred habitat for the species in question (forested sites for *U. tyleri*, locations with high breeding site density for the remaining species; Figure 2). Therefore, some caution may be needed to avoid unusually frequent fires in terrestrial locations that support high densities of frog breeding sites. In contrast, all four species of frogs were found in locations that had been subject to complete absence of fire during our study window, suggesting that fire exclusion is unlikely to be a threatening process.

From a statistical perspective, our results were unusual in that they showed strong effects of interactions between variables that, when treated independently, had low explanatory power. Although this phenomenon was present in the models for all four species, it was especially evident for *L. peronii*, where the interaction between breeding site density and the number of previous fires was the only statistically significant term (from 7 in total; Table S1). We could have improved the parsimony of our final models by testing smaller subsets of terms, and particularly by allowing independent effects of time since fire and the number of previous fires. However, the interaction between these variables was important because they are inherently linked quantities that collectively describe the impact of sequential fires on fauna

(Foster et al., 2015). Therefore, including both terms allowed us to investigate their collective importance, without testing a larger number of more parsimonious models that made less ecological sense. This approach provides two points for consideration in future disturbance ecological research. First, there is a difference between the most parsimonious model and that which best describes the fire regime, and so researchers may need to consider more carefully whether their terms are dependent or independent from ecological first principles, rather than by model fit. Second, investigating higher-order interactions among predictor variables are data intensive (e.g., this study, Haslem et al., 2016), meaning that investigating these effects may not be straightforward in smaller studies with limited replication. In such cases, ecologists may need to supplement analysis of broadscale monitoring data with targeted surveys, experimental manipulations (Foster et al., 2015) or computer simulations of dominant processes (Conlisk et al., 2015) to adequately investigate important patterns in their data and minimize the risk of adverse biodiversity outcomes.

One final—and potentially overlooked—result of our research is the sheer ubiquity of frogs in this landscape. Despite our study sampling a range of terrestrial vegetation types without regard to the location of aquatic frog habitats, we still managed to detect frogs in 92% of trap locations. Although these findings support earlier research on the ubiquity of *C. signifera* in terrestrial habitats (Lauck, 2005), our results were more surprising for other species. For example, *U. tyleri* defends territories during the breeding season (Robertson, 1986), a trait that might suggest high site fidelity, yet we found this species at 50% of our study locations. Similarly, we found individuals of *H. australiacus* at 12 different sites on 14 occasions (Table 1), suggesting that this species is likely to be quite widespread, despite being difficult to detect (see also Penman et al., 2008). Our results are particularly novel when we consider that this study took place during the Millennium drought, a period characterized by long-term below-average rainfall in this region (van Dijk et al., 2013), and therefore likely below-average frog movement. Therefore, our results demonstrate that further work to quantify terrestrial habitat use is essential for understanding the structure and dynamics of frog assemblages.

5 | CONCLUSIONS

Fire is an important generator of landscape dynamism (Tulloch et al., 2016) that drives complex spatial and temporal variation in plant and animal assemblages (Smith et al., 2016; Zeigler & Fagan, 2014). In this study, we observed strong variation in the relationship between frog occurrence and time since the last fire, variation that was relatable to both the isolation of those sites from suitable breeding habitats, and the number of previous fires at each study location. These results suggest that the same species could be considered as either a fire specialist, or fire averse, depending on the context of the study used to make that classification. Fauna inhabiting heterogeneous study systems—that is, those characterized by strong spatial variation in vegetation type, topography or fire regimes—are unlikely to display consistent responses to time since fire.

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BIOSKETCH

The authors are current and former members of the Conservation and Landscape Ecology research group at the Australian National University, which investigates methods for quantifying and ameliorating the effects of landscape change on biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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