

Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire?

Martin J. Westgate, Don A. Driscoll and David B. Lindenmayer

M. J. Westgate (martin.westgate@anu.edu.au), D. A. Driscoll and D. B. Lindenmayer, The Fenner School of Environment and Society, The Australian National Univ., Canberra, ACT 0200, Australia.

Fire is a common form of recurrent disturbance in many ecosystems, but ecological theory has a poor record of predicting animal responses to fire, at both species and assemblage levels. As a consequence, there is limited information to guide fire regime management for biodiversity conservation. We investigated a key research gap in the fire ecology literature; that is, the response of an anuran assemblage to variation in the fire return interval. We tested two hypotheses using a spatially-explicit fire database collected over a 40 year period: 1) species richness would peak at intermediate levels of disturbance. 2) Species with traits which enabled them to escape fire – burrowing or canopy dwelling – would be better able to survive fires, resulting in higher levels of occurrence in frequently burned sites. We found no evidence for either a reduction in species richness at locations with short fire return intervals, or a peak in species richness at intermediate levels of disturbance. Although we found some support for individual species responses to fire return intervals, these were inconsistent with the interpretation of burrowing or climbing being functional traits for fire-avoidance. Instead burrowing and climbing species may be more likely to be disadvantaged by frequent fire than surface dwelling frogs. More generally, our results show that many species in our study system have persisted despite a range of fire frequencies, and therefore that active management of fire regimes for anuran persistence may be unnecessary. The responses of anurans to fire in this location are unlikely to be predictable using simple life-history traits. Future work should focus on understanding the mechanistic underpinnings of fire responses, by integrating information on animal behavior and species' ecological requirements.

Fire is a common form of disturbance in many ecosystems worldwide. Because fire strongly influences the composition of biotic communities (Bond et al. 2005), it is concerning that many regions are expected to suffer increases in the size, frequency and severity of fires as a result of climate change (Dale et al. 2001, Westerling et al. 2006). Past changes to fire regimes have been associated with significant losses of biodiversity, either as a result of fire suppression (Zackrisson 1977, Backer et al. 2004) or overly frequent prescribed burns (Andersen et al. 2005). Preventing similar losses of biodiversity from recurring in the future will be difficult because managing plant and animal populations against a backdrop of environmental change involves great uncertainty (Conroy et al. 2011). Ignoring uncertainty in favor of applying 'rules of thumb' to fire management (such as the 'pyrodiversity paradigm') is undesirable because such rules provide neither a plan for learning, nor surety of positive conservation outcomes (Parr and Andersen 2006). Therefore, research is urgently needed to identify management practices that balance the risks of fire-related mortality in animal populations – and damage to human infrastructure – against the need to reduce fuel loads and maintain fire-dependent communities (Driscoll et al. 2010a).

Community ecological theory provides a number of testable hypotheses regarding the potential effects of disturbance, but few hypotheses have been comprehensively investigated

for animals (Parr and Chown 2003, Clarke 2008, Driscoll et al. 2010b), or in relation to different components of the fire regime (Gill 1977). For this paper, we investigated whether anuran responses to the fire return interval (FRI) were consistent with two hypotheses. First, the intermediate disturbance hypothesis (IDH, sensu Connell 1978) suggests that diversity of responses within an assemblage will lead to a peak in species richness where species at different points on the disturbance–sensitivity gradient can coexist. However, there is mixed support for the IDH in studies of both plant and animal communities (Mackey and Currie 2001, Lindenmayer et al. 2008a). Second, evidence from studies of plants (Lavorel and Garnier 2002) and animals (Moretti et al. 2009, Langlands et al. 2011) suggests that species that share relevant functional traits will respond similarly to disturbance, but this hypothesis has not been investigated for anurans, despite evidence of trait-correlated extinction risks in this taxon (Murray and Hose 2005).

We investigated each of these hypotheses in turn, beginning with whether anuran species richness showed a peaked relationship with FRI. If anuran populations take a long time to recover from the effects of single fires, short FRIs can lead to local extinction (Driscoll and Roberts 1997). The FRI might also have indirect effects on anuran populations by influencing canopy cover (Fisher et al. 2009) or changing the composition of riparian vegetation (McWilliams et al.

2007), both of which have been shown to influence habitat suitability for some anuran species (Hamer et al. 2002, Skelly et al. 2002). Consequently, we investigated two plausible relationships between FRI and anuran species richness. First, we looked for evidence of a peaked response to increasing FRIs (congruent with the IDH), that would suggest inter-species variation in resilience to disturbance. Second, we tested for a linear, positive response to increasing FRIs, that would suggest that fire was a threatening process for anurans in our study location (Schurbon and Fauth 2003).

Our second hypothesis was that anuran species with particular shared traits would be better able to persist in locations with short FRIs. Although breeding ponds and streams may act as refugia from fire (Pilliod et al. 2003), many anuran species use aquatic sites only on a seasonal basis (Semlitsch 2008), or in some cases, only during short breeding events (Penman et al. 2008). Therefore we would expect that anuran species that use terrestrial locations in fire-prone regions would show adaptations to avoid fire-related mortality. We investigated two potential adaptations to fire. First, increased mobility may enable anurans to flee oncoming fires, either by climbing to avoid low severity fires that leave the canopy unscathed, or by enabling directional movement away from the fire front (Grafe et al. 2002). Second, burrowing may allow animals to shelter from fires that might otherwise kill them (Driscoll and Roberts 1997). In both cases, we could reasonably hypothesize that species with one of these traits might occur more often in locations with short fire return intervals than species lacking any such traits.

The current lack of knowledge regarding animal responses to fire frequency is a key research gap (Driscoll et al. 2010b) that has limited the ability of ecologists to provide advice to policy-makers about optimal fire management for biodiversity conservation (Clarke 2008, Driscoll et al. 2010a). Studies such as ours are therefore important in contributing to the debate about whether ecological theories can be used to guide appropriate fire management for animal conservation, and whether it is possible to develop contingent theory to apply in specific cases (Parr and Andersen 2006, Driscoll and Lindenmayer 2012).

Methods

Study area and anuran fauna

Booderee National Park is located in the Jervis Bay Territory, southeastern Australia (approximate midpoint is 35°10'S, 150°40'E; for map see Fig. 1), and covers the majority of the southern peninsula of Jervis Bay. At the time of our study, vegetation in the park consisted primarily of eucalypt forest (45.1%), although patches of heath (15.3%) and woodland (12.9%) were common (Taws 1997). Soils were primarily sandy over sandstone geology. Upland areas typically had shallow soil, dominated by heaths, and were characterized by high levels of soil moisture following rain. Forested areas had low runoff and deep soils (Taylor et al. 1995). Rainfall averaged over 1200 mm per year (Bureau of Meteorology 2010).

In the 40 years preceding our study, there were 194 recorded fires in Booderee National Park. The majority of fires were small (median size 4.95 hectares), low- to medium-intensity controlled burns, that occurred between August and January (late winter to mid-summer). Although small uncontrolled fires were relatively common, only two large (> 1000 ha) wildfires occurred during this period (in 1973 and 2003).

Booderee National Park contains six anuran species in each of the families Myobatrachidae (southern frogs) and Hylidae (tree frogs; Cogger 1996). As with many anurans, these families consist of species with an aquatic juvenile stage and a largely terrestrial adult stage (Tyler 1994).

Survey methods

We used aural surveys to detect calling anurans at 44 potential breeding sites, and completed between four and eight (mean = 5.25) surveys at each site, each lasting five minutes, between August 2007 and February 2008. We measured temperature and humidity during field surveys using a portable weather meter.

We collected a number of site-level covariates for use in modeling of anuran species richness and occurrence

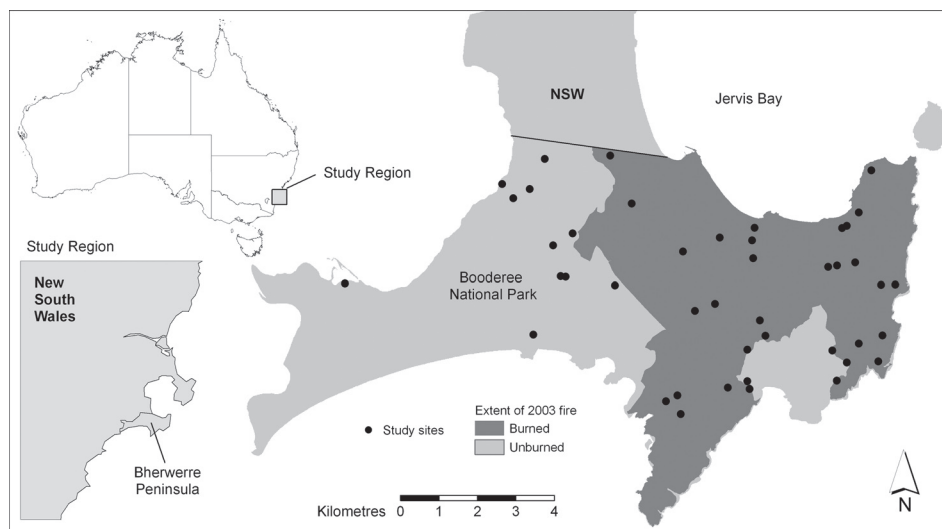


Figure 1. Map of the study area.

(Table 1). We estimated water-body width (in metres) and calculated the proportion of visits during which a site contained water as a surrogate for the hydroperiod. We also included two measures of terrestrial vegetation, each taken from a different source. We first counted the number of tree stems within a 10 × 10 m quadrat positioned 5 m from the water's edge at each site. Our second variable was the proportion of forest within a 200 m buffer centered on each survey location, calculated from a vegetation map for the area (Taws 1997). We chose these attributes of terrestrial habitat because they have been shown to strongly influence anuran assemblage composition in other ecosystems (Skelly 1999, Werner et al. 2007).

We investigated four variables as potential predictors of detectability: temperature, humidity, Julian date, and soil moisture deficit (or SMD; Finkele et al. 2006), the latter being calculated using data from the Bureau of Meteorology (2010). We log-transformed all continuous variables for normality where required, and standardized them to a standard deviation of one and mean zero.

Intermediate disturbance hypothesis

Our fire history data were derived from a GIS database maintained by staff at Booderee National Park, that gave the date and precise spatial extent of all fires in the area in the 40 years preceding the survey period (i.e. all fires since 1968). Ideally we would have investigated the effect of time since fire, or of the minimum fire return interval, on anuran populations; however 32 of our 46 sites (70%) were burned in a single, relatively recent wildfire (in 2003), meaning that our data were too unbalanced for this to be informative.

We calculated mean FRI as the length of data collection period, divided by the number of fires that had occurred at each site plus one. Using this formula, sites that were unburned were given a return interval equal to the length of the study period (40 years), which is likely to be an underestimate. However, the alternative of averaging across all known FRIs was unavailable to us, since 29 sites in our study area (63%) had been burned twice or less (meaning that the number of known inter-fire intervals was ≤ 1). To account for variation in of FRIs between sites, we also calculated the maximum period of time that each site had remained unburned (i.e. the maximum FRI).

We used a multi-stage process to assess the relationship between mean or maximum FRI and species richness. First, we grouped data from all visits to each site, and used Chao's (1984) method to estimate total (as opposed to observed)

species richness, which we log transformed for later analysis. Second, we used hierarchical partitioning of generalized linear models (GLM's; McCullagh and Nelder 1989) to determine the proportion of variance explained by each candidate variable (including mean and maximum FRIs). Third, we ranked a series of models by AICc weight, each including a unique combination of variables that we had selected by virtue of their explaining > 10% variance in species richness (as indicated by hierarchical partitioning). Fourth, mean and maximum FRI were added to the 'final' model – both linearly and quadratically – to see if either variable led to a reduction in AICc. We found that a Gaussian error distribution fitted residuals well, and better described the distribution of log-transformed Chao richness than a Poisson model. If a quadratic FRI term was included in the final model, and resulted in a peaked relationship between richness and the FRI, we considered this evidence of a response consistent with the IDH (Mackey and Currie 2001). In contrast, a negative linear response would support Schurbon and Fauths' (2003) finding that very short FRIs can be detrimental to anuran species richness.

Fire responses in relation to species traits

In our anuran assemblage, five species could be considered effective burrowers. *Limnodynastes dumerilii* and *Uperoleia tyleri* are morphologically adapted for burrowing (Sanders and Davies 1984), as is the locally rare *Heleioporus australiacus* (Penman and Brassil 2010). *Limnodynastes peronii* has been observed to be a capable burrower, despite lacking morphological adaptations for burrowing (Barker et al. 1995). Finally, *Pseudophryne bibronii* constructs burrows as egg deposition sites (Woodruff 1976). Two myobatrachids with poor burrowing abilities occur in our study area; *Crinia signifera* and *Paracrinia haswelli*.

Hylids are often highly mobile, and most species from this family are likely to be able to climb to some extent; but few species are likely to be regular canopy-dwellers. For example, *L. freycineti* is a ground-dwelling frog that prefers heaths over tall forests. Similarly, *Litoria jervisiensis* and *L. nudidigitus* are both commonly associated with reeds and low-lying riparian vegetation, rather than trees. In contrast, we observed individuals from three species (*L. peronii*, *L. tyleri* and *L. dentata*) calling from trees during this study (see also Barker et al. 1995), and we consequently classified these species as potential canopy dwellers.

Table 1. Species observed during this study. 'Sites' and 'Visits' columns give the number of observations, while figures in brackets give this value as a proportion of all observations.

	Species	Sites	Visits	Traits
Myobatrachidae	<i>Crinia signifera</i>	40 (0.86)	142 (0.61)	None tested
	<i>Uperoleia tyleri</i>	16 (0.34)	52 (0.21)	Burrowing
	<i>Paracrinia haswelli</i>	14 (0.30)	38 (0.16)	None tested
	<i>Limnodynastes peronii</i>	10 (0.20)	21 (0.09)	Burrowing
	<i>Pseudophryne bibronii</i>	4 (0.09)	6 (0.03)	Burrowing
	<i>Limnodynastes dumerilii</i>	2 (0.05)	6 (0.03)	None tested
Hylidae	<i>Litoria peronii</i>	13 (0.30)	40 (0.16)	Climbing
	<i>Litoria jervisiensis</i>	9 (0.20)	26 (0.10)	None tested
	<i>Litoria nudidigitus</i>	8 (0.18)	18 (0.08)	None tested
	<i>Litoria freycineti</i>	5 (0.11)	7 (0.03)	None tested
	<i>Litoria dentata</i>	3 (0.07)	3 (0.01)	Climbing
	<i>Litoria tyleri</i>	3 (0.07)	3 (0.01)	Climbing

Our approach to investigating whether species with shared functional traits displayed similar responses to mean or maximum FRIs was twofold. First, we used fourth-corner analysis (Dray and Legendre 2008) to test whether interspecies variation in responses to hydrological, vegetation or FRI gradients was attributable to groups of species defined by shared burrowing or climbing traits. We then tested whether individual species showed statistically significant linear responses to mean or maximum FRIs, using the model by MacKenzie et al. (2002) for occupancy given low detection. If models for species with strong climbing or burrowing abilities contained fewer fire variables, or weaker ‘effects’ of fire (where those variables were selected) than models for species that lacked either of those abilities, we would consider this to be evidence that burrowing or climbing were traits that facilitate persistence in frequently burned locations.

We constructed occupancy models using the package ‘unmarked’ (Fiske and Chandler 2010) in the R statistical program (R Core Development Team 2009). We selected a final model (for each species) using a multi-stage approach, first testing whether AICc was reduced by two or more by the addition of any of our four detection covariates (Arnold 2010). We then tested whether the addition of vegetation or hydrological covariates further improved model fit, comparing nine likely candidate models against a null model (that included only detection covariates). We labeled this our ‘habitat’ model. We then ranked ‘detection only’, ‘detection + habitat’, ‘detection + mean or max FRI’ and ‘detection + habitat + mean or max FRI’ models using AICc weight. This was a useful approach because of the possibility of correlation between fire and vegetation covariates, given that heaths might support shorter FRIs than forests in our study region (Attiwill 1994). Comparison of models with and without fire effects against a null model enabled the relative support for fire and habitat effects to be evaluated, in a similar manner to the hierarchical partitioning approach used for species richness GLMs.

Results

Intermediate disturbance hypothesis

We detected 12 species across 44 sites, six each from the families Hylidae and Myobatrachidae (Table 1). Most sites

had low species richness, with 17 sites (39%) supporting only one species and a further 11 sites (25%) inhabited by only two species. The highest species richness at a single site was six species, but seven sites (16%) contained this many species. Sites had burned between zero ($n = 4$) and seven times ($n = 1$) since 1968, with the median value being two fires per site ($n = 15$), and the next most common value being four fires per site ($n = 9$).

Hierarchical partitioning showed that 75% of explained variance (total explained variance = 43%) could be attributed to the interaction between width and hydroperiod. A further 11% could be attributed to the number of trees, while only 3% was attributable to the proportion of forest within 200 metres. Of the FRI variables, a quadratic relationship with mean FRI explained most variance (3.8%). The remaining FRI variables in combination explained 6% of total variance.

We found that a GLM containing all variables that explained >10% variance only marginally improved fit over a model that lacked ‘number of trees’ as a covariate ($\Delta\text{AICc} = -0.03$). Moreover, a model that included width, hydroperiod and their interaction was a better fit to the data ($\Delta\text{AICc} = -1.10$) than a model that included hydroperiod, width, and number of trees, and we accordingly selected the former as our ‘final’ model. This model suggested that species richness was highest in large waterbodies ($\beta_{(\text{width})} = 0.22 \pm 0.08$, $t_{(1,40)} = 2.69$, $p = 0.01$), but only where those waterbodies contained water during a high proportion of visits ($\beta_{(\text{hydroperiod})} = 0.14 \pm 0.08$, $t_{(1,40)} = 1.74$, $p = 0.089$; $\beta_{(\text{interaction})} = 0.16 \pm 0.08$, $t_{(1,40)} = 1.90$, $p = 0.064$; Fig. 2a–b).

Adding a linear term for mean FRI to our existing species richness model reduced model fit ($\Delta\text{AICc} = 1.73$), and the statistical significance of this variable was low ($p = 0.63$). Adding mean FRI as a quadratic variable did marginally improve fit ($\Delta\text{AICc} = -0.71$), and predicted a peak in species richness at a mean FRI of 10 years (predicted richness = 2.86 ± 0.10), 1.39 species higher than a return interval of ≥ 40 years (predicted richness = 1.47 ± 0.27), and 2.40 species more than a return interval of five years (predicted richness = 0.46 ± 0.76 ; Fig. 2c). However, this variable was not statistically significant ($p = 0.12$). Similarly, model fit was not improved by adding maximum FRI to the model, either linearly ($\Delta\text{AICc} = 1.98$, $p = 0.91$) or quadratically ($\Delta\text{AICc} = 1.24$, $p = 0.41$).

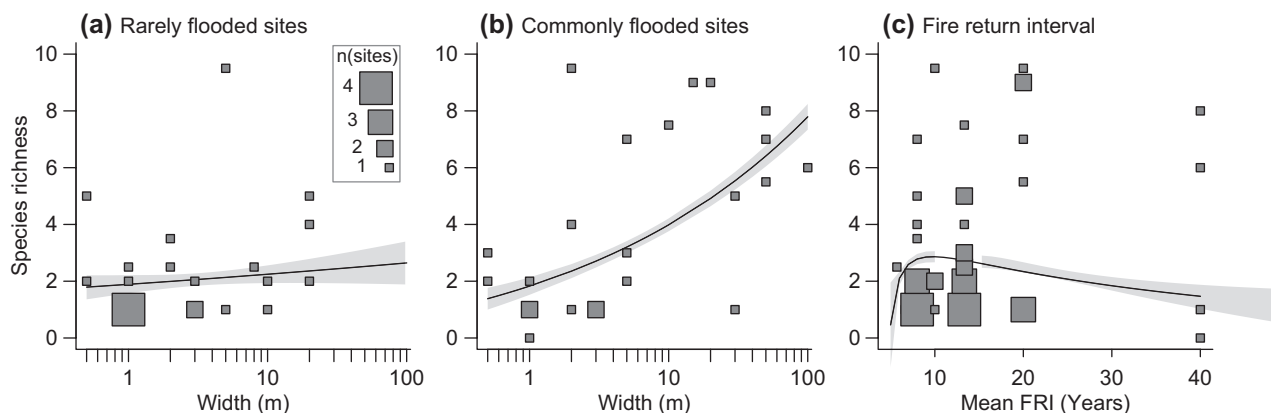


Figure 2. Predicted species richness for rarely (a) and commonly (b) flooded sites, with increasing waterbody width. The quadratic model for mean FRI is given in (c). Filled regions show 95% confidence intervals. Size of squares shows the number of sites at each point.

Fire responses in relation to species traits

Fourth-corner analysis showed that climbing species were significantly more likely to occur in larger waterbodies ($F = 3.46$, $p = 0.032$) that contained water during more visits ($F = 3.86$, $p = 0.024$), but were unaffected by FRIs ($F_{(\text{mean FRI})} = 2.11$, $p = 0.09$, $F_{(\text{max FRI})} = 1.21$, $p = 0.21$). In contrast, burrowing species were more likely to occur only in locations with longer maximum FRIs ($F = 3.05$, $p = 0.034$), but did not show a significant relationship with mean FRI ($F = 2.52$, $p = 0.055$). When we compared species with either of these fire-avoidance traits (i.e. all burrowing and climbing species, $n = 7$) against species lacking them ($n = 5$), we found that species with fire-avoidance traits occurred in significantly larger sites ($F_{(\text{width})} = 3.70$, $p = 0.01$), with significantly longer mean ($F = 6.27$, $p = 0.002$) and maximum ($F = 5.66$, $p = 0.003$) FRIs. This is the opposite pattern from that expected at the onset of our study.

Models of occupancy rates that contained FRI variables had high AICc weight for six of eight species (Fig. 3), but in most cases these were only slight improvements on models that contained only hydrological or vegetation covariates (Table 2). Although some models containing mean or maximum FRI were poorly supported, for three species lacking canopy-dwelling or fossorial tendencies occupancy models suggested negative responses to increasing FRIs (Fig. 3a–c). Two species with strong burrowing abilities were found to occur less often in areas with short

maximum FRIs (*Lim. peronii*: $\beta = 0.87 \pm 0.51$, $p = 0.092$; *U. tyleri*: $\beta = 0.87 \pm 0.51$, $p = 0.088$; Fig. 3e–f), as was a third myobatrachid with weak burrowing abilities (*P. haswelli*: $\beta = 1.42 \pm 0.79$, $p = 0.073$). Model fit was not improved by including FRI in the occupancy model for the only canopy-dwelling species with sufficient data for modeling to occur (*Litoria peronii*). Full model selection statistics, along with coefficient values, standard errors and p-values from the models with lowest AIC for each species are provided in Appendix 1.

Discussion

We quantified the distribution of anurans in relation to habitat and fire return interval (FRI) gradients, and compared our results to predictions based on the intermediate disturbance hypothesis (Connell 1978). We also compared the fire responses of taxa with strong and weak burrowing and climbing abilities, leading to some surprising results. There was no evidence for either a reduction in species richness with decreasing FRIs, or a peak in species richness at intermediate levels of disturbance. There was limited support for responses to FRI for six species, however these responses were inconsistent with the interpretation of burrowing or climbing being functional traits for fire-avoidance. We further discuss these results in the remainder of our paper.

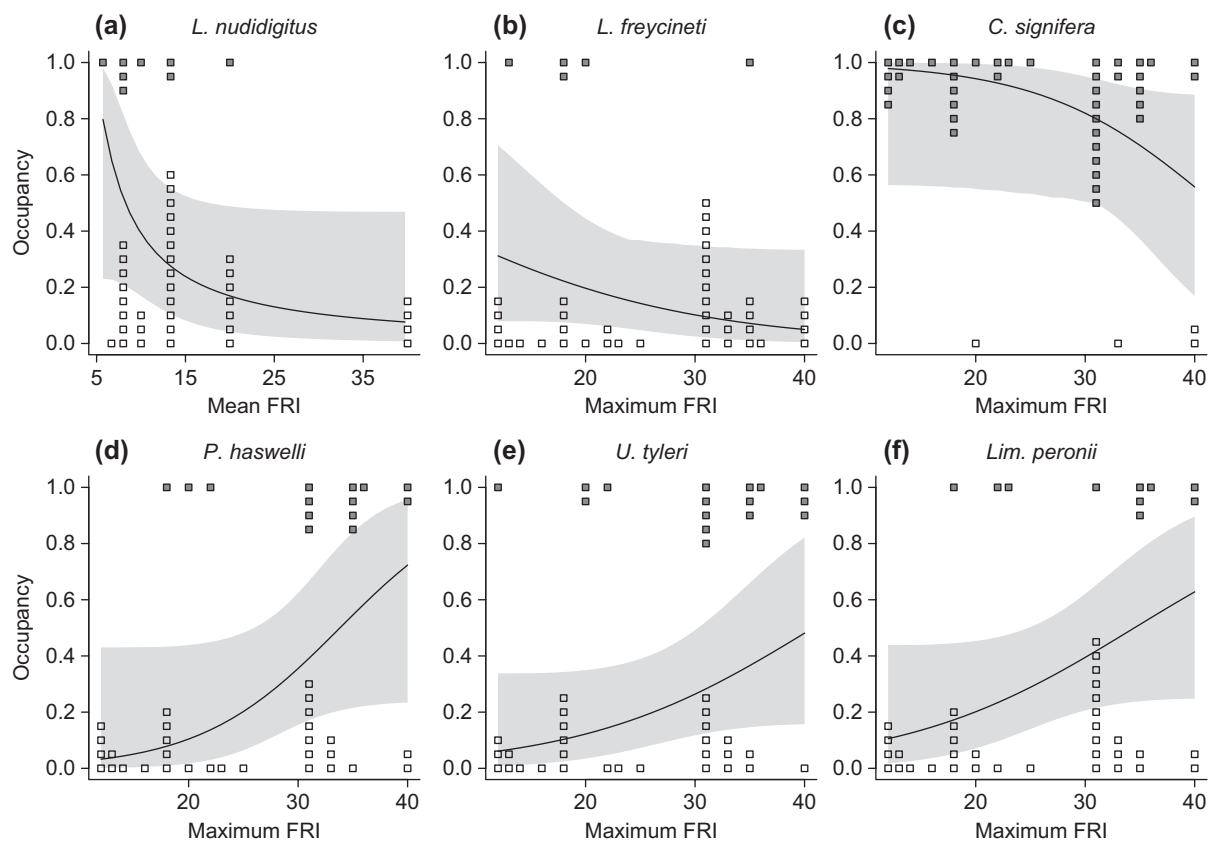


Figure 3. Effect of mean or maximum FRI on occupancy of individual species according to models with the lowest AICc for that species. Filled regions show 95% confidence intervals, while squares are histograms of the number of absences (open squares) or presences (filled squares) at each point on the FRI gradient.

Table 2. AICc of alternative candidate occupancy models for each species. The model with the lowest AICc for each species is given in bold. For full explanation, see text.

Species	Detection only	Habitat	Mean FRI	Max FRI	Habitat + Mean FRI	Habitat + Max FRI
<i>Crinia signifera</i>	285.25 (0.16)	284.97 (0.18)	286.73 (0.08)	284.49 (0.23)	286.63 (0.08)	284.16 (0.27)
<i>Limnodynastes peronii</i>	119.81 (0.02)	114.75 (0.23)	117.06 (0.07)	117.64 (0.05)	114.28 (0.29)	113.89 (0.35)
<i>Paracrinia haswelli</i>	137.73 (0.00)	119.21 (0.25)	134.74 (0.00)	132.93 (0.00)	120.79 (0.12)	117.38 (0.63)
<i>Uperoleia tyleri</i>	178.89 (0.00)	168.00 (0.32)	175.65 (0.01)	174.90 (0.01)	168.66 (0.23)	167.36 (0.44)
<i>Litoria freycineti</i>	59.42 (0.27)	60.58 (0.15)	60.39 (0.17)	60.02 (0.20)	61.48 (0.10)	61.08 (0.12)
<i>Litoria jervisiensis</i>	107.58 (0.00)	92.64 (0.62)	105.94 (0.00)	107.10 (0.00)	94.94 (0.20)	95.05 (0.18)
<i>Litoria nudidigitus</i>	99.87 (0.10)	98.89 (0.17)	98.53 (0.20)	100.36 (0.08)	97.61 (0.32)	99.55 (0.12)
<i>Litoria peronii</i>	145.90 (0.00)	121.98 (0.67)	144.39 (0.00)	146.37 (0.00)	124.67 (0.17)	124.82 (0.16)

Intermediate disturbance hypothesis

We found no compelling evidence that species richness was significantly related to either mean or maximum FRIs – in contrast to the predictions of the intermediate disturbance hypothesis (IDH). Why this should be the case is unclear, but one possibility is that fire does not qualify as a disturbance for anurans at breeding sites. For example, the IDH assumes that few species will be able to survive in frequently disturbed locations, or otherwise be incapable of rapidly recolonizing them following local extinction (Connell 1978, Mackey and Currie 2001). Because water-bodies can act as refugia, fire is unlikely to result in high mortality, with indirect fire effects likely to have a stronger influence on anuran assemblage composition (via such mechanisms as increased runoff or vegetation succession; Pilliod et al. 2003). Similarly, while the effects of fire on anuran dispersal rates are unclear (Means et al. 2004), Lindenmayer et al. (2008a) highlight that post-fire recovery of vegetation in our study area can be rapid, suggesting that increased risks of desiccation or predation in the post-fire terrestrial environment should be temporary. In combination, the above arguments suggest that some assumptions of the IDH poorly match anuran life histories, potentially reducing the relevance of this theory for predicting the relationship between anuran species richness and the FRI.

An alternative explanation for our findings could be that the IDH does apply to the fire responses of anuran communities, but that our study was unable to detect it. Our results show that a peaked curve could fit the relationship between species richness and FRI, after other covariates had been taken into account (Fig. 2c), but also that this was a weak and non-significant relationship. Statistical power to detect any result consistent with the IDH would be improved in assemblages with high species richness. While possible, we do not consider this to be the most likely interpretation of our results because our study had sufficient power to detect other patterns of interest – namely statistically significant effects of water-body width and hydroperiod on species richness (see also Skelly et al. 1999, Werner et al. 2007).

Although we found low species richness in some locations with short FRIs, and some tendency towards reduced incidence of burrowing and climbing species in frequently burned locations, we found little evidence overall that short FRIs lead to reduced species richness. This contrasts with evidence from Schurbon and Fauth (2003), who demonstrated that short FRIs in some areas of the southeastern United States are negatively and linearly correlated with

amphibian species richness. Unfortunately, there are many possible factors that could account for the differences in our respective findings. We evaluated different water-body types (streams and ponds) and sizes, within a range of vegetation types, while these were factors controlled for in the study design used by Schurbon and Fauth (2003, 2004). There were also large differences in the fauna of our respective studies, with long-leaf pine-associated amphibian assemblages containing salamanders in addition to anurans. The anurans of our respective studies are also likely to have evolved under very different fire regimes (Glitzenstein et al. 1995, Gill and Williams 1996). Despite these differences, our results are consistent with work on other animal taxa in our study region (Lindenmayer et al. 2008a, b). It is possible, therefore, that the fauna of our study region is better adapted to persist in the presence of frequent fire than anurans in some North American locations.

Fire responses in relation to species traits

Several of our results do not support the hypothesis that species with burrowing or climbing traits were better able to persist in frequently burned locations. First, fourth-corner analysis showed that inter-species variation in responses to hydrological, vegetation and FRI gradients was not attributable to groups of species defined by shared burrowing or climbing traits. Second, species with and without burrowing or climbing traits were shown to have similar responses to the FRI. For example, *Lim. peronii* and *U. tyleri* are capable of burrowing, while *P. haswelli* is not; but all three species showed a positive response to increasing fire return intervals. Third, relationships between occupancy and FRIs were only weakly supported for most species (low AICc weights; Table 2), suggesting any effect of FRIs on occupancy were slight. Fourth, responses for burrowing species were opposite to those expected, with two burrowing species (*Lim. peronii* and *U. tyleri*) becoming more common as FRIs increased, rather than being more common in locations with short FRIs as we had expected. The evidence is less clear for climbing species, since two species with this trait (*L. tyleri* and *L. dentata*) were very rare in our dataset. However, similar lines of reasoning apply; *Litoria peronii* is a stronger climber than *L. jervisiensis*, but neither species showed any response to FRIs.

Our fourth-corner results suggest that burrowing and climbing abilities may marginally increase species vulnerability to short FRIs, and not decrease vulnerability as we

had anticipated. Although initially puzzling, this makes sense if we consider burrowing or canopy-dwelling as desiccation-avoidance traits, rather than as traits to avoid fire-related mortality. While most amphibians are obliged to complete their migrations during short periods following rainfall, burrowing enables some anurans to persist in terrestrial locations during the periods between successive rain events (Penman et al. 2006). Similarly, arboreal anurans are often large and have high cutaneous resistance (Tracy et al. 2010). A shared consequence of both traits may therefore be reduced desiccation (and increased survival) during dispersal between widely-spaced breeding ponds. Such traits would be highly beneficial in regions with high temporal heterogeneity in the availability of required habitat such as breeding ponds (Kisdi 2002). If so, one additional consequence of desiccation-avoidance traits would be an increased risk of individuals being away from aquatic refugia during rare but catastrophic fire events. Therefore, species with desiccation-avoidance traits could be more, rather than less, susceptible to fire-related mortality than species that spend more time near water. Future work could evaluate whether anuran desiccation-avoidance traits play a similar functional role to dispersal-correlated traits in other animal taxa (such as flight in invertebrates, Barton et al. 2011, Driscoll and Weir 2005).

Management implications

What are the key implications of our results for fire regime management in our study region? Three species were shown to have higher occupancy in locations with short mean (*L. nudidigitus*) or maximum (*L. freycineti* and *C. signifera*) fire return intervals. However, these species were either very rare (*L. nudidigitus* and *L. freycineti*) or very common (*C. signifera*), and there was little difference between models that contained and did not contain FRI variables in terms of fit ($\Delta AIC_c < 3$ across all models for all three species; Table 2), suggesting that these results might be a statistical artifact. Studies of these species that had a better balance of occupied and unoccupied breeding sites would most likely prove enlightening as to their actual responses to fire return intervals.

Our findings suggest that frequent burning risks reducing occupancy rates for three ground-dwelling myobatrachids for which meaningful data were available; *Lim. peronii*, *P. haswelli* and *U. tyleri*. While there was no change in species richness with decreasing FRIs, our fourth-corner results further suggest that terrestrial-adapted anurans may be disadvantaged by short FRIs. This result is of some concern given that prescribed burning rates required to appreciably reduce the incidence of unplanned fire are predicted to be less than once in five years (Bradstock et al. 1998), a rate with the potential to drive a number of species towards regional extinction. For each species, estimated probability of occurrence reached its mean value when the maximum FRI was ~20 years or more (Fig. 3), although mean FRIs could be lower than this, with species richness peaking at a mean FRI of 10 years (Fig. 2c). These results suggest that species can recover from occasional short fire intervals (say fires five years apart), provided that long (>20 year) inter-fire intervals occur shortly thereafter.

While our results suggest that FRIs have only a limited influence on anuran species richness at present, future

changes to fire regimes are likely in our study region (south-eastern New South Wales; Cary 2002), as this area is forecast to receive reduced rainfall under future climate scenarios (Hennessy et al. 2007). Because larger breeding sites supported a disproportionately high species richness of anurans in our study area (Fig. 2b), drying could reduce the availability of valuable breeding habitats. While none of the species we have discussed are currently of conservation concern (Clayton et al. 2004), the combination of drought and increased fire frequency could be detrimental to population viability at local scales, with consequences for ecosystem processes (Beard et al. 2003).

Conclusions

We found no evidence that species richness of anurans was reduced by short FRIs. While we did find limited evidence for a relationship between occurrence and FRI for six species, these models were weakly supported in most cases, and were also inconsistent with hypothesized responses. In general, the majority of species were shown to be tolerant of variation in the fire regime, even (in some cases) where this involved exposure to high fire frequencies. Instead of fire, the majority of variation in anuran species richness and occupancy was explained by gradients of water-body size and hydroperiod. We therefore suggest that there is limited value in actively maintaining particular FRIs in an attempt to provide 'optimal' fire-maintained communities for individual anuran species in our study area (Parr and Andersen 2006). Maintaining a range of fire return intervals at anuran breeding habitats should be sufficient to avoid negative effects of inappropriate fire regimes on anuran species.

Acknowledgements – The authors are greatly indebted to the people of Wreck Bay Aboriginal Community on whose land this research was conducted. We thank the staff at Booderee National Park who assisted this research, particularly N. Dexter and M. Hudson. We thank C. MacGregor for valuable advice and support, and J. Wood for statistical advice. Our work was greatly improved by feedback from K. Stagoll and S. Bond. MJW was funded by a PhD scholarship provided by the ANU, and fieldwork funding was provided by The Australian National University's Vice-Chancellors fieldwork grants scheme.

References

- Andersen, A. N. et al. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. – *Austral Ecol.* 30: 155–167.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – *J. Wildlife Manage.* 74: 1175–1178.
- Attwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. – *For. Ecol. Manage.* 63: 247–300.
- Backer, D. M. et al. 2004. Impacts of fire-suppression activities on natural communities. – *Conserv. Biol.* 18: 937–946.
- Barker, J. et al. 1995. A field guide to Australian frogs. – Surrey Beatty and Sons.
- Barton, P. S. et al. 2011. Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. – *Biol. J. Linn. Soc.* 102: 301–310.

- Beard, K. H. et al. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. – *J. Trop. Ecol.* 19: 607–617.
- Bond, W. J. et al. 2005. The global distribution of ecosystems in a world without fire. – *New Phytol.* 165: 525–538.
- Bradstock, R. A. et al. 1998. Bushfire risk at the urban interface estimated from historical weather records: consequences for the use of prescribed fire in the Sydney region of southeastern Australia. – *J. Environ. Manage.* 52: 259–271.
- Bureau of Meteorology. 2010. Climate data for Point Perpendicular Lighthouse.
- Cary, G. 2002. Importance of a changing climate for fire regimes in Australia. – In: Bradstock, R. A. et al. (eds), *Flammable Australia*. Cambridge Univ. Press, pp. 26–48.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. – *Scand. J. Stat.* 11: 265–270.
- Clarke, M. F. 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? – *Wildlife Res.* 35: 385–394.
- Clayton, M. et al. 2004. CSIRO list of Australian vertebrates: a reference with conservation status. – CSIRO Publishing.
- Cogger, H. G. 1996. Reptiles and amphibians of Australia. – Reed Publishers.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. – *Science* 199: 1302–1310.
- Conroy, M. J. et al. 2011. Conservation in the face of climate change: the roles of alternative models, monitoring and adaptation in confronting and reducing uncertainty. – *Biol. Conserv.* 144: 1204–1213.
- Dale, V. H. et al. 2001. Climate change and forest disturbances. – *Bioscience* 51: 723–734.
- Dray, S. and Legendre, P. 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. – *Ecology* 89: 3400–3412.
- Driscoll, D. A. and Roberts, D. 1997. Impact of fuel-reduction burning on the frog *Geocrinia lutea* in southwest Western Australia. – *Aust. J. Ecol.* 22: 334–339.
- Driscoll, D. A. and Weir, T. 2005. Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. – *Conserv. Biol.* 19: 182–194.
- Driscoll, D. A. and Lindenmayer, D. B. 2012. Framework to improve the application of theory in ecology and conservation. – *Ecol. Monogr.* 82: 129–147.
- Driscoll, D. A. et al. 2010a. Resolving conflicts in fire management using decision theory: asset-protection versus biodiversity conservation. – *Conserv. Lett.* 3: 215–223.
- Driscoll, D. A. et al. 2010b. Fire management for biodiversity conservation: key research questions and our capacity to answer them. – *Biol. Conserv.* 143: 1928–1939.
- Finkele, K. et al. 2006. National daily gridded soil moisture deficit and drought factors for use in prediction of Forest Fire Danger Index in Australia. Research Report 119. – Bureau of Meteorology, Melbourne.
- Fisher, J. L. et al. 2009. Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. – *Biol. Conserv.* 142: 2270–2281.
- Fiske, I. and Chandler, R. 2010. Unmarked: a package for ecological analysis in R. – *J. Stat. Software.* 93: 1–23.
- Gill, A. M. 1977. Fire and the Australian flora: a review. – *Aust. For.* 38: 4–25.
- Gill, A. M. and Williams, J. E. 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. – *For. Ecol. Manage.* 85: 261–278.
- Glitzenstein, J. S. et al. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. – *Ecol. Monogr.* 65: 441–476.
- Grafe, T. U. et al. 2002. Frogs flee from the sound of fire. – *Proc. R. Acad. Sci. B* 269: 999–1003.
- Hamer, A. J. et al. 2002. Management of freshwater wetlands for the endangered green and golden bell frog (*Litoria aurea*): roles of habitat determinants and space. – *Biol. Conserv.* 106: 413–424.
- Hennessy, K. et al. 2007. Australia and New Zealand. – In: Parry, M. L. et al. (eds), *Climate change 2007: impacts, adaptation and vulnerability. Contrib. Working Grp II to the 4th Assess. Rep. of the Intergovernmental Panel on Climate Change*. Cambridge Univ. Press, pp. 507–540.
- Kisdi, E. 2002. Dispersal: risk spreading versus local adaptation. – *Am. Nat.* 159: 579–596.
- Langlands, P. R. et al. 2011. Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. – *J. Anim. Ecol.* 80: 558–568.
- Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – *Funct. Ecol.* 16: 545–556.
- Lindenmayer, D. B. et al. 2008a. Testing hypotheses associated with bird responses to wildfire. – *Ecol. Appl.* 18: 1967–1983.
- Lindenmayer, D. B. et al. 2008b. How predictable are reptile responses to wildfire? – *Oikos* 117: 1086–1097.
- MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – *Ecology* 83: 2248–2255.
- Mackey, R. L. and Currie, D. J. 2001. The diversity–disturbance relationship: is it really strong and peaked? – *Ecology* 82: 3479–3492.
- McCullagh, P. and Nelder, J. A. 1989. Generalized linear models. – Chapman and Hall.
- McWilliams, S. R. et al. 2007. Effects of prescribed fall burning on a wetland plant community, with implications for management of plants and herbivores. – *Western N. Am. Nat.* 67: 299–317.
- Means, D. B. et al. 2004. Amphibians and fire in longleaf pine ecosystems: response to Schurbon and Fauth. – *Conserv. Biol.* 18: 1149–1153.
- Moretti, M. et al. 2009. Taxonomical vs functional responses of bee communities to fire in two contrasting climatic regions. – *J. Anim. Ecol.* 78: 98–108.
- Murray, B. R. and Hose, G. C. 2005. Life-history and ecological correlates of decline and extinction in the endemic Australian frog fauna. – *Austral Ecol.* 30: 564–571.
- Parr, C. L. and Chown, S. L. 2003. Burning issues for conservation: a critique of faunal fire research in southern Africa. – *Austral Ecol.* 28: 384–395.
- Parr, C. L. and Andersen, A. N. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. – *Conserv. Biol.* 20: 1610–1619.
- Penman, T. D. and Brassil, T. E. 2010. Management of amphibian populations in Booderee National Park, southeastern Australia. – *Herpetol. Conserv. Biol.* 5: 73–79.
- Penman, T. D. et al. 2006. Meteorological effects on the activity of the giant burrowing frog (*Heleioporus australiacus*) in southeastern Australia. – *Wildlife Res.* 33: 35–40.
- Penman, T. D. et al. 2008. Spatial ecology of the giant burrowing frog (*Heleioporus australiacus*): implications for conservation prescriptions. – *Aust. J. Zool.* 56: 179–186.
- Pilliod, D. S. et al. 2003. Fire and amphibians in North America. – *For. Ecol. Manage.* 178: 163–181.
- Sanders, J. and Davies, M. 1984. Burrowing behaviour and associated hindlimb myology in some Australian hylid and leptodactylid frogs. – *Aust. Zool.* 21: 123–142.
- Schurbon, J. M. and Fauth, J. E. 2003. Effects of prescribed burning on amphibian diversity in a southeastern US National Forest. – *Conserv. Biol.* 17: 1338–1349.

- Schurbon, J. M. and Fauth, J. E. 2004. Fire as friend and foe of amphibians: a reply. – *Conserv. Biol.* 18: 1156–1159.
- Semlitsch, R. D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. – *J. Wildlife Manage.* 72: 260–267.
- Skelly, D. K. 1999. Distributions of pond-breeding anurans: an overview of mechanisms. – *Isr. J. Zool.* 47: 313–332.
- Skelly, D. K. et al. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. – *Ecology* 80: 2326–2337.
- Skelly, D. K. et al. 2002. Forest canopy and the performance of larval amphibians. – *Ecology* 83: 983–992.
- Taws, N. 1997. Vegetation survey and mapping of Jervis Bay Territory: a report to Environment Australia. – Taws Bot. Res.
- Taylor, G. et al. 1995. Geology, geomorphology, soils and earth resources. – In: Cho, G. et al. (eds), Jervis Bay: a place of cultural, scientific and educational value. Aust. Nature Conserv. Agency, pp. 41–52.
- Tracy, C. R. et al. 2010. Not just small, wet, and cold: effects of body size and skin resistance on thermoregulation and arboreality of frogs. – *Ecology* 91: 1477–1484.
- Tyler, M. J. 1994. Australian frogs: a natural history. – Cornell Univ. Press.
- Werner, E. E. et al. 2007. Amphibian species richness across environmental gradients. – *Oikos* 116: 1697–1712.
- Westerling, A. L. et al. 2006. Warming and earlier spring increase western US forest wildfire activity. – *Science* 313: 940–943.
- Woodruff, D. S. 1976. Courtship, reproductive rates and mating system in three Australian *Pseudophryne* (Amphibia, Anura, Leptodactylidae). – *J. Herpetol.* 19: 313–318.
- Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. – *Oikos* 29: 22–32.

Supplementary material (available as Appendix O19863 at <www.oikosoffice.lu.se/appendix>). Appendix 1.