Quantifying the effects of fire on frogs in Booderee National Park

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A thesis submitted for the degree of Doctor of Philosophy of The Australian National University, Canberra

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Litoria peronii
Declaration

This thesis is my own work, except where otherwise acknowledged (see preface and acknowledgements).

[Signature]

Martin Joseph Westgate

May 2013
Preface

Structure of the thesis

This thesis is structured as four articles on a related theme. For this reason, each chapter is formatted as a separate manuscript with its own figures and references, and is written in the plural first person (‘we’ instead of ‘I’). Further, the introduction is not intended as a literature review; each chapter begins by reviewing the literature necessary for that chapter. Where I refer to an earlier chapter, I will do so using the published citation for that article, or by chapter number where that article is still in preparation or review.

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Author attributions

All of the papers presented in this thesis were (or shall be) published with multiple authors. In each case, I am the first author, having conducted all data analysis and having written the first draft of each article. In subsequent edits, I integrated comments on each work provided by my coauthors: primarily by my supervisors (Don Driscoll and David Lindenmayer); but also by other authors where stated on the cover page for that chapter (i.e. Chris MacGregor in Chapter 4, and Gene Likens in the Appendix). The only exceptions to these statements occur in the appendix, in which section 5.1 combines paragraphs written by David Lindenmayer and myself, while the first draft of section 5.2 was written by David Lindenmayer. In addition to authorship of the final work, chapter 4 includes analysis of a seven-year dataset of terrestrial frog captures in Jervis Bay, collected mostly by Christopher MacGregor as part of David Lindenmayer’s Jervis Bay Fire Experiment.
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Thesis Abstract

Recurrent wildfires strongly affect the distribution and composition of biotic communities, and can also be highly destructive to human populations and infrastructure. Consequently, a number of fire management approaches (such as fire suppression, prescribed burning and selective clearing) are routinely implemented in many countries, with the aim of reducing the risk of catastrophic fires. While some of these approaches are known to be incompatible with the persistence of some plant and animal species, the extent to which inappropriate fire management is a threatening process for frog populations is largely unknown. Any effects of fire on frog populations that do occur are likely to be complex, because fire both kills individual animals, and may also influence frog movement through terrestrial locations (i.e. migration and dispersal). Further research on this topic would also be useful from a scientific perspective, in that frog populations can serve as interesting test cases for the investigation of fire ecology theories, which have typically been constructed for other animal taxa.

In this thesis, I address these research gaps on frog responses to fire, through a program of research undertaken in Booderee National Park, southeastern Australia. The resulting papers are arranged by increasing spatial scale, moving from responses of frog assemblages at breeding ponds (chapters 1 & 2), to frog behavior in the pond margin (chapter 3), to terrestrial movements at the landscape scale (chapter 4). In combination, these studies constitute a detailed investigation of the effects of recurrent fire on frog populations. This body of research represents an in-depth assessment of the viability of ecological theory for explaining variation in frog assemblages following fire.
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Context statement

Frogs and Fire

Recurrent wildfires have strong effects on the distribution and composition of biotic communities across large areas of the earth’s surface (Bond et al. 2005; Bowman et al. 2009; Bradstock et al. 2012). In addition to the important ecological role that fires play in terrestrial ecosystems, fires can have catastrophic effects on human populations and infrastructure (Gibbons et al. 2012). The need to mitigate the risk of catastrophic fires has lead to the adoption of a range of techniques for attempting to manage the size, frequency and severity of fires, including selective clearing of native vegetation, prescribed burning and fire suppression (Agee and Skinner 2005; Gill and Allan 2008). However, many species of plants and animals are dependent on particular fire regimes, some of which are incompatible with fire management approaches such as widespread fire suppression (e.g. Templeton et al. 2011). Further, the extent to which it has been possible to emulate natural or indigenous fire regimes has been limited by increasing land use intensity (among other factors; see Gill and Williams 1996). Therefore, identifying fire regimes that allow persistence of biodiversity – while still preserving key human infrastructure – is a major challenge for applied ecological research (Pausas et al. 2008; Driscoll et al. 2010a).

A logical approach to dealing with uncertainty regarding the effects of fire on biodiversity would be through the use of adaptive management, in which management activities are designed as experiments that guide improvements in future practice (see Walters and Holling 1990; Williams et al. 2009; Keith et al. 2011). However, experimental trials of competing fire management practices are difficult to implement (Driscoll et al. 2010b), particularly at the spatial and temporal scales at which fires typically occur (although see Andersen et al. 2005; van Wilgen et al. 2007). Further, biotic responses to fire regimes may occur over decades or even centuries (Haslem et al. 2011), and these scales are too long to provide meaningful feedback to management. These problems – combined with broader issues such as limited
interaction between management and research agencies (Russell-Smith et al. 2003; Stankey et al. 2003), and the difficulties of long-term monitoring and research (Lindenmayer and Likens 2011) – hinder attempts to apply adaptive management to problems at the interface of fire management and biodiversity management (for a full discussion, see the Appendix).

While adaptive management is often difficult to apply, these difficulties do not preclude the application of ecological research to conservation problems (Sutherland et al. 2004). In fact, even a basic understanding of a species’ ecological traits can be informative of their potential responses to fire regimes (Moretti and Legg 2009). Unfortunately, advances in the science of predicting the effects of fire on biotic communities have been more rapid for plant assemblages (Bradstock and Kenny 2003; Pausas et al. 2004) than for animal populations or assemblages (Parr and Chown 2003; Clarke 2008). A number of factors have reduced our ability to adequately describe animal responses to fire, but particularly important have been difficulties in quantifying how fire influences animal movements (including foraging, migration and dispersal) through complex and often fragmented environments (Amarasekare and Possingham 2001; Parsons and Gosper 2011). Consequently, fire management for conservation could be significantly improved through greater investigation of the fire responses of animal taxa, particularly those where dispersal has a strong influence on population dynamics.

In this thesis, I present the results of a series of research studies designed to empirically assess the response of frog populations to fire regimes in Booderee National Park, located in the Jervis Bay Territory on the southeast coast of Australia. My aim was to provide a foundation for improved fire management, to be incorporated with information on the fire responses of other taxonomic groups in the same location (see Lindenmayer et al. 2008a-c).

Research on the fire ecology of frog populations remains at an early stage, and so predicting the effects of any given fire regime on frog populations and assemblages remains difficult. For example, the effects of single fires on frog populations can be either severe (Driscoll and Roberts 1997) or undetectable (Hossack and Corn 2007), depending on the extent to which
frogs remain in terrestrial locations during fire. Further, in cases where individual frogs are killed by fire, it follows that recurrent fires might constitute a threatening process for assemblages of breeding frogs. However, the only example of a study demonstrating such a pattern that I know of (Schurbon and Fauth 2003) proved controversial (see Means et al. 2004; Robertson and Ostertag 2004; Schurbon and Fauth 2004). Finally, the extent to which fire affects migration and dispersal is unknown (see Semlitsch 2008 for a discussion of these processes), despite the importance of these processes for the persistence of frog populations (e.g. see Grant et al. 2010). While it is reasonable to expect that fire would reduce the availability of suitable microhabitats, and thereby reduce survival (Rittenhouse and Semlitsch 2007), there is some evidence that fire can actually increase movement rates for some species (Roznik et al. 2009). To resolve some of these uncertainties, in this thesis I investigate the effect of fires on frog populations both at breeding sites, and in terrestrial locations.

Besides the need to resolve the uncertainties that I have discussed above, there are a number of important reasons why further research on the fire ecology of frog populations is necessary. First, the complex life cycles displayed by many frog species make them useful test cases for theories developed to describe the fire ecology of other animal taxa (e.g. the habitat accommodation model (Fox et al. 2003); patch mosaic burning theory (Parr and Andersen 2006); and the effects of fire on landscape resistance (Vogt et al. 2009)). Second, research on factors that influence the persistence of frog populations is especially urgent in the context of ongoing declines resulting from the spread of chytrid fungus (Beebee and Griffiths 2005; Skerratt et al. 2007; Wake and Vredenburg 2008). Already, this pathogen is likely to have caused the extinction of one species from our study area (the Green and Golden Bell Frog, *Litoria aurea* (White and Pyke 2008), a species known to be highly sensitive to chytrid infection (Stockwell et al. 2010)). Therefore, one important goal of fire management is risk-avoidance. In this case, risk-avoidance would involve ensuring that ongoing land management practices do not increase pressure on already vulnerable frog populations. For these reasons, my
thesis is timely in attempting to address important gaps in the literature on frog ecology and conservation.

Summary of outcomes

In the following thesis (chapters 1-4), I present a series of research in which I use space-for-time substitution to infer the effects of historical fires on present-day frog assemblages (for examples of this approach see Driscoll and Henderson 2008; Langlands et al. 2011). I begin (chapter 1) by focusing on responses of frogs to fire at frequently flooded breeding sites, and our ability to use theory to accurately predict those responses. Specifically, I 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. I 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 I 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.

In chapter 2, I investigate the efficacy of a fire-management approach known as the pyrodiversity paradigm, which suggests that – as a rule of thumb – maintaining a fine-grained, patchy mosaic of fire histories should benefit biodiversity. Although this approach is conceptually appealing, critics argue that this approach could conceivably be used to justify any program of prescribed burning. My aim was to test (1) whether pyrodiversity metrics more strongly influenced frog species richness and composition than local fire histories, and (2) at what spatial scale pyrodiversity effects (if any) were most evident. I found that models of frog species richness and composition that took into account spatial variability in fire regimes ('pyrodiversity') provided better fit than models that accounted only for local effects of fire.
However, my results did not support the pyrodiversity paradigm for several reasons, namely: (1) Inclusion of pyrodiversity measures led to only marginal improvements in model fit; (2) Species richness responded negatively to pyrodiversity; and (3) Diversity of fire histories had different effects on richness and composition than did diversity of fire ages, suggesting that the term 'pyrodiversity' lacks precision. Instead, frequent fires close to breeding sites might constitute a threatening process for some frog species. Rather than following simple rules of thumb, my results suggest that, in this location, fire management for biodiversity conservation requires fire regimes that are appropriate to the spatial and temporal scales at which target species respond to environmental variation and disturbance.

In the final section of my thesis (chapters 3 & 4), I broaden the scope of my work to investigate terrestrial occurrence by frogs. I begin this section by investigating frog movement at fine scales around breeding ponds (chapter 3), a process that is essential for understanding factors that limit or promote animal dispersal in fragmented landscapes. In particular, topography is a major factor influencing the movement behaviour of many animal species, and therefore the extent of functional connectivity between habitat patches. For pond-breeding frogs, areas of low topographic relief (such as streams or drainage lines) offer damp microhabitats that can facilitate movement through otherwise dry landscapes. However, the extent of topographic bias of frog movements has rarely been quantified. I used a replicated study to compare captures in high- and low-relief transects for three frog species in my study area, and found that I captured frogs significantly more often on low-relief transects. However, capture rates decreased with increasing distance from water at similar rates on both high-relief and low-relief transects, and I observed few differences between adult and juvenile movements. My results suggest that although low-relief drainage lines are important for the pond-breeding frogs in question, ecologists and landscape managers should not discount the role of high-relief locations. Because low-relief drainage lines represent a small proportion of the pond margin, >90% of movements are likely to occur across high-relief locations. Therefore, for the species that I studied, buffer zones designed to conserve only hydrological networks would provide insufficient protection of
frequently used pond margins. In addition, drainage lines are unlikely to act as vital movement networks facilitating connectivity between breeding ponds. Instead, movement across slopes may be most important for facilitating functional connectivity.

In my final chapter, I build on my earlier findings by investigating occurrence of frogs in terrestrial locations at landscape scales (chapter 4). Conserving migratory species requires that breeding and overwintering habitats are maintained, along with the movement corridors that connect them. For migratory frogs, however, the properties of vital terrestrial habitats and movement corridors are often unknown. In this chapter, I relate captures of frogs in 109 terrestrial locations collected over seven years to the density of surrounding breeding sites. I then test for effects of topographic, vegetation and disturbance gradients on frog emigration, terrestrial habitat use, and landscape resistance. I show that for the species that we studied, ecological gradients have a strong influence on emigration rates, but very little influence on terrestrial habitat selection or landscape resistance at this scale. Fire frequency was the only variable to influence frog emigration rates, while vegetation and topography influenced frog occurrence in terrestrial locations. My results challenge the suggestion that landscape resistance and terrestrial habitat selection are universal mechanisms that drive the distribution of migratory frogs at landscape scales.

**Summary**

In summary, my thesis outlines a detailed investigation of the effects of recurrent fire on frog populations. In the following chapters I will show that fire can influence the composition of frog breeding assemblages (chapters 1 & 2), with some species responding positively and other negatively to some aspects of the fire regime. I will then show that frogs use a large proportion of the whole margin of frog breeding ponds, potentially leaving those populations vulnerable to fires that occur in any direction relative to breeding pond (chapter 3). Finally, I will show that fires at breeding sites reduce the number of frogs captured in nearby traps for some species, but that fire has no influence on terrestrial habitat use or landscape resistance for the species that I
studies (chapter 4). Consequently, this body of research represents both a source of information on the effects of fire on frog populations in my study location, as well as an in-depth assessment of the viability of ecological theory for explaining these effects.
References


Chapter 1

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

Limnodynastes peronii
Abstract

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.
Introduction

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 (Backer, et al. 2004, Zackrisson 1977) 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. 2010).

Community ecological theory provides a number of testable hypotheses regarding the potential effects of disturbance, but few hypotheses have been comprehensively investigated for animals (Clarke 2008, Driscoll, et al. 2010, Parr and Chown 2003), 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 (Lindenmayer, et al. 2008, Mackey and Currie 2001). Second, evidence from studies of plants (see Lavorel and Garnier 2002) and animals (Langlands, et al. 2011, Moretti, et al. 2009) 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 also might 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 (e.g. 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. 2010) that has limited the ability of ecologists to provide advice to policymakers about optimal fire management for biodiversity conservation (Clarke 2008, Driscoll, et al. 2010). 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 (Driscoll and Lindenmayer 2012, Parr and Andersen 2006).

Methods

Study area and anuran fauna

Booderee National Park is located in the Jervis Bay Territory, south-eastern Australia (approximate midpoint is 35° 10'S, 150° 40'E; for map see Figure 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 1200mm per year (Bureau of Meteorology 2010).

[Figure 1]

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 (see 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 by 10 metre quadrat positioned five metres from the waters’ edge at each site. Our second variable was the proportion of forest within a 200 metre buffer centered on each survey location, calculated from a vegetation map for the area (Taws 1997). We chose these attributes of aquatic habitat because they have been shown to strongly influence anuran assemblage composition in other ecosystems (Skelly 2001, Werner, et al. 2007).

We investigated four variables as potential predictors of detectability: temperature, humidity, Julian date, and soil moisture deficit (or SMD; see 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 44 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 \( \leq 1 \)). To account for variation in the distribution 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.

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 inter-species 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 2010). 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/max FRI’ and ‘detection + habitat + mean/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 supports shorter FRIs than forests in our study region (Attiwill 1994). Comparison of models with and without fire effects against a null model enables 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 (see above).

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 10 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 (ΔAICc = -0.03). Moreover, a model that included width, hydroperiod and their interaction was a better fit to the data (ΔAICc = -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 (β_{width}=0.22 ± 0.08, t_{(1,40)}=2.69, P=0.01), but only where those waterbodies contained water during a high proportion of visits (β_{hydroperiod}=0.14 ± 0.08, t_{(1,40)}=1.74, P=0.089; β_{interaction}=0.16 ± 0.08, t_{(1,40)}=1.90, P=0.064; see figure 2a, b).

Adding a linear term for mean FRI to our existing species richness model reduced model fit (ΔAICc= 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 (ΔAICc= -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; figure 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 (ΔAICc= 1.98, P=0.91) or quadratically (ΔAICc= 1.24, P=0.41).

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_{mean FRI}= 2.11, P=0.09, F_{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.

[Table 2]

Models of occupancy rates that contained FRI variables did have high AICc weight for six of eight species (Figure 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 (Figure 3 a-c). Two species with strong burrowing abilities were found to occur less often in areas with short maximum FRIs ($L. \text{peronii}: \beta=0.87 \pm 0.51$, $P=0.092$; $U. \text{tyleri}: \beta=0.87 \pm 0.51$, $P=0.088$; figure 3e, f), as was a third myobatrachid with weak burrowing abilities ($P. \text{haswelli}: \beta=1.42 \pm 0.79$, $P=0.073$). 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 ($L. \text{peronii}$). Coefficient values, standard errors and $P$ values from the models with lowest AICc for each species are provided in Table A1.

[Figure 3]

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.

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 re-colonizing 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. (2008) 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 (Figure 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 south-eastern 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 (see Gill and Williams 1996, Glitzenstein, et al. 1995). Despite these differences, our results are consistent with work on other taxa in our study region (Lindenmayer, et al. 2008, 2008). 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

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 AICs weights; see 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* & *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 (e.g. 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 (see 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, e.g. 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 & C. signifera) fire return intervals. However, these species were either very rare (L. nudidigitus & 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 (ΔAICc <3 across all models for all three species; see 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 & 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 (Figure 3), although mean FRIs could be lower than this, with species richness peaking at a mean FRI of 10 years (Figure 2c). These results suggest that species can recover from occasional short fire intervals (say fires 5 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; see 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 (Figure 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 (see 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

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scholarship provided by the ANU, and fieldwork funding was provided by The Australian National University's Vice-Chancellors fieldwork grants scheme.

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Tables and Figures

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.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Sites</th>
<th>Visits</th>
<th>Traits</th>
</tr>
</thead>
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<tr>
<td>Myobatrachidae</td>
<td><em>Crinia signifera</em></td>
<td>40 (0.86)</td>
<td>142 (0.61)</td>
<td>None tested</td>
</tr>
<tr>
<td></td>
<td><em>Uperoleia tyleri</em></td>
<td>16 (0.34)</td>
<td>52 (0.21)</td>
<td>Burrowing</td>
</tr>
<tr>
<td></td>
<td><em>Paracrinia haswelli</em></td>
<td>14 (0.30)</td>
<td>38 (0.16)</td>
<td>None tested</td>
</tr>
<tr>
<td></td>
<td><em>Limnodynastes peronii</em></td>
<td>10 (0.20)</td>
<td>21 (0.09)</td>
<td>Burrowing</td>
</tr>
<tr>
<td></td>
<td><em>Pseudophryne bibronii</em></td>
<td>4 (0.09)</td>
<td>6 (0.03)</td>
<td>Burrowing</td>
</tr>
<tr>
<td></td>
<td><em>Limnodynastes dumerillii</em></td>
<td>2 (0.05)</td>
<td>6 (0.03)</td>
<td>Burrowing</td>
</tr>
<tr>
<td>Hylidae</td>
<td><em>Litoria peronii</em></td>
<td>13 (0.30)</td>
<td>40 (0.16)</td>
<td>Climbing</td>
</tr>
<tr>
<td></td>
<td><em>Litoria jervisienisis</em></td>
<td>9 (0.20)</td>
<td>26 (0.10)</td>
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<td><em>Litoria nudidigitus</em></td>
<td>8 (0.18)</td>
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<tr>
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<td><em>Litoria freycineti</em></td>
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<td>7 (0.03)</td>
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<td><em>Litoria dentata</em></td>
<td>3 (0.07)</td>
<td>3 (0.01)</td>
<td>Climbing</td>
</tr>
<tr>
<td></td>
<td><em>Litoria tyleri</em></td>
<td>3 (0.07)</td>
<td>3 (0.01)</td>
<td>Climbing</td>
</tr>
</tbody>
</table>
Table 2: AICc of alternative candidate occupancy models for each species. The model with the lowest AICc for each species is given in bold. See text for full explanation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Detection only</th>
<th>Habitat</th>
<th>Mean FRI</th>
<th>Max FRI</th>
<th>Habitat + Mean FRI</th>
<th>Habitat + Max FRI</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crinia signifera</em></td>
<td>285.25 (0.16)</td>
<td>284.97 (0.18)</td>
<td>286.73 (0.08)</td>
<td>287.49 (0.23)</td>
<td>286.63 (0.08)</td>
<td>284.16 (0.27)</td>
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<td><em>Limnodynastes peronii</em></td>
<td>119.81 (0.02)</td>
<td>114.75 (0.23)</td>
<td>117.06 (0.07)</td>
<td>117.64 (0.05)</td>
<td>114.28 (0.29)</td>
<td>113.89 (0.35)</td>
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<tr>
<td><em>Paracrinia haswelli</em></td>
<td>137.73 (0.00)</td>
<td>119.21 (0.25)</td>
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<td>117.38 (0.63)</td>
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<tr>
<td><em>Uperoleia tyleri</em></td>
<td>178.89 (0.00)</td>
<td>168.00 (0.32)</td>
<td>175.65 (0.01)</td>
<td>174.90 (0.01)</td>
<td>168.66 (0.23)</td>
<td>167.36 (0.44)</td>
</tr>
<tr>
<td><em>Litoria freycineti</em></td>
<td>59.42 (0.27)</td>
<td>60.58 (0.15)</td>
<td>60.39 (0.17)</td>
<td>60.02 (0.20)</td>
<td>61.48 (0.10)</td>
<td>61.08 (0.12)</td>
</tr>
<tr>
<td><em>Litoria jervisiensis</em></td>
<td>107.58 (0.00)</td>
<td>95.64 (0.62)</td>
<td>105.94 (0.00)</td>
<td>107.10 (0.00)</td>
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</tr>
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<td><em>Litoria nudidigitus</em></td>
<td>99.87 (0.10)</td>
<td>98.89 (0.17)</td>
<td>98.53 (0.20)</td>
<td>100.36 (0.08)</td>
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<td><em>Litoria peronii</em></td>
<td>145.90 (0.00)</td>
<td>121.98 (0.67)</td>
<td>144.39 (0.00)</td>
<td>146.37 (0.00)</td>
<td>124.67 (0.17)</td>
<td>124.82 (0.16)</td>
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</table>
Figure 1: Map of the study area.
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 2c. Filled regions show 95% confidence intervals. Size of squares shows the number of sites at each point.
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.

a) *L. nudidigitus*  
b) *L. freycineti*  
c) *C. signifera*  
d) *P. haswelli*  
e) *U. tyleri*  
f) *Lim. peroni*
Table A1: Coefficient values, standard errors and P values from the models with lowest AIC for each species

<table>
<thead>
<tr>
<th>Species</th>
<th>Variable</th>
<th>Occupancy ((\hat{y}))</th>
<th>Detection ((p))</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Est.</td>
<td>SE</td>
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<tr>
<td>Litoria freycineti</td>
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<tr>
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<td>Max FRI</td>
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<tr>
<td></td>
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<td>0.65</td>
</tr>
<tr>
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<td>Hydrop.</td>
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</tr>
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<td>Forest</td>
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<td>0.51</td>
</tr>
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<td>Width</td>
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<td>0.54</td>
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<td></td>
<td>Max FRI</td>
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<td>0.51</td>
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<tr>
<td>Paracrinia haswelli</td>
<td>Intercept</td>
<td>-1.18</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Width</td>
<td>1.71</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>Hydrop.</td>
<td>1.64</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
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<tr>
<td></td>
<td>Max FRI</td>
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<td>Upperolea tyleri</td>
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<td>Max FRI</td>
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</table>
Chapter 2

Does pyrodiversity influence frog species richness or composition?

*Pseudophryne bibronii*
ABSTRACT

Aim: The pyrodiversity paradigm is a rule of thumb, which suggests that creating a fine-grained, patchy mosaic of fire histories will enable managers to maintain biodiversity in fire-prone regions. However, further research is required before the pyrodiversity paradigm can be widely and safely adopted. For this paper, we tested: (1) whether pyrodiversity metrics more strongly influenced frog species richness and composition than local fire histories, and (2) at what spatial scale any pyrodiversity effects were most evident.

Location: Jervis Bay, southeastern Australia

Methods: We used aural surveys of frogs at 44 breeding sites to determine species richness and composition. We then took two fire metrics – the time since last fire, and length of the longest period without fire in the preceding 40 years – and used them to calculate two pyrodiversity metrics (i.e. Shannon’s diversity of fire classes in the region surrounding each breeding site), for a range of buffer widths. Finally, we tested whether models of species richness and composition containing pyrodiversity metrics performed better than models describing the local fire regime, or models without fire effects.

Results: We found that models that incorporated spatial variability in fire regimes (‘pyrodiversity’) provided marginally better fit to frog species richness and composition data than competing models. However, species richness displayed a weak, negative response to pyrodiversity.

Main Conclusions: We found no evidence that instituting a patchy mosaic of fire ages would benefit frog populations or assemblages. Instead, frequent fires might constitute a threatening process for some frog species, albeit a weak one. Further, diversity of fire histories had different effects on richness and composition than did diversity of fire ages, suggesting that the term ‘pyrodiversity’ lacks precision.
INTRODUCTION

Protection of human and ecological assets from severe wildfires are common goals for landscape managers in fire-prone locations (Gill & Allan, 2008; Gibbons et al., 2012). However, quantifying the effectiveness of fire management activities (such as prescribed burning or fire suppression) for biodiversity conservation remains difficult. As a result, fire management occurs in a context of ecological uncertainty (Driscoll et al., 2010a), occasionally leading to the adoption of inappropriate fire regimes that result in biodiversity loss (Burgman et al., 2006; Woinarski & Recher, 1997). Consequently, preventing further losses requires research that quantifies the biodiversity outcomes of alternative fire regimes.

In the absence of data quantifying the effects of fire on biodiversity, the pyrodiversity paradigm has sometimes been used to guide fire management actions (Parr & Andersen, 2006; Clarke, 2008). This approach advocates the creation of a fine-grained mosaic of varying fire ages, and is based on the premise that highest biodiversity will occur where habitat for both fire-tolerant and fire-intolerant species occurs in close proximity (Bradstock et al., 2005). Although the pyrodiversity paradigm has received some empirical support (e.g. Bliege Bird et al., 2012), it has also been criticized on the grounds that most fires add diversity to an existing fire mosaic. Consequently, almost any program of prescribed burning could conceivably be justified under the pyrodiversity paradigm (Driscoll et al., 2010b), potentially even those that involve burning of species-rich fire refugia (Taylor et al., 2012).

A logical approach to resolving these disputes is to quantitatively test the efficacy of the 'pyrodiversity begets biodiversity' hypothesis. However, work on this topic has been hindered by the notorious difficulties associated with testing the effects of fire on biodiversity (Chen & Taylor, 2012), and on animal populations and assemblages in particular (Parr & Chown, 2003; Clarke, 2008). Some authors have taken the view that if a community lacks fire responses of
any kind, then the pyrodiversity paradigm will be invalid (Davies et al., 2012). Others have tested the predictive power of pyrodiversity metrics against alternative measures of the fire regime, such as the time since fire (Taylor et al., 2012), or the frequency of fires in a given location (Bradstock et al., 2005). While these have been important contributions, we argue that two key criticisms of the pyrodiversity paradigm have yet to be adequately addressed.

First, the pyrodiversity paradigm states that fine-grained mosaics are desirable, but provides little guidance as to the upper or lower bounds of desirable fire sizes, frequencies, or intensities (Driscoll et al., 2010b). In some locations, traditional practices can provide a baseline for managing fire in a patchy manner (Cissel et al., 1999), but these are often either unknown, or difficult to implement (Bowman, 1998). An alternative approach is to determine how the relationship between the fire regime and biodiversity changes with increases in the size of the region in which pyrodiversity is measured. The scale at which model fit is maximized can then be interpreted as the scale at which most species respond to pyrodiversity (see Ficetola et al., 2008). Although species that use the landscape at fine spatial scales can benefit from small fire sizes (Bliege Bird et al., 2008), studies that investigate or account for scale when measuring fire effects are rare (Clarke, 2008).

Second is the broader question of how the term ‘pyrodiversity’ should be interpreted. Some authors have interpreted the pyrodiversity paradigm as stating that managers should maximize the diversity of fire ages in a given area (e.g. Taylor et al., 2012). A potentially important extension of this work is that species or communities might respond to the spatial diversity of aspects of the fire regime other than the time since the last fire (Faivre et al., 2011). For example, variation in fire intensity can cause patchy fire mosaics after a single fire; but spatial variation in fire intensity is difficult to quantify. A more tractable approach is to calculate the spatial diversity of inter-fire intervals, which could be interpreted as the diversity of fire histories in a given region. Such metrics may be particularly important where species or communities respond primarily to the interval between successive fires in a given location, rather than the time since a single fire has occurred (e.g. Lindenmayer et al., 2008).
In this paper, we investigate the two problems described above for a pond-breeding frog assemblage. Although we are unaware of any studies that have investigated the effect of pyrodiversity on frog assemblages to date, there are several reasons why we might expect pyrodiversity to be important. First, some frog species respond positively, and others negatively, to increasing fire frequencies (Westgate et al., 2012a), suggesting that locations with a diversity of fire frequencies might support combinations of species that would not otherwise co-occur. Second, there is increasing recognition that processes that impact frog populations in terrestrial areas—such as development (Harper et al., 2008) or logging (Semlitsch et al., 2009)—can have a strong influence on nearby breeding assemblages. Fire is one such process, as it can kill terrestrial frogs (Driscoll & Roberts, 1997). Finally, recent evidence suggests that effects of fires on frog populations can be long-lasting (Hossack et al., 2012), in which case the fire history of the region surrounding a breeding pond could have subtle, long-term effects on breeding assemblages. For these reasons, we argue that further investigation is warranted regarding the potential effects of pyrodiversity on frog populations and assemblages.

In testing the applicability of the pyrodiversity paradigm, we build on earlier work where we tested the extent to which the history of inter-fire intervals at frog breeding sites explained variation in the occurrence or richness of frog species (Westgate et al., 2012a). However, we have yet to address the role of spatial variation in fire regimes, and so we expand on that work here by asking (1) whether pyrodiversity metrics more strongly influenced frog species richness and composition than local fire histories, and (2) at what spatial scale any pyrodiversity effects were most evident. We anticipated that spatial diversity in fire histories might plausibly influence frog assemblages (Russell et al., 1999), but would most likely be related to diversity of fire histories rather than diversity of fire ages (Schurbon & Fauth, 2003). Further, because most individual frogs do not move large distances from breeding sites (Westgate et al., 2012b; Semlitsch & Bodie, 2003), we anticipated that pyrodiversity would influence frog communities at relatively fine spatial scales.
A considerable amount of work is still required before the pyrodiversity paradigm can be reliably used as a rule-of-thumb for fire management in a biodiversity conservation context (Bradstock et al., 2005; Clarke, 2008; Driscoll et al., 2010a; Parr & Andersen, 2006). Further, to the best of our knowledge, frogs are a taxon for which the predictions of patch-mosaic burning theory have yet to be empirically tested. In this paper, we address a number of criticisms of patch-mosaic burning for the first time, for a taxon that has received little research attention in the fire ecology literature.

METHODS

Study area and survey methods

Our study area was Booderee National Park, located on the southern peninsula of Jervis Bay, southeastern Australia (Fig. 1). The study area has high rainfall relative to inland locations at the same latitude (Bureau of Meteorology, 2010), with the result that it has both a relatively rich frog fauna, and a number of reliably flooded streams and wetlands (Westgate et al., 2012a). Booderee National Park supports 12 frog species, evenly split between the families Myobatrachidae (southern frogs) and Hylidae (tree frogs; Cogger, 1996). One species has recently become extinct from our study area (Litoria aurea; see White & Pyke, 2008), while the invasive cane toad (Bufo marinus) does not occur there at the time of writing.

We identified 119 sites that might plausibly flood at some point during the year, and used five-minute aural surveys to detect calling males on at least four occasions per site between August 2007 and February 2008 (max visits = 8, mean = 5.25). For this study, we analyzed data from only those sites that flooded for an appreciable period (typically for two consecutive visits undertaken ~2 weeks apart), and could therefore be assumed to be available for colonization by breeding frogs (n= 44).

[Fig. 1]
Variables

We calculated three response variables to quantify properties of the frog assemblage in our study location. Our first variable was species richness, calculated as the sum of all species located at a given site. Our second and third response variables were the first two axes of a correspondence analysis (Greenacre, 1984) of species occurrences across all sites at which any species were detected (n=43). These two variables are referred to as CA1 and CA2 from this point on.

We calculated two ‘habitat’ and four ‘fire’ raster datasets with 20 metre resolution, using the ‘raster’ R package (Hijmans & Van Etten, 2012). We derived our two habitat covariates from a map of vegetation and land cover types by interpreting and categorizing information on the structural properties of those vegetation types (Taws, 1997; Ingwersen, 1976). Our first habitat variable was an index of canopy height, with low values representing low vegetation types such as grasslands, sedgelands and heaths, while high values denoted sclerophyll forests and rainforests. Our second habitat variable was more specific to frog habitat requirements, and ranked vegetation and land cover types in proportion to the availability of water that they supported. Consequently, low values denoted locations that were either saline (e.g. saltmarsh) or very dry (e.g. *Eucalyptus pilularis* forest), while high values denoted locations that retained either water close to the surface (e.g. wet heath) or open water (lakes and waterholes). Details of our rankings of vegetation and land cover types according to these categories are given in Fig. A1.

We calculated two ‘local’ fire variables: the time since the last fire (TSF) and the length of the maximum fire return interval to have occurred in the last 40 years (maximum FRI). In both cases, the maximum possible value was 40 years, for locations that were unburned during the period for which data were available; however such locations made up only a small proportion of the total dataset (13.5% by area). Further, where a location had only been burned once, we calculated the maximum fire return interval as the longest period without fire in that 40-year
period. Consequently, our approach may underestimate the ‘true’ maximum interval in infrequently burned locations due to dataset constraints. We log-transformed both surfaces prior to any further analysis.

We used our two fire-related raster datasets to calculate two pyrodiversity metrics: Diversity of fire ages (which used the TSF layer); and diversity of fire histories (which used the maximum FRI layer). We calculated both of our pyrodiversity metrics using Shannon’s diversity index, such that the range of fire values within a buffer was scaled by their proportional coverage within that buffer (see Taylor et al., 2012). Consequently, this approach incorporates information on the spatial diversity of fire ages or histories, but ignores the magnitude of any differences in fire ages or histories. Fortunately, the range of fire ages in our system was relatively low (particularly in relation to locations where fire ages may differ by a century or more, e.g. Nimmo et al., 2012), and so the effect of this loss of information on our results is likely to be minimal. Our final stage was to divide each pyrodiversity value by the proportion of the buffer area that was within the study area, effectively normalizing each pyrodiversity metric for edge effects.

Statistical Analysis

Our first stage of analysis was to create and rank models of species richness and composition that contained non-fire covariates only. We used Generalised Linear Models (McCullagh & Nelder, 1989) with a Poisson distribution and a log link to model species richness, while we used a Gaussian distribution for both species composition models. At this stage, we created four candidate models for each response variable: a null model with no covariates; two that contained one each of vegetation structure and water availability; and one that contained both vegetation structure and water availability. We then ranked these four models by AICc weight (Burnham & Anderson, 2002). We selected the best combination of covariates by choosing the model with the lowest AICc, except that models containing an additional variable were selected
only if they resulted in a reduction in AICc of two or more (Arnold, 2010). We conducted all analyses in the R statistical package (R Core Development Team, 2010).

Our second stage of analysis was to test the scale at which each of our three frog assemblage metrics responded to pyrodiversity. Shannon’s diversity index will change according to the size of the buffer used to define the region surrounding each site, and so we calculated six versions of each of our two pyrodiversity measures (time since fire, maximum fire return interval). The buffer widths that we used to calculate our pyrodiversity metrics were 50, 100, 250, 500, 1000 and 1500 metres. We added each of these 12 measures to our existing ‘habitat only’ models, and determined how the coefficient of each pyrodiversity variable changed as we increased the scale at which it was measured. We selected the ‘best’ buffer distance as that with the 95% confidence interval of the coefficient that showed greatest distance from (or smallest overlap with) zero, for each response variable.

Our final stage of analysis was to compare five fire-related models for each response variable (i.e. species richness or composition). Our null model included only habitat covariates selected at stage one. The remaining models all included the selected habitat covariate(s), plus one of the four possible fire covariates: max FRI; TSF; diversity of max FRI; or diversity of TSF (where the final two variables were measured at the ‘optimal’ scale identified in our second stage of analysis). As in our first stage of analysis, we ranked these models by AICc weight. We concluded by plotting predicted values derived from the highest-ranked model.

RESULTS

Frog species richness and composition

Our aural surveys detected twelve species, of which six were tree frogs (family Hylidae) and six ground frogs (family Myobatrachidae). Species richness was strongly left-skewed; although only three sites were occupied by a single species, a further 11 sites contained only two species. Species-poor sites were dominated by *Crinia signifera*, which occurred at all sites that contained any species ($n_{sites}=43$), while *Pseudophryne bibronii* occurred at 35 sites. The top
The five most common species were all Myobatrachids (also included were *Uperoleia tyleri* (*n* (sites)=17), *Paracrinia haswelli* (*n* (sites)=15) and *Limnodynastes peronii* (*n* (sites)=14)), with *Litoria peronii* being the most common Hylid (*n* (sites)=13). Five sites had eight or more species, with maximum richness at a single site being 10 species.

Correspondence analysis showed that sites containing still-waterbody specialists (such as *Litoria peronii, Paracrinia haswelli, Litoria jervisiensis* and either or both *Limnodynastes* spp.) represented a distinct compositional unit (Fig. 2). Two other compositional units were distinguishable using correspondence analysis: common generalists (*C. signifera* and *P. bibronii*); and a more disparate group containing Hylids with unusual habitat requirements (*Litoria freycineti, L. nudidigitus & L. dentata*).

Our first modelling stage showed that frog species richness and composition were strongly influenced by water availability, but not by vegetation structure. For both species richness and CA2, the model containing only water availability had the highest AICc weight (0.52 and 0.68 respectively), indicating high support. For CA1, the model with the lowest AICc included both water availability and vegetation structure, but only decreased AICc by 1.07 over the next highest-ranking model, which contained water availability only.

**Scale of measurement of pyrodiversity**

In most cases, the scale at which pyrodiversity was measured had only a limited effect on the strength of its relationship with species richness or composition. In particular, the estimated coefficient for a given buffer width was never outside of the 95% confidence intervals estimated for any other width (Fig. 3). Further, both pyrodiversity measures gave generally similar results when used to predict the same response variable: both diversity of TSF and diversity of maximum FRI were negatively related to species richness; while these same variables were both positively related to CA1. We only detected a difference in the sign of pyrodiversity coefficients for CA2, with diversity of TSF having a positive coefficient, and diversity of maximum FRI a negative coefficient.
Although support for pyrodiversity variables was low at most spatial scales that we investigated, there were some important trends. In our models of CA1, overlap of the 95% confidence intervals with zero was substantially lower for diversity of maximum FRI than for diversity of TSF, while the opposite was true for CA2. Further, the ‘optimal’ scale for measuring pyrodiversity was generally shown to be at fine scales, with 50 metres being selected three times and 250 metres twice.

Comparison of fire metrics

After accounting for scale effects, pyrodiversity metrics outperformed local measures of the fire regime in all models (Table 1). In particular, the highest-ranking models for both species richness and CA2 included diversity of TSF as a covariate. However, neither model had high support, with the top model improving AICc by only 0.82 for species richness, and 0.83 for CA2, relative to the null model (which included ‘water availability’ as the only covariate in each case). In contrast, the best-fitting model for CA1 included diversity of maximum FRI, and was strongly supported with a ΔAICc of -2.44, relative to a model that lacked any fire effects.

Each response variable also had a different order of high-ranking models. For species richness, the two pyrodiversity metrics (diversity of either TSF or maximum FRI) outperformed the null model, but local fire variables (TSF and maximum FRI) did not. For CA1, models containing maximum FRI or diversity of maximum FRI outperformed those containing either TSF variable. The opposite was true for CA2, with models containing TSF or diversity of TSF outperforming models including either maximum FRI or diversity of maximum FRI.

Taking the highest-ranked model as ‘final’ for each response variable, we found that species richness increased significantly with water availability ($\beta = 0.35 \pm 0.07$, $P < 0.001$), but decreased with increasing diversity of TSF ($\beta = -0.16 \pm 0.09$, $P = 0.095$). However, the latter result was not
statistically significant, and appeared to be strongly influenced by outliers; the scale at which diversity was measured for this model (i.e. within a 50 metre buffer) meant that most sites had zero pyrodiversity (Fig. 4(d)). In contrast, CA1 showed a negative relationship with water availability ($\beta = -0.30 \pm 0.16$, $P = 0.058$), and a positive relationship with diversity of maximum FRI ($\beta = 0.34 \pm 0.16$, $P = 0.034$). Finally, CA2 also showed a negative relationship with water availability ($\beta = -0.50 \pm 0.16$, $P = 0.004$) and a positive relationship with diversity of TSF ($\beta = 0.30 \pm 0.16$, $P = 0.076$).

[Fig. 4]

DISCUSSION

In this paper, we tested whether pyrodiversity influenced the richness or composition of frog assemblages, and if so, at what spatial scale. A positive relationship between frog species richness and pyrodiversity would indicate that the pyrodiversity paradigm was a potentially useful approach for directing fire management activities for the conservation of frog assemblages. We found that although pyrodiversity metrics (i.e. those metrics that quantified the spatial diversity of fire ages or histories surrounding each breeding site) provided better fit to frog species richness and composition than variables that accounted only for local effects of fire, their effects were relatively weak, and were largely inconsistent with the predictions of the pyrodiversity paradigm. We discuss these results and their implications in the remainder of our paper.

Our results suggest that pyrodiversity has only limited effects on the composition and richness of frog assemblages in our study area. Although pyrodiversity was always selected as the top-ranked variable describing species richness or composition, pyrodiversity variables only marginally increased fit relative to models that contained either no fire variables, or alternative metrics describing the fire regime (Table 1). Only in one case was a pyrodiversity variable a statistically significant predictor of species richness or composition (CA1 responded significantly to the diversity of maximum FRI; Fig 4(e)). Instead, our work showed frog
species richness and composition were predominantly influenced by water availability (see also Skelly, 2001). Therefore, it is unlikely that a decision to institute patchy fire mosaics would strongly influence frog populations, presuming that managers sought to avoid overly frequent fires near breeding sites (Westgate et al., 2012a) or other potential fire refugia (Taylor et al., 2012).

Despite generally weak effects of pyrodiversity, we found that increased pyrodiversity was associated with a shift from species-rich assemblages to locations that contained only *L. nudidigitus* (in relation to diversity of maximum FRI) or *L. dentata* (in relation to diversity of TSF). Such a relationship between species composition and pyrodiversity could result from a number of processes. The fact that both CA axes were also correlated with water availability is suggestive that *L. nudidigitus* and *L. dentata* may be dry location specialists, in which case these species’ apparent relationship with pyrodiversity may result from the fact that drier locations are more flammable. An alternative explanation could be that these frog species require resources that occur at distinct seral stages, as has been described for some animal taxa (e.g. the partridge pigeon (*Geohaps smithii*; Fraser et al., 2003), Leadbeater’s possum (*Gymnobelideus leadbeateri*; Smith & Lindenmayer, 1992)). For example, unburned locations may support high densities of rest and elevated calling sites, while burned locations can have decreased soil water repellency in *Eucalypt* forests (Doerr et al., 2006), potentially leading to higher moisture retention in soils and corresponding increases in frog survival (Rittenhouse et al., 2009).

However, further research would be required to determine the precise mechanistic basis of the frog responses to pyrodiversity that we have observed.

We also found that the effects of pyrodiversity metrics were largely invariant with increasing spatial scale (Fig. 3). In particular, we found that the 95% confidence intervals of pyrodiversity coefficients overlapped zero at nearly every scale for which we measured pyrodiversity. Nevertheless, it is important to recognise that our approach to detecting the effects of pyrodiversity on frog assemblages was only sensitive to changes in the probability of frog occurrence at breeding sites. Therefore, it is possible that fire could strongly influence frog
dispersal rates or abundance at large distances from water, and still not be detected by our study. We suggest that further investigation of such effects is warranted, particularly given evidence suggesting that slight variations in dispersal rates can strongly influence the viability of frog populations (Grant et al., 2010).

In general, our results suggest that PMB theory is of little usefulness in predicting frog responses to fire regimes in our study location, for two reasons. First, the relationship that we observed between species richness and pyrodiversity – although not statistically significant – was negative, in contrast to the hypothesis that pyrodiversity begets biodiversity (Parr & Andersen, 2006). Second, our results suggest that the term ‘pyrodiversity’ lacks sufficient precision to be used as the basis for fire management decisions. This was because the diversity of fire histories was a significant predictor of CAI, while a more common metric (diversity of fire ages) influenced different metrics of frog assemblage structure, and models containing this variable had low AICc weight (Table 1). Consequently, our results suggest that spatial and temporal diversity of fire regimes can each have differential impacts on individual species (Bradstock et al., 2005), and therefore on the structure and richness of frog assemblages (Schurbon & Fauth, 2003; Westgate et al., 2012a). By not taking this variation into account, PMB theory lacks the conceptual tools need to be usefully predictive of population dynamics in our study system.

CONCLUSIONS

In this paper, we investigated the relationship between pyrodiversity, and the richness and composition of frog assemblages. We found limited support for any fire effects on frog assemblages, and those relationships that we did identify did not support the view that ‘pyrodiversity begets biodiversity’. Instead, pyrodiversity may have a moderate negative effect on species richness. Further, diversity of fire ages and diversity of fire histories influenced different components of species composition, though further research on the interaction between hydroperiod and pyrodiversity gradients would be necessary to determine the mechanisms at
play here. Based on this evidence, we suggest that the pyrodiversity paradigm would be a poor basis for fire management of frog populations in our study location. More broadly, we suggest that managers should consider the mechanisms underlying biotic responses to fire regimes before implementing any given fire management plan (Driscoll et al., 2010b), rather than adopting a blanket view about the usefulness (or lack thereof) of the pyrodiversity concept.
REFERENCES


Table 1: AICc values of models with different fire variables, with weights given in parentheses.

The ‘best’ model selected at each analysis stage is shown in bold.

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<th>Predictor Variables</th>
<th>Modelling stage</th>
<th>Predictor Variables</th>
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<td>131.99 (0.07)</td>
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FIGURE LEGENDS

Fig 1: a) Map of the study area showing survey locations as dots. Additional plots show patterns of time since fire (b) and maximum fire return interval (c).

Fig 2: Correspondence analysis of frog species occurrences at 43 occupied breeding sites. Circles represent sites with identical species composition, while the size of each circle gives the number of sites containing each unique combination of species.

Fig. 3: Effect of buffer size on pyrodiversity coefficients. Error bars give 95% confidence intervals. Note that vertical axes have different scales between plots. Distances selected for inclusion in later analysis stages are shown with a white square.

Fig. 4: Predictions of variable effects for variables included in the three final model of species richness or composition. Error bars give 95% confidence intervals. Values on the X axes give the number of standard deviations from the mean.
FIGURES

Fig. 1

a) Scale (Kilometers)

b) Time Since Fire (Years)

c) Maximum FRI (Years)
Fig A1: Vegetation communities ranked according to axes used in this paper

Key (vegetation classifications from Taws, 1997)
- FdEp Eucalyptus pilularis dry forest
- FwEp Eucalyptus pilularis wet sclerophyll forest
- FdEb Eucalyptus botryoides dry forest
- FsEb Eucalyptus botryoides wet sclerophyll forest
- FsCg Casuarina glauca swamp forest
- FdEpan Eucalyptus paniculata dry forest
- FdBi Banksia integrifolia dry forest
- RIAFL Littoral rainforest
- RdBi Backhousia myrtifolia dry rainforest
- RpCa Ceratopetalum apetalum warm temperate rainforest
- WdBi Banksia integrifolia dry woodland
- WdBi Banksia serrata dry woodland
- WdEg Eucalyptus gummifera dry woodland
- WdEesEg Eucalyptus sclerophylla - E. gummifera dry woodland
- WdEesEg Eucalyptus sieberi - E. gummifera dry mallee
- WmAm Arvicantha marina mangrove woodland
- WsMl Melaleuca linearifolia swamp woodland
- MdEg Eucalyptus gummifera dry mallee
- MdEpan Eucalyptus poniculata dry mallee
- SsLp Leptospermum polygalifolium swamp shrubland
- SsMc Melaleuca capitata swamp shrubland
- SsMc Melaleuca ericifolia swamp shrubland
- SsMs Melaleuca squarrosa swamp shrubland
- HlcBf Baeckea imbricata coastal heath
- HldAd Allocasuarina distyla dry heath
- HiBe Banksia ericifolia intermediate heath
- HiSi Sprengelia incarnata intermediate heath
- HwLJ Wet heath
- HkAd Allocasuarina distyla rocky heath
- ScAsL1 Acacia sophorae - Leptospermum laevigatum coastal shrubland
- ScL1 Leptospermum laevigatum coastal shrubland
- SdAd Allocasuarina distyla dry shrubland
- SdAv Allocasuarina verticillata dry shrubland
- SkAdMc Allocasuarina distyla - Melaleuca capitata rocky shrubland
- VwGc Gohnia clarkei wet sedgeland
- Vglm Issolepis nudosa grassy sedgeland
- VsBa Banoea articulata swamp sedgeland
- VsEs Eleocharis spiculata swamp sedgeland
- VsSh Schoenus brevifolius swamp sedgeland
- VwL1 Lepidosperma forsythii wet sedgeland
- JvJk Juncus kraussii saltmarsh rushland
- JlL1 Lomandra longifolia tussock rushland
- GcSh Spinifex bursutus coastal grassland
- GcSv Sporobolus virgincus coastal grassland
- K Kikuyu grassland
- PeP Former pine plantation
- PsE Eucalyptus plantation
- Q Water
- D Disturbed areas
Chapter 3

Limited influence of stream networks on the terrestrial movements of three wetland-dependent frog species

Paracrinia haswelli
Abstract

Quantifying functional connectivity is essential for understanding factors that limit or promote animal dispersal in fragmented landscapes. Topography is a major factor influencing the movement behaviour of many animal species, and therefore the extent of functional connectivity between habitat patches. For pond-breeding frogs, areas of low topographic relief (such as streams or drainage lines) offer damp microhabitats that can facilitate movement through otherwise dry landscapes. However, the extent of topographic bias of frog movements has rarely been quantified. We used a replicated study to compare captures in high- and low-relief transects, for three species from a pond-breeding frog community in southeastern Australia. We captured frogs significantly more often on low-relief transects. However, capture rates decreased with increasing distance from water at similar rates on both high-relief and low-relief transects, and we observed few differences between adult and juvenile movements. Our results suggest that although low-relief drainage lines are important for the pond-breeding frogs in question, ecologists and landscape managers should not discount the role of high-relief locations. Because low-relief drainage lines represent a low proportion of the pond margin, >90% of movements are likely to occur across high-relief locations. Therefore, for the species that we studied, buffer zones designed to conserve only hydrological networks would provide insufficient protection of frequently used pond margins, while drainage lines are unlikely to act as vital networks facilitating connectivity between breeding ponds. Our study suggests that movement across slopes may be most important for facilitating functional connectivity.
1. Introduction

Habitat fragmentation, caused by large-scale human modification of ecosystems, is a major driver of biodiversity loss (Fahrig 2003; Kingsford et al. 2009; Lindenmayer and Fischer 2006). Conceptual landscape models which emphasize patch-matrix habitat distributions (derived from Island Biogeography Theory; MacArthur and Wilson 1967) can be useful for describing fragmented landscapes, and have therefore been influential throughout the development of landscape ecology (Haila 2002). Applications of these models commonly assume that viable metapopulations are maintained by dispersal (Hanski 1998; Leibold et al. 2004), while acknowledging that dispersal can be strongly influenced by properties of the intervening matrix (Vogt et al. 2009). Quantifying the extent to which parts of the landscape facilitate animal movement - a concept known as ‘functional connectivity’ (Baguette and Van Dyck 2007; Lindenmayer and Fischer 2007) - provides a basis for understanding the effects of matrix alteration on patch-dependent animal populations (see Storfer et al. 2010).

Functional connectivity is a particularly relevant concept for frog populations. Pond-breeding frogs are commonly described as a naturally occurring model of a fragmented system, because ponds appear like patches in a terrestrial matrix (Bradford et al. 2003; Marsh and Trenham 2001). For this reason, metapopulation theory (Hanski 1998) has commonly been used as a model for describing frog populations (Smith and Green 2005). However, dispersal rates are highly variable between frog species (e.g. Driscoll 1997; Smith and Green 2006), and the role of landscape resistance in explaining this variation remains unclear (Stevens et al. 2006). In particular, topographic features represent barriers to movement in some species and locations (e.g. Funk et al. 2005; Richards-Zawacki 2009; Richter-Boix et al. 2007) but not others (e.g. Davis and Roberts 2005; Driscoll 1998; Zhan et al. 2009). Functional connectivity therefore provides a framework for investigating the influence of landscape variation on frog dispersal and for deciding, in turn, which management interventions are likely to be effective for conservation (see Petranka and Holbrook 2006).
Although there has been much research into terrestrial habitat use by frogs (Baldwin and deMaynadier 2009; Bulger et al. 2003; Parker and Anderson 2003; Patrick et al. 2008; Semlitsch and Bodie 2003), relatively little work has focused on the concept of functional connectivity at fine spatial scales (although see e.g. Popescu and Hunter 2011; Stevens et al. 2006; Todd et al. 2009). This is unusual given that conditions in the pond margin can strongly influence both landscape resistance (Semlitsch et al. 2009) and emigration orientation (Mazerolle and Vos 2006; Timm et al. 2007b), thereby inducing large differences in functional connectivity between patches at landscape scales. It is important, therefore, that investigations of landscape resistance for frogs include research into behaviour at the pond margin.

In this paper, we describe a study designed to address the question: Do frogs preferentially use areas of low topographic relief within pond margins? High-relief movement paths require more energy to cross than low relief paths (Lowe et al. 2006), and contain proportionally fewer damp microhabitats that provide refugia from desiccation (Rittenhouse et al. 2009). Further, there is evidence both that some species rely on drainage-lines to facilitate terrestrial movements (Rittenhouse and Semlitsch 2007), but also that overland dispersal can be an important process facilitating species persistence in some cases (Grant et al. 2010; Hazell et al. 2001). These examples suggest that the role of topographically defined barriers and movement corridors warrants further attention in relation to functional connectivity for frogs. However, the influence of topography on frog movements has received proportionally less attention than factors such as vegetation structure (e.g. see Semlitsch et al. 2009 and references therein).

We used a replicated, trap-based approach to quantify fine-scale variation in frog movement behaviour, taking into account several sources of variation including the effects of rainfall, migration, demography, and distance from water on capture rates, as well as topography. Our guiding assumption was that the need to avoid desiccation is an important mechanism driving spatial and temporal variability in frog terrestrial movements. Consequently, we anticipated that captures in relation to topographic relief would be influenced by both distance from water and rainfall.
Insights into the influence of topography on frog movements are important because they have practical implications for conservation efforts. In particular, frog species with a high proportion of hydrological network-biased movement will be effectively conserved using buffer zones surrounding streams and breeding ponds (see Semlitsch and Bodie 2003), while species which predominantly display overland movements will not. More generally, our study provides a direct, replicable test of landscape resistance. Such studies are rare, but are fundamental to understanding and managing connectivity in fragmented landscapes (Fahrig 2007).

2. Methods

2.1. Study area

Our study area was Booderee National Park, in the Jervis Bay Territory, south-eastern Australia (approximate coordinates 35°10' S 150°40' E; see Fig. 1). The park covers the majority of the southern peninsula of Jervis Bay. It is owned by the Wreck Bay Aboriginal Community, and co-managed in association with the Australian Department of Sustainability, Environment, Water, Population and Communities (SEWPaC). The study region has a temperate climate, with average annual rainfall of approximately 1200 mm that is largely consistent year-round. The majority of the park consists of Eucalyptus botryoides and Eucalyptus pilularis forest on deep sandy soils, but patches of woodland and coastal heath are also common, predominantly on shallow soils at higher elevations (Taws 1997).

Booderee National Park contains a number of lakes and ponds formed by the blockage of existing drainage lines by sand dunes (Jones et al. 1995). These pools provide breeding habitat for the majority of frog species in the park (Westgate et al. 2012), although some species adapted to breed in ephemeral pools in coastal heaths also occur in our study area (Penman and Brassil 2010). We chose five such ponds for this study, all of greater than five metres diameter and surrounded by eucalypt forest. All five ponds remained flooded for the duration of the investigation. At each site, we identified a single drainage line at provided the majority of
inflow from runoff, although none of these contained continuously flowing water for the duration of the study period.

The frog community in Booderee National Park consists of thirteen species split between the families Myobatrachidae (southern frogs, seven species) and Hylidae (tree frogs, six species). Both families include species that require open water for breeding (Cogger 1996). Because hylids cannot be reliably sampled using pitfall traps (Todd et al. 2007), we focused this study on Myobatrachids.

2.2. Study design

Our study was primarily designed to investigate variation in frog movements between high and low relief locations in pond margins. However, topography has the potential to influence movement patterns of frogs through a number of mechanisms. First, low-relief locations collect and retain moisture more effectively than high-relief locations, thereby providing more favourable microclimates for frogs. Second, vegetation structure and composition can vary across topographic gradients in riparian locations (Merrill et al. 2006). Finally, the identity and abundance of both predator and prey species vary in relation to the above processes (e.g. Camper 2009; Seagle and Sturtevant 2005). Although we attempted to control for differences in vegetation and flowing water between high and low relief transects, our study therefore tested the combined effect of a suite of co-varying topographically-dependent attributes on frog movements.

We used a replicated trapping design to investigate the occurrence of frogs in relation to three spatial variables (distance from water, topography, and direction of movement), and two temporal variables (rainfall and Julian date). Our approach provides a different interpretation from pitfall trapping studies that investigate habitat use: rather than testing whether traps in more suitable locations detect more frogs, we tested whether some traps detected a larger number of frog movements as a result of their location. Comparatively few studies have used a trapping approach to investigate frog movements (although see Timm et al. 2007b), with many
authors instead using radio-tracking data to describe the behaviour of a small number of individual animals (e.g. Bulger et al. 2003; Rittenhouse and Semlitsch 2007; Sztatecsny and Schabetsberger 2005). Our approach allowed direct comparison of use of different terrestrial locations in an experimental framework.

We established two transects at each pond, with each transect running for 200 metres from a point within 5 m of the waters’ edge (Fig. 1). We chose 205 m as our maximum study distance because it was the mean minimum core terrestrial habitat area identified by Semlitsch & Bodie (2003) in their meta-analysis of movement studies of 19 frog species. Trapping at distances shorter than 205 m would therefore be unjustified by the ecological literature, while larger distances were logistically unfeasible. The first transect (low-relief) at each pond followed a drainage line, with the second transect (high-relief) placed at the point on the waters’ edge with the steepest slope that occurred within 90 degrees of compass orientation of the first transect. Each transect consisted of six drift fences at 40 m intervals, with each fence oriented parallel to the waters’ edge. Fences were five metres long and had a 10 litre pitfall bucket buried on each side, with the rim positioned at ground level. These two buckets were used to differentiate between individuals moving away from water (caught on the close-to-water side of the fence), from those moving toward water. We added a ‘lip’ (~5 cm wide) at the rim of each bucket to stop frogs from climbing out of the pitfall traps.

[Fig. 1]

In our study design, we controlled for a number of factors that had the potential to introduce confounding in the key drivers of variation in frog movement behaviour. First, we ensured that transects did not cross boundaries (either those between adjoining vegetation types, or roads or tracks), which could confound our analysis of the effect of distance from water on capture rates (Carthew et al. 2009). Second, we released all captured individuals on the opposite side of the drift fence from where they had been captured, to minimize any effect of the study design on total distance travelled. Third, we ensured that vegetation structure varied as little as possible
between low-relief and high-relief transects, to avoid confounding between vegetation type and topography.

Our study design included 120 buckets (5 sites x 2 transects x 6 distance classes x 2 directions), checked daily from 12th August to 17th September 2008 (37 days). This period includes the spring peak breeding season for a number of Australian frog species (Barker et al. 1995; Lemckert and Mahony 2008). We took all captured animals to a nearby field station, where we weighed them and took four morphological measures; snout-vent length, tibia length, head width, and internarial distance. We photographed and clipped one toe from each animal to enable individual identification, before re-releasing each animal on the opposite side of the fence at which they had been captured. We re-opened our traps at the end of summer (between 17th January and 28th February 2009; 42 days) to collect data on dispersing juveniles. During this second period, we repeated our trapping method exactly, except that recapture rates from the first trapping period (eight recaptures from 475 captures, or <2%) were too low for the continuation of toe clipping to be necessary or justifiable. We differentiated adults and juveniles by plotting snout-vent length against tibia length and looking for discontinuities in size. The minimum SVL measurements for adults calculated using this method were 16.0 mm for Crinia signifera, 22.5 mm for Paracrinia haswelli, and 20.0 mm for Uperoleia tyleri (Fig A.1).

2.3. Statistical analysis

We modeled occurrence of frogs in traps using Generalized Linear Mixed Models (GLMMs; Pinheiro and Bates 2000). Using GLMMs enabled us to quantify the probability of capturing an animal at each trap in relation to both spatial and temporal covariates. Since this was a trap-level analysis with low recapture rates, we excluded records of second captures of single individuals from our analysis. Site-level fixed effects were: distance from water (0 – 200 m), topographic relief (high or low) and direction (toward or away from water). Visit-level fixed effects were the amount of rainfall in the previous 24 hours (log-transformed) and Julian date. To account for our nested study design, and to enable us to investigate both visit-level and site-level covariates,
we included five levels of nested random effects: visit (38 visits per bucket for the spring trapping period); bucket (n=120); fence (n=60, 10 for each of six distance classes); transect (n=10, five each for high- and low- topographic relief) and site (n=5).

Our approach to modeling these data was to create a single model that we applied to all species, enabling us to compare relative effect sizes of each covariate across species. We included all variables as additive fixed effects, plus a small number of possible interactions that we used to test for particular responses to spatially and temporally varying conditions. First, we tested whether frogs could move more easily along low-relief transects (interaction between distance & transect). Second, we tested whether frogs moved further following rain (interaction between rainfall & distance). Third, we tested whether frogs were more restricted to low-relief locations in the absence of rainfall (interaction between transect & rainfall). Finally, we tested whether nature of the interaction between topographic relief and distance from water was affected by rainfall (i.e. a three-way interaction between these variables). Our approach was different from the more common method of choosing a ‘best’ model with fewer covariates; we felt that such an approach was inappropriate because of the constraints of our study design, and also because of non-trivial issues regarding the interpretation of information criteria for selection between models that include random effects (Greven and Kneib 2010; Vaida and Blanchard 2005). We used the lme4 package (Bates et al. 2011) in the R statistical program (R Core Development Team 2010) for all analyses.

To compare captures of adults versus juveniles, we used Fishers exact test to compare proportions of captures in each of four classes. Fisher’s exact test works by comparing the proportion of captures from a dataset in two sets of binary categories. In each case, the first binary variable was the number of adult versus juvenile captures. In three tests for each species, we chose corresponding variables that evenly divided the total number of traps in half. These variables were simplified versions of our spatial variables of interest, i.e. topography (high versus low relief), distance from water (0-80 m versus 120-200 m), and direction of travel (towards or away from water). Where Fishers test gave a P value ≤0.05, we took this as
evidence of a significant difference in adult versus juvenile captures for the spatial comparison in question.

2.4. **Quantifying the importance of high versus low relief locations**

The final stage of our analysis was to estimate the total proportion of frogs using high or low relief landscape elements. This was important because the approach employed thus far - directly comparing frog occurrence on high-relief versus low-relief transects - implied that both transect types represent equal proportions of the pond edge, an assumption that was clearly invalid for the ponds in question.

To quantify the relative availability of high and low relief locations, we used satellite imagery to measure the circumference of each pond, and the proportion of the circumference in each topographic class. We then multiplied the number of captures on each transect type (high or low relief) by the proportion of the pond edge in each of the respective classes. This gave us an estimate of relative frog abundance in high versus low relief locations. We then converted our estimated abundance data to percentages, and averaged the percentage of individuals using high versus low relief locations across all sites.

3. **Results**

We captured a total of 965 frogs from seven species: 538 in our spring trapping period, and 427 in our summer trapping period. However, during our spring trapping period, three species - *Pseudophryne bibronii, Litoria jervisensis* and *Heleioporus australiacus* - were represented by only a single individual, and we captured only four adults from a fourth species (*Limnodynastes peronii*). This left three species that were sufficiently common to enable us to construct models of adult occurrence from our spring trapping dataset: *Crinia signifera* (n=171), *Paracrinia haswelli* (n=174) and *Uperoleia tyleri* (n=130). These three species are all small (<50 mm), pond-dwelling members of the family Myobatrachidae (Cogger 1996).
We found that capture probabilities decreased significantly with increasing distance from water, and increased significantly following rainfall, for all three species (Table 1). However, the effect of topography on capture rates varied between species, and was strongly mediated by both rainfall and distance from water. For *C. signifera*, increased captures following rainfall were concentrated on low-relief transects ($\beta_{\text{distance:transect:rain}} = 0.23 \pm 0.13$, P = 0.078). There was a similar effect for *P. haswelli*, with the majority of additional captures following rainfall occurring at short distances from water ($\beta_{\text{transect:rain}} = 0.15 \pm 0.08$, P = 0.067). Finally, captures of *U. tyleri* were higher on low-relief than high-relief transects after rainfall; but this pattern was reversed during drier periods (Fig. 2). Supplementary analysis of individual distance classes showed that captures were significantly higher on low-relief transects at distances of up to 80m from water for both *C. signifera* (P=0.010) and *P. haswelli* (P=0.032) but only at the shortest distance class from water for *U. tyleri* (P=0.01).

[Table 1]

We found limited evidence of migratory movement in spring, with only *U. tyleri* showing evidence of higher levels of movement towards water ($\beta_{\text{direction}} = 0.57 \pm 0.30$, P = 0.061).

Capture rates also increased throughout the trapping period for both *U. tyleri* ($\beta_{\text{date}} = 0.11 \pm 0.01$, P<0.001) and *C. signifera* ($\beta_{\text{date}} = 0.04 \pm 0.01$, P<0.001). Increasing captures over time in these species was not due to confounding with rainfall, since rainfall and time were poorly correlated (Pearson’s correlation = 0.16), with high rainfall events occurring almost weekly throughout the study period (rainfall > 10 mm on days 12, 18 & 26).

[Fig. 2]

Results from our second trapping period (in late Summer/early Autumn) were less conclusive than those from our spring trapping period. Although we captured a reasonable number of juvenile frogs in our second trapping period (*C. signifera* = 28, *P. haswelli* = 145, *U. tyleri* = 32), most were from a single site (n=171, 83%), and we did not observe any mass dispersal events. These factors limited the degree of inference that could be drawn from linear models of
the kind constructed for adult captures. We therefore restricted our analysis to comparison of the proportion of adult and juvenile captures between different treatments (Table 2). Fisher’s exact test showed no significant difference between adults and juveniles of any species, in terms of the proportion of individuals captured on low-relief versus high-relief transects (P values: C. signifera = 0.36; P. haswelli = 0.45; U. tyleri = 0.84), or with increasing distance from water (P values: C. signifera = 0.82; P. haswelli = 0.19; U. tyleri = 0.79). The only significant difference between adult and juvenile captures was that juvenile P. haswelli were significantly more likely to move away from water than were adults of the same species (P=0.006).

[Table 2]

Using satellite imagery, we found that the total circumference of ponds averaged 658 metres, while low relief locations chosen for investigation in our study averaged 28 metres of the pond boundary (<6%). This suggested that our raw data on relative numbers of captures (see Table 2) were not representative of the overall importance of high- versus low- relief locations in pond riparian margins. Although 67% of captures on average were on low-relief transects (C. signifera =71%; P. haswelli =74%; U. tyleri =56%), once these numbers were weighted according to the area covered by steep and shallow slopes, we found that >90% of all animals would be likely to occur in relatively high-relief locations (C. signifera =91%; P. haswelli =89%; U. tyleri =95%).

4. Discussion

For this study, we aimed to quantify the extent of topographic bias in the movement behaviour of three frog species. We found that low-relief drainage lines providing the majority of inflow into breeding ponds were preferentially used by these frogs. More specifically, we found statistically significant differences in frog occurrence between high- and low- relief transects for all three species, although this effect was mediated by rainfall and distance to water (Fig. 2). While this would appear to reinforce the importance of drainage lines as priority locations for frog movements, one third of all captures were on high-relief transects, which was a higher
proportion than we had expected at the outset of the study. Because drainage lines are linear features of landscapes that cover only a small proportion of pond edge, we were able to show that the absolute proportion of individuals from these three species that preferentially used low-relief locations is likely to be small.

Our finding that only a small proportion of frogs use low-relief pond margins, a pattern that was consistent for all three species for which data were available, has important implications for landscape planning and frog conservation. Some authors (e.g. Baldwin et al. 2006; Roe and Georges 2007) have suggested that reducing the radius of buffers around breeding ponds, and proportionally increasing the width of buffers centered on stream networks, would increase the representation of commonly used areas for semi-aquatic herpetofauna without increasing overall land allocation to conservation. Our results contrast with that view; a drainage-line buffer in this location would conserve areas used during <10% of frog movements for the species that we studied (see also Bulger et al. 2003). Our results suggest that circular buffers around breeding ponds would be a more appropriate use of resources for the conservation of valuable terrestrial locations (see Calhoun et al. 2005; Semlitsch and Bodie 2003). Rather than conflicting with earlier research, however, these results reinforce the deeper message that empirical testing of frog movement behaviour is important to ensure that buffers meet their goals of conserving viable frog populations (Gamble et al. 2007; Goates et al. 2007).

Use of high-relief transects by frogs was unexpectedly high in our study. This is particularly surprising considering that most studies of amphibian movements in riparian areas either use fences as enclosures to capture all migrating individuals (e.g. Gibbons et al. 2006; Regosin et al. 2005), or else increase trap effort with increasing distance from water, such that a constant proportion of pond edge is represented at each distance class (e.g. Patrick et al. 2008). Such an approach was impossible in our study because drainage lines are linear features. Our methodology would therefore lead us to expect decreasing captures with distance on high-relief transects, simply as a result of lower proportional survey effort with increasing distance from water. However, if drainage lines act as movement corridors for frogs (Rittenhouse and
Semlitsch 2007), we would not expect a corresponding decrease in captures on low-relief transects. We were surprised, therefore, to find that capture rates decreased at similar rates with increasing distance from water on both high-relief and low-relief transects (Fig. 2). Although this result might have eventuated by chance if frogs commonly moved parallel to the pond edge, such movement is inconsistent with perpendicular movement observed for *U. tyleri*. Therefore, the available evidence suggests that drainage lines are not acting as movement corridors. Instead, low-relief locations are functionally similar to high-relief transects, but with higher densities near the pond edge.

Despite our finding of decreasing occupancy of frogs with increasing distance from water (consistent with Semlitsch and Bodie 2003), some frogs used terrestrial areas at large distances from water during the breeding season. Locations up to 80 meters from water – a distance which exceeds mandated buffer zone widths in some jurisdictions (Goates et al. 2007) – had a >20% probability of capturing *C. signifera* or *U. tyleri* following rainfall (Fig. 2). This finding has two important implications. First, buffer zones up to 80 m from the waters' edge may be used throughout the breeding season, most likely for foraging. Interestingly, this is lower than some estimates; for example, *C. signifera* can be ubiquitous at distances of up to 500 m from water in some locations (Lauck 2005). This reinforces the importance of comparatively large buffer zone widths (Harper et al. 2008). Second, locations >80 m from water supported a smaller increase in captures following rain, suggesting that rainfall did not increase the likelihood of long-distance adult movements (i.e. migration or dispersal). Although weather can strongly influence the probability of dispersive movements in frogs (Gibbons et al. 2006; Timm et al. 2007a) as well as in other animal taxa (e.g. Walls et al. 2005), our results support the view that favorable weather conditions may not initiate migratory or dispersive movements (see also Semlitsch 2008).

Our finding that terrestrial locations were commonly used by the frog species that we studied was exemplified by one species in particular. High captures of *Uperoleia tyleri* in high-relief and long distance-from-water locations might have been influenced by high levels of
territoriality among male *U. tyleri* (Robertson 1986). This is because territoriality could mitigate against concentration of individuals in locations with favourable microhabitat characteristics. More importantly, however, *U. tyleri* was the only species for which there was evidence of migratory behaviour during our spring trapping period. This evidence included an initial absence of captures for this species (first capture on day 10), and some directional movement ($\beta_{\text{direction}} = 0.57 \pm 0.30, P=0.061$). The fact that we found no corresponding evidence of topographically-biased movement for this species suggests that *U. tyleri* uses high-relief locations during migration and/or dispersal. These findings support our assertion that high-relief locations are likely to be important for ongoing persistence of local breeding populations for this species (see Harper et al. 2008).

We found no evidence for a difference in terrestrial movements between adults and juveniles of any species. The only exception was that directional movement of juveniles was greater than for adults in *P. haswelli* (Table 1). This difference was expected given that metamorphic juveniles must begin their movements from water (and can therefore only move away from their natal ponds), whereas adults may occur at a range of distances from water at the beginning of their migratory period. While these results may appear surprising given that juveniles are commonly thought to be the dispersive phase in the frog life cycle (Semlitsch 2008), contrary evidence does exist for some species. Smith and Green (2006), for example, report that movements of Fowler’s Toads (*Bufo fowleri*) are not demographically biased. Given the importance of juvenile dispersal for predicting demographic variation and the persistence of frog populations (Swanack et al. 2009), juvenile-biased dispersal should be carefully tested for, rather than assumed, in frog species.

To what extent are our results relevant for describing functional connectivity across landscapes? The answer to this question depends upon the extent to which our results are representative of dispersive movements for the species in question. Although there are prominent examples where frogs have made long-distance directed movements toward breeding sites (Sjogren-Gulve 1998), there is also evidence of frog species following undirected movement paths (Rothermel
2004; Schwarzkopf and Alford 2002). In the latter case, dispersal would result from a series of small foraging movements, rather than being a deliberate behaviour (Hawkes 2009; Van Dyck and Baguette 2005). Even if foraging and dispersal are different behaviours, we are unaware of any evidence suggesting that topographic bias in frog movements varies between foraging and dispersal. In this case, our finding of limited differences between adult and juvenile behaviour (Table 2) supports the argument that our results are representative of general movement behaviour for the species in question. The available evidence therefore suggests that strong topographically-biased dispersal is unlikely at landscape scales for the species that we studied. This also implies that isolation of breeding ponds will predominantly be influenced by distance rather than topography, decreasing pond isolation, and thereby reducing the probability of local extinction (Griffen and Drake 2009; Johst et al. 2011). However, studies at larger spatial scales would be necessary to confirm these expectations (Hovestadt et al. 2011; Jacobson and Peres-Neto 2010).

5. Conclusions

Our study has shown that – for the pond-breeding frogs that we examined – the majority of individuals used terrestrial areas that were not located on drainage lines. This leads to two important conclusions for frog conservation in this location. First, buffer zones designed to conserve only hydrological networks would provide insufficient protection of locations that were commonly used by frogs in this study. Second, drainage lines are unlikely to be vital networks facilitating connectivity between breeding ponds for the species that we studied. Underlying these unexpected responses to topography were a series of unexpected movement behaviours in the frog species in question. These included: (1) near-continuous use of terrestrial areas at large distances (up to 80 metres) from water during the breeding season. (2) Low incidence of directional or migratory movement. (3) Limited differences between adult and juvenile movements. Focusing on the nexus between fine-scale movement behavior and landscape scale connectivity has therefore provided novel insights into behaviors which underlie variation in terrestrial movement behaviour by frogs in this location. However, further work is
required to determine the extent to which the patterns we have identified apply more generally. In particular, larger frogs are generally capable of dispersing with low risk of dehydration (Tracy et al. 2010), while frogs that are closely related, but ecologically dissimilar, may use terrestrial locations in different ways (Rowley and Alford 2007; Tracy et al. 2010). Along with identification and prioritization of at-risk habitats (Baldwin and deMaynadier 2009), anchoring estimates of functional connectivity in an understanding of animal behavior at relevant spatial scales (Van Dyck and Baguette 2005) is therefore an important goal for amphibian conservation in future.

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Table 1: Variable estimates from Binomial GLMMs. Values with $P \leq 0.05$ are given in bold.

<table>
<thead>
<tr>
<th>Type</th>
<th>Variable</th>
<th>$C. \text{ signifera}$</th>
<th>$P. \text{ haswelli}$</th>
<th>$U. \text{ tyleri}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial</td>
<td>Intercept</td>
<td>$-3.11 \pm 0.68 \ (P &lt;0.001)$</td>
<td>$-2.05 \pm 0.57 \ (P =0.001)$</td>
<td>$-6.64 \pm 0.74 \ (P &lt;0.001)$</td>
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<tr>
<td></td>
<td>Distance from water</td>
<td>$-0.64 \pm 0.16 \ (P &lt;0.001)$</td>
<td>$-0.87 \pm 0.20 \ (P &lt;0.001)$</td>
<td>$-0.43 \pm 0.20 \ (P =0.030)$</td>
</tr>
<tr>
<td></td>
<td>Steep topography</td>
<td>$-0.91 \pm 1.01 \ (P =0.368)$</td>
<td>$-0.87 \pm 0.85 \ (P =0.304)$</td>
<td>$2.18 \pm 0.82 \ (P =0.008)$</td>
</tr>
<tr>
<td></td>
<td>Moving towards water</td>
<td>$0.13 \pm 0.21 \ (P =0.533)$</td>
<td>$-0.10 \pm 0.25 \ (P =0.670)$</td>
<td>$0.57 \pm 0.30 \ (P =0.061)$</td>
</tr>
<tr>
<td>Temporal</td>
<td>Rainfall</td>
<td>$0.44 \pm 0.20 \ (P =0.031)$</td>
<td>$0.66 \pm 0.21 \ (P =0.002)$</td>
<td>$1.39 \pm 0.30 \ (P &lt;0.001)$</td>
</tr>
<tr>
<td></td>
<td>Date</td>
<td>$0.04 \pm 0.01 \ (P &lt;0.001)$</td>
<td>$0.001 \pm 0.01 \ (P =0.986)$</td>
<td>$0.11 \pm 0.01 \ (P &lt;0.001)$</td>
</tr>
<tr>
<td>Interactions</td>
<td>Distance: Topography</td>
<td>$-0.32 \pm 0.31 \ (P =0.306)$</td>
<td>$0.05 \pm 0.33 \ (P =0.889)$</td>
<td>$-0.96 \pm 0.38 \ (P =0.011)$</td>
</tr>
<tr>
<td></td>
<td>Distance: Rainfall</td>
<td>$0.10 \pm 0.07 \ (P =0.128)$</td>
<td>$0.15 \pm 0.08 \ (P =0.067)$</td>
<td>$-0.10 \pm 0.11 \ (P =0.387)$</td>
</tr>
<tr>
<td></td>
<td>Topography: Rainfall</td>
<td>$-0.45 \pm 0.36 \ (P =0.213)$</td>
<td>$-0.39 \pm 0.37 \ (P =0.285)$</td>
<td>$-1.54 \pm 0.43 \ (P &lt;0.001)$</td>
</tr>
<tr>
<td></td>
<td>D:T:R</td>
<td>$0.23 \pm 0.13 \ (P =0.078)$</td>
<td>$0.08 \pm 0.15 \ (P =0.591)$</td>
<td>$0.56 \pm 0.19 \ (P =0.003)$</td>
</tr>
</tbody>
</table>
Table 2: Number and proportion (in parentheses) of captures of adult and juvenile frogs from three species. P values show significance of fishers’ exact tests on proportions of adult and juvenile captures in each category, with values ≤0.05 give in bold.

<table>
<thead>
<tr>
<th>Criteria</th>
<th>C. signifera</th>
<th>P. haswelli</th>
<th>U. tyleri</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juvenile</td>
<td>Adult</td>
<td>P</td>
</tr>
<tr>
<td><strong>Within 80m of water</strong></td>
<td>20 (0.71)</td>
<td>128 (0.75)</td>
<td>0.816</td>
</tr>
<tr>
<td><strong>On low-relief transects</strong></td>
<td>23 (0.82)</td>
<td>121 (0.71)</td>
<td>0.259</td>
</tr>
<tr>
<td><strong>Moving towards water</strong></td>
<td>18 (0.64)</td>
<td>84 (0.49)</td>
<td>0.157</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>28</td>
<td>171</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1: Map of the study area, showing a schematic of the trapping design.
Fig. 2: Probability of occurrence with increasing distance from water, as given by GLMMs. Columns give results for each species, while rows give results for different amounts of rainfall. Solid lines (filled squares) give estimates for low-relief transects; dashed lines (open circles) give estimates for high-relief transects.
Fig. A.1: Tibia length (TL) versus Snout-Vent length (SVL) for the three most abundant species in our study. Dashed lines give ‘cut-off’ SVL’s used to differentiate adults from juveniles in this study.

- **a) Crinia signifera**
  - Cutoff SVL = 16.0 mm

- **b) Paracrinia haswelli**
  - Cutoff SVL = 22.5 mm

- **c) Uperoleia tyleri**
  - Cutoff SVL = 20.0 mm
Chapter 4

Quantifying the effect of disturbance on frog migration

Uperoleia tyleri
Abstract

Conserving migratory species requires that breeding and overwintering habitats are maintained, along with the movement corridors that connect them. For migratory frogs, however, the properties of vital terrestrial habitats and movement corridors are often unknown. Here, we relate captures of frogs in 109 terrestrial locations collected over seven years to the density of surrounding breeding sites. We then test for effects of topographic, vegetation and disturbance gradients on frog emigration, terrestrial habitat use, and landscape resistance. We show that for the species that we studied, ecological gradients have a strong influence on emigration rates, but very little influence on terrestrial habitat selection or landscape resistance at this scale. Fire frequency was the only variable to influence frog emigration rates, while vegetation and topography influenced frog occurrence in terrestrial locations. Our results challenge the suggestion that landscape resistance and terrestrial habitat selection are universal mechanisms that drive the distribution of migratory frogs at landscape scales.
**Introduction**

Many animal species use spatially-distinct habitats during different seasons, or at different stages of the life cycle (Dingle & Drake 2007). This life-history strategy enables animals to exploit seasonal resource pulses, but also increases their exposure to a broader suite of threatening processes that manifest in different locations (e.g. Cherel et al. 2013). As a result, population-wide declines can occur rapidly in migratory taxa, sometimes in response to geographically distant ecological or anthropogenic impacts (Tottrup et al. 2012). Predicting the likely effects of such impacts, and identifying conservation actions that will ameliorate them, requires detailed knowledge of how species use spatially-discontinuous habitats and movement corridors (Martin et al. 2007; Marfil-Daza et al. 2012).

Many frog species display seasonal migratory movements (Semlitsch 2008) that range in scale from tens to hundreds of meters, or even several kilometers (Smith & Green 2005). While these movements are considerably shorter (and less frequently studied) than the migrations of larger or more mobile species such as birds (Tottrup et al. 2012) or mammals (Berger 2004), they have the identical effect of rendering migratory frogs vulnerable to threatening processes that occur in either breeding (aquatic) or non-breeding (terrestrial) habitats (Baldwin et al. 2006; Harper et al. 2008). Consequently, an interesting question is the extent to which processes that influence the success of bird or mammal migrations also influence frogs.

In this paper, we investigate the ecological properties that determine high-quality aquatic and terrestrial frog habitats, quantify the extent of landscape resistance to frog movements, and test the vulnerability of frog populations to disturbance by fire. In combination, these can processes limit frog distributions at the landscape scale, meaning that further study of their effects is a vital step for conservation of migratory frog populations (see Stevens & Baguette 2008; Murphy et al. 2010). Unfortunately, few earlier works have been able to investigate the distribution of frogs across whole landscapes (although see Semlitsch et al. 2009 and references therein), largely as the result of logistical difficulties distinct from those faced in studies of mammal or
bird migrations. We overcome these hindrances by combining data on terrestrial occurrence at 109 sites over seven years (from a pitfall trap study conducted over ~14,000 trap nights) with aural survey data on the distribution of species at known breeding sites, leading to unprecedented insights into frog movement behavior at the landscape scale.

Our guiding question was ‘How do vegetation structure, topography and fire influence frog occurrence in terrestrial locations?’ In addressing this question, we began by recognizing that terrestrial capture rates should be proportional to the density of occupied breeding sites in the vicinity of the trap location (Fig. 1a). We then identified and tested three mechanisms by which ecological gradients could potentially influence frog capture rates. First, breeding sites with high adult abundance, or with more favorable ecological properties, are likely to produce larger numbers of emigrants (Gibbons et al. 2006). We investigated this possibility by testing how weighting breeding site density estimates by ecological gradients affected the fit of models of frog capture rates in terrestrial locations (Fig. 1b). Second, frogs may select terrestrial habitats with particular properties, in which case ecological gradients should additively influence capture rates, irrespective of density (Fig. 1c). Finally, frog capture rates should be inversely proportional to the resistance of the landscape to frog movements (Storfer et al. 2010), in which case the effect of an ecological gradient would interact with breeding site density (Fig. 1d).

Understanding the relative influence of these three processes on frog distributions important for understanding the dynamics of animal populations (Murphy et al. 2010).

[Fig. 1]

Our trap-based approach enabled us to test detailed predictions – raised by earlier research in our study system – regarding the effects of vegetation structure, fire, or topography on emigration, terrestrial habitat use, and landscape resistance. First, we anticipated that fire would primarily influence the rate of emigration, as the fire return interval can influence occurrence of frogs at breeding sites (Westgate et al. 2012a), while corresponding evidence that fire affects landscape resistance is comparatively rare (although see Roznik et al. 2009). Second, we
predicted that topographic slope would have only a moderate influence on landscape resistance to frog movements in this location (Westgate et al. 2012b). Finally, we expected that vegetation structure would influence frog occurrence in terrestrial locations. However, vegetation structure can influence both the total number of emigrants (Skelly et al. 2002) as well as landscape resistance (Patrick et al. 2008), and so we did not attempt to predict which of these effects would be the strongest in our study.

Understanding the habitat requirements of migratory species is vital if conservation actions are to be effective (Marfil-Daza et al. 2012). For frogs, landscape-wide studies are required to provide information on the requirements of frog species for particular terrestrial locations (Bartelt et al. 2011). By combining high survey effort and a novel study design that includes both terrestrial and breeding site data, we hope to advance understanding of ways to promote frog conservation in disturbance-prone ecosystems.

Material and methods

Study area and species

Our study area was Booderee National Park, an ~60 km² peninsula on the southeast coast of Australia (Fig. 2), which was a valuable study location for a number of reasons. First, coastal New South Wales has relatively high rainfall throughout the year (Bureau of Meteorology 2010), meaning that nights that are suitable for frog movement are more common than at inland locations at the same latitude. Second, the Park contains a variety of aquatic habitats for breeding amphibians including creeks, pools and lakes (Roe & Georges 2007). Finally, Booderee National Park supports a range of vegetation types and fire histories (Lindenmayer et al. 2008b), which might influence both landscape resistance and quality of aquatic habitats for frogs.

[Fig. 2]
Booderee National Park contains twelve frog species from two families. Six species of Hylidae (tree frogs) are highly mobile and difficult to trap using pitfalls, but are readily detected by call. Conversely, six species of Myobatrachidae (southern frogs) are readily detected using both pitfall traps and call surveys. One species listed as vulnerable occurs there (*Heleioporus australiacus*), while a second (*Litoria aurea*) has gone locally extinct in the last decade.

**Sampling methods**

We quantified frog occurrence in terrestrial locations using pitfall traps. We selected locations for pitfall trapping sites using a random stratified approach. First, we stratified the landscape according to vegetation type (following data provided by Taws 1997). We then randomly selected 10 locations within each of the 12 most common vegetation types. Finally, we replaced any vegetation patches that were not large enough to contain a 100 metre transect without crossing into a different vegetation type. Each trap site consisted of three 20 metre drift fences, 20 metres apart, each with a 20 litre pitfall trap at each end. Our first trapping period was in May and June of 2003, which was followed by a large fire in December 2003 which burned ~50% of the peninsula. We repaired damaged sites and recommenced trapping in February 2004. We subsequently trapped for three consecutive days per year, between the months of November and February until 2010 (for full details of our trapping design, see Lindenmayer *et al.* 2008b). For the purposes of this analysis, we counted a ‘survey year’ as beginning in July rather than January. This meant that consecutive spring and summer trapping periods would be counted as having occurred in the same year, despite typically occurring in October and February (respectively). Sites that were not surveyed annually for the whole study period were excluded from our analysis (n=11), leaving a total of 109 sites for analysis.

To examine the effect of proximity to breeding sites on frog capture rates, we gathered an additional dataset with information on the distribution of frog breeding sites. We identified potential frog breeding sites using a range of methods, including discussions with local people, use of maps, and visual encounter surveys in July 2007. In this way, we identified 119 sites that we considered likely to flood after rain, which we selected independently from the 109 pitfall
trap sites. Of these 119 sites, only 44 were permanently flooded, though 93 contained some water at least once during the study period. We then used aural surveys to quantify the ranked abundance of each frog species at each potential breeding site. Each survey lasted five minutes, and we visited each site at least eight times between spring and autumn 2007/08 (for map see Fig. 2).

Covariates

We calculated four covariates that could influence the probability of detecting frogs using pitfall traps in this landscape. Our first covariate was a factorial variable that tested for differences in detection probability between years. Our remaining variables quantified daily variation in temperature, humidity, and soil moisture deficit (as a surrogate for aridity; see Finkele et al. 2006). We calculated all of our daily weather covariates using data provided by the Bureau of Meteorology (http://www.bom.gov.au).

To account for the fact that aquatic-breeding frogs occur with decreasing frequency with increasing distance from water (Semlitsch & Bodie 2003), we calculated the density of known breeding sites for each species and included this covariate as a predictor of frog occurrence. We calculated density of breeding sites using Baddeley and Turner's (2005) approach, which calculates the number of points per unit area using a Gaussian weighting function. Because density estimates will always be higher away from the edges of the study region, and this can bias study results, we used an approach that corrected the resulting density estimate for edge effects.

We calculated four variables that described the environment at each pitfall trap or breeding site using spatially-explicit raster datasets. Our first variable was slope, which influences both variation in water availability across the landscape, and a species' ability to traverse that landscape (Murphy et al. 2010). We calculated slope from a Digital Elevation Model (DEM) of the Jervis Bay region. This raster was available at 20 metre resolution, and we used this as the
standard for all other raster datasets used in this study (see below), enabling direct comparison between variables.

Our second variable was 'vegetation structure', which ranked land cover classes from areas with very low canopy heights (sedgelands, heaths and shrublands) through to areas with high canopy heights (tall forest and rainforest). We calculated this variable by ranking vegetation classes according to information provided by Ingwerson (1976) and Taws (1997) in their respective vegetation surveys in our study area (see Fig. A1 for rankings of land cover classes used for this paper). Including this variable in our analyses was important because broad-scale vegetation structure can strongly influence both occurrence of frogs at breeding sites (Skelly et al. 2002), and frog movement behaviour in terrestrial areas (Semlitsch et al. 2009).

Our remaining variables described the fire regime at each pitfall trap or breeding site. We derived two fire variables from a dataset showing the boundaries of each fire to have occurred in Booderee National Park in the 40 years preceding our investigation of frog calling behaviour (i.e. since 1968). Our first fire variable was the mean fire return interval (FRI), which we calculated as the length of the period for which data were available (40 years), divided by the number of fires that each location had been subject to in that time plus one. Our second fire variable was the maximum FRI, which we calculated as the maximum length of time that each site had remained unburned within the last 40 years.

Statistical analysis

We used MacKenzie et al.'s (2002) approach to model occurrence of frogs in terrestrial locations. This approach was necessary to account for low detection rates resulting from attempts to capture frogs at large distances from water (Semlitsch & Bodie 2003), and to enable us to quantify temporal variation in detection probabilities. We ran all analyses using the package ‘unmarked’ (Fiske & Chandler 2010) in the R statistical program (R Core Development Team 2010).
We began by testing a range of visit-level (detection) covariates. We tested eight models in total, including a null model with no detection covariates. Each of our first four models tested the effect of a single covariate on frog detection rates: either one of our weather-related variables (aridity, humidity and maximum temperature); or a factorial variable that allowed for inter-year variation in detection rates (described as ‘year’ from here on). Our remaining three models tested for effects of year in combination with either aridity, humidity or maximum temperature. We used an information-theoretic approach (Burnham & Anderson 2002) to choose a final set of detection covariates. This involved comparing the fit of each model using AICc, and choosing the model that provided the most parsimonious fit. In all our model selection stages, we accepted the inclusion of an extra term if it led to a decrease in AICc of two or more (Arnold 2010). Consequently, the model with the highest AICc weight was not always chosen as a ‘final’ model using our approach.

We then began a three-stage process of determining which spatial covariates to include in each model, as a means of identifying ecological gradients that influenced emigration rates from breeding sites, terrestrial habitat use, or landscape resistance.

Our first stage was to create a series of hypotheses about how ecological gradients might influence emigration from breeding sites. Our reasoning on how to account for variation in emigration rates was as follows: If emigration from a breeding site is low, then its’ contribution to the number of individuals in nearby terrestrial locations (i.e. contribution to pond density effects) will be lower than it would otherwise have been. We can account for this in our ‘pond density’ estimates by giving that site a lower ‘weight’ in the density estimate calculation. For example, frequent fire might kill frogs and reduce the number of emigrants, in which case frequently burned sites are given low weight in the density calculation. However, it also worth considering that this hypothesis is invalid, and that frequent fire would have no effect or even a positive effect on emigration.
To account for all of the possible effects that ecological covariates could have on emigration rates, we constructed seven density surfaces, each using a different method to assign weight to frog breeding sites in the density calculation. The first density surface used only known breeding sites, and assigned each breeding site equal (unit) weight (Fig 1a). The second surface assigned weights in proportion to the average ranked-abundance of a frog species at each location. This second approach tested the assumption that locations close to large populations would receive more emigrants than those close to small populations. The remaining surfaces tested whether weighting the density estimate using environmental covariates provided better fit to frog capture data (Fig 1b). We tested six ‘environmental’ variables, each derived from one of our four raster datasets. In order, these density surfaces assigned higher weight to breeding sites in tall vegetation types; with low slope; with high mean or maximum FRI’s (implying higher emigration from rarely burned sites); or with low mean or maximum FRI’s (implying higher emigration from frequently burned sites).

Our second stage of analysis was to test the relative fit of these seven density surfaces; and by extension, compare competing hypotheses regarding the factors that influence frog emigration from breeding sites. We therefore tested all seven density surfaces as predictors of frog occurrence at trap locations, as well as null model without any site-level covariates. In each case (i.e. for all seven density models), we selected a width for our density estimation kernel (i.e. the distance over which density of breeding sites is measured) by iteratively increasing the size of the kernel from 400 metres to ten kilometers. We then identified the distance at which fit increased most strongly, by identifying the highest residual in a model of AICc fit against distance. This method avoided an issue whereby overall fit was low, but increased or decreased consistently over distance, leading to unrealistically high or low movement distances.

Our final stage of analysis was to determine whether local environmental covariates (i.e. values of raster datasets extracted for each pitfall trap location) improved fit of models of species occurrence, relative to models that only contained detection and/or density covariates. In our models at this stage of analysis, we tested for both additive and interactive effects of vegetation
structure, slope, and mean and maximum FRIs. We interpreted additive effects of local variables to imply variation in terrestrial habitat quality along that gradient (Fig 1c), while interactive effects would imply variation in landscape resistance along that gradient (Fig 1d). In addition to a ‘null’ model containing only a density covariate, this approach gave a total of nine candidate models, which we ranked by AICc weight to determine a ‘final’ model for each species.

Results

Detectability

Using pitfall traps at 109 sites over seven years (a total of 13,734 trap nights; for map see Fig. 1), we captured individuals from seven species of ground-dwelling frogs (family Myobatrachidae). Of these seven species, we captured four species sufficiently often to allow us to model occurrence at trap locations: *Limnodynastes peronii* (n (visits)=290, n (individuals)=1691), *Crinia signifera* (n (visits)=210, n (individuals)=442), *Uperoleia tyleri* (n (visits)=124, n (individuals)=282), and *Pseudophryne bibronii* (n (visits)=123, n (individuals)=236). We detected the remaining three species — *Paracrinia haswelli* (n (individuals)=62), *Limnodynastes dumerilii* (n (individuals)=37) and *Heleioporus australiacus* (n (individuals)=16) — on ≤21 occasions each (<0.1% of all visits).

We found that high survey effort across multiple years was necessary to compensate for low and annually variable detection rates. Overall, total detections varying between 49 in 2009 (0.15 detections per site per day) and 260 in 2007 (0.79 detections per site per day). Comparisons of detection probability models by AICc showed that ‘year’ was the best-fitting detection covariate for every species, while models that did not include year as a covariate had low AICc weight (<0.01) for all four species. Addition of a weather covariate only improved model fit for one species (*U. tyleri*), providing some evidence that humidity influenced detection rates for this species (Table 1). However, inclusion of humidity in the model for *U. tyleri* did not sufficiently reduce AICc to be selected in the final model (ΔAICc = -0.62). Detection rates for all species showed similar trends over time, in that they all peaked in the same year (2007; see Fig. 3 a-d).
Density of breeding sites

Breeding site density surfaces were significant predictors of frog occurrence in terrestrial locations for all four species. Weighting density estimates by mean fire return interval (FRI) provided the best model for *L. peronii*, while maximum FRI provided the best model for *P. bibronii* and *U. tyleri*. Consequently, these species were more likely to be captured if there were long periods where nearby locations containing breeding populations had remained unburned during the preceding 40 years. In contrast, the highest ranked model for *C. signifera* included a response to vegetation structure, implying that this species is more likely to be detected when nearby breeding sites are in forest than in heath.

Each species responded to density of breeding sites at a different spatial scale. In increasing order, optimal kernel widths for each species were 411 metres (*C. signifera*); 746 m (*U. tyleri*); 868 m (*L. peronii*); and 1475 m (*P. bibronii*). There was no significant correlation between the scale at which species responded to breeding site density, and either the number of breeding sites occupied by that species (r = 0.35) or the number of trap sites at which each species was captured (r = 0.12).

Habitat selection and landscape resistance

For our final stage of analysis, we took the top-ranked density surface for each species, and tested whether adding 'local' covariates (i.e. values of ecological gradients measured at each pitfall trap location) explained any further variation in occurrence of that species. We interpreted an additive relationship between density and an ecological variable to indicate variation in terrestrial habitat selection. In contrast, if we observed a multiplicative relationship – in which the effect of local covariates was greater at low densities – we would take this to imply variation in landscape resistance along that gradient.

For two of four species, we found that models that included trap-level covariates improved model fit (as measured by AICc weight, see Table 1). For *L. peronii*, support for the final model
was strong ($\Delta$AICc = -2.91 over the next best model, -15.16 over a model with no local covariates), and showed that occurrence of this species increased significantly with increasing density ($\beta = -1.95 \pm 0.57$, $P < 0.001$) and decreased with increasing slope ($\beta = -1.33 \pm 0.45$, $P = 0.003$); but that the effect of slope increased at high densities ($\beta = -0.89 \pm 0.48$, $P = 0.063$). For *C. signifera*, models containing trap-level vegetation as a covariate strongly improved model fit ($\Delta$AICc < -12.26 over a model with no local covariates), with the additive model having best overall fit ($\Delta$AICc = -2.22 over density * vegetation model). The final model for this species contained significant effects of both breeding site density ($\beta = 0.66 \pm 0.30$, $P = 0.03$), and vegetation type ($\beta = -0.98 \pm 0.27$, $P < 0.001$), suggesting lower occurrence in taller, more structurally simple vegetation types (i.e. forests).

For our remaining two species, models containing density as the only covariate were either the top-ranked model (*P. bibronii*), or higher ranked models contained more covariates but with limited change in AIC ($\Delta$AICc = 0.95 between top-ranked and null model for *U. tyleri*).

However, density of breeding sites was a significant predictor of occurrence for both species (*P. bibronii*; $\beta = 0.64 \pm 0.27$, $P = 0.018$; *U. tyleri*; $\beta = 1.60 \pm 0.39$, $P < 0.001$).

[Fig. 3]

**Discussion**

Lack of knowledge about species ecological requirements is a key hindrance to the effective conservation of species with complex life histories (Marfil-Daza et al. 2012; Radchuk et al. 2012). Although many frog species are known to migrate between terrestrial and aquatic habitats (Semlitsch 2008), few studies have described frog distributions at landscape scales (Bartelt et al. 2011), while even fewer have done so by directly quantifying terrestrial occurrence as we have done here. Further, our high level of spatial and temporal replication mean that the results we present are a more detailed evaluation of landscape-scale frog distributions than has been possible in earlier studies (e.g. Regosin et al. 2005). We discuss our
findings, as well as their implications for the management and conservation of frog populations, in the remainder of our paper.

We found that density of breeding sites, and the properties of those breeding sites, had a stronger influence on frog occurrence in terrestrial locations than did trap-level covariates, implying low terrestrial habitat selection and landscape resistance (Fig 3 e-h). This is surprising given the amount of attention that landscape resistance has received in the ecology literature (Vogt et al. 2009; Storfer et al. 2010). While it is possible that our study area was too small for landscape resistance to be detectible, this seems unlikely, for two reasons. First, our current results are consistent with an earlier study, in which we showed low influence of topography on frog movements at fine spatial scales (Westgate et al. 2012b). Second, our study area contains a number of structurally distinct vegetation types separated by strong ecotones (Lindenmayer et al. 2008a), which should influence both landscape resistance and habitat selection. One possible reason for the lower-than-expected landscape resistance that we report may be that those environments where strong landscape resistance has been reported have typically displayed even stronger variation in elevation (e.g. Murphy et al. 2010) or vegetation structure (e.g. Janin et al. 2009) than occurred in our study area. This suggests that conditions that are highly threatening to frog survival in terrestrial areas are more likely to induce landscape resistance, and consequently influence frog distributions.

Our finding that the distribution of aquatic habitats explains a large proportion of variation in frog distributions at this scale is an important result, because breeding sites are considerably easier to identify and manage than are frog terrestrial habitats or movement corridors. It also means that conserving individual breeding ponds and their terrestrial margins (Semlitsch & Bodie 2003; Calhoun et al. 2005), or groups of breeding sites that occur in close proximity (and therefore constitute meaningful ‘management units’; see Roe & Georges 2007), is likely to be an effective management strategy in our study area. However, the distance at which frogs responded to breeding site density in our study – which should be considered as baselines for identifying where subpopulations are likely to be connected by dispersal – were large, ranging
from 410 to 1475 metres. These are distances are much larger than buffers implemented in many locations (Goates et al. 2007), though they are also considerably smaller than the maximum distances at which frogs have been recorded to move (Smith & Green 2005).

Whether such buffers are an adequate management tool for frog conservation in other locations will depend on the relative importance of dispersal, terrestrial habitat selection, and breeding site quality for the persistence of frog populations in each study system.

While our results generally support the idea of using aquatic breeding habitat to identify high-priority conservation areas for frogs, another of our results suggests caution. Specifically, our models of breeding site density showed that occurrence of *C. signifera* was best explained by proximity to forested breeding sites (Table 1), but also that occurrence of this species was lower in forested environments than in heath (Fig 3c). Consequently, our study is unusual in showing an inversion of habitat preferences between breeding and non-breeding locations within a single frog species. Such dramatic changes in habitat preferences between breeding and non-breeding seasons have previously been documented in birds (Marfil-Daza et al. 2012) and butterflies (Radchuk et al. 2012), but not in frogs to our knowledge. However, this result can be explained when we consider that many large, productive waterbodies in our study area occur in forests, while heaths retain higher overall soil moisture. Therefore, this result appears to reflect this species’ need for damp microhabitats (Rittenhouse et al. 2009), rather than for vegetation types with particular structural characteristics. None-the-less, this result suggests that caution be taken when assessing the locations and relative importance of breeding and non-breeding habitats for migratory taxa.

Our findings regarding the effects of fire on frog populations in this environment were highly unexpected. Our initial anticipation was that frog breeding sites would act as refugia from fire (Pilliod et al. 2003), while fire would strongly influence habitat selection and landscape resistance by destroying moist rest sites necessary for frog survival in terrestrial locations (Rittenhouse et al. 2009). Instead, the opposite was true; we found stronger effects of fire in aquatic than terrestrial areas. Why this should be is unclear, but it seems likely that frequent fire
at breeding sites reduces frog population sizes through mortality for three of four species (i.e. all except C. signifera). Two of these species (U. tyleri and P. bibronii) call from terrestrial locations, which may increase their vulnerability to fire during breeding aggregations (see also Driscoll & Roberts 1997). It is less clear, however, why fire should have no detectible influence on frog terrestrial habitat selection or landscape resistance in our study area. One possibility is that the effects of fire in terrestrial areas are too fleeting to have strong influences on frog populations. For example, post-fire recovery of vegetation is rapid in our study environment (Lindenmayer et al. 2008a), which would reduce the effect of fire on landscape resistance. Similarly, frog population densities are low at even moderate distances from water (Westgate et al. 2012b), in which case fire-related mortality would also be low. In combination, these observations may be sufficient to explain the lack of response to terrestrial fires that we observed in our study.

Finally, our finding of strong inter-species variation in responses to ecological gradients – while not unprecedented – is unusual given that all four species that we studied co-occur in many breeding ponds in our study area. In particular, we found that only two species responded to the same combination of ecological gradients (P. bibronii & U. tyleri), and only because these species showed no response to terrestrial gradients. Such strong inter-species variation is analogous to migratory patterns in birds, where species that overwinter in different locations will coexist at breeding sites (McCulloch et al. 2003), or vice versa (Cherel et al. 2013). As with migratory birds, this result implies that frog species that co-occur at breeding habitats will respond differently to the threatening processes that occur in overwintering locations (Marfil-Daza et al. 2012). Potential examples include differential responses to development of upland habitats between sympatrically breeding frog species (Calhoun et al. 2005; Cushman 2006), or to spatial variation in habitat quality (e.g. Richter-Boix et al. 2007).
Conclusions

In this study, we have shown that the terrestrial distribution of frog species is strongly influenced by the density of breeding sites in the vicinity and their ecological properties, but less strongly to the ecological properties of potential terrestrial habitats and movement corridors. Our findings challenge the view that landscape resistance is a consistently important factor influencing the distribution of frog species at landscape scales. They also show that flooded breeding sites are not always adequate refugia from fire; instead fire may induce mortality in a number of species, and particularly those that call from terrestrial locations. In combination, these results show that frog species requirements for non-breeding and breeding habitats are neither interchangeable, nor predictable without careful investigation.

Acknowledgements

This work was made possible by support of the staff at Booderee National Park, as well as the people of the Wreck Bay Aboriginal community, on whose land this work was conducted. A number of staff and volunteers contributed to trapping for this project, particularly Mason Crane, Damian Michael, and Rebecca Montague-Drake. Feedback from Karen Ikin, Laura Rayner, and two anonymous referees improved an earlier draft of this manuscript.
References


### Tables and Figures

**Table 1:** Model selection statistics used to identify covariates that gave best fit to occupancy data for each species. Values give AICc, with weights in parentheses. Selected models at each modeling stage (taking into account >2 ΔAIC rule) are given in bold

<table>
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<td>Year + Temp</td>
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</table>
Figure 1: Hypothetical results and their ecological implications

a. Stochastic Metapopulation or Patchy Population
   - Trap occupancy rate
   - Density of occupied breeding sites

b. Deterministic Metapopulation or Patchy Population
   - Density of occupied, high quality breeding sites

c. One of above + terrestrial habitat selection
   - Trap occupancy rate
   - Shallow slopes
   - Steep slopes
   - Density of occupied breeding sites

d. One of above + landscape resistance
   - Shallow slopes
   - Steep slopes
Figure 2: Map of the study area, showing call survey (dots) and pitfall trap locations (crosses).
Figure 3: Predicted detection rates given annual variation (top row) and occupancy rates in relation to breeding site density (bottom row), taken from final models for each species (columns). Lines show the values of present or absent sites in this study. Error bars give 95% confidence intervals. Effects of ecological variables on terrestrial habitat selection not shown (see text). Where a ‘local’ covariate was included in the final model (e-f), low values of that variable (10% quantile) are shown as dashed lines, with high values (90% quantile) shown as solid lines.
### Appendix

**Fig. A1:** Values assigned to vegetation categories, as used in the 'vegetation structure' variable used in this article.

<table>
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<tr>
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<tr>
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<td>VwGc</td>
</tr>
<tr>
<td>0.0</td>
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</tbody>
</table>

**Keys (vegetation classifications from Taws 1997):**
- **FdEp** Eucalyptus pilularis dry forest
- **FwEp** Eucalyptus pilularis wet sclerophyll forest
- **FdB** Eucalyptus baxteri dry forest
- **FdBw** Eucalyptus baxteri wet sclerophyll forest
- **FsG** Cassinia glauca swamp forest
- **FdEpC** Eucalyptus paniculata dry forest
- **FdBi** Banksia integrifolia dry forest
- **WdBi** Banksia integrifolia dry woodland
- **WdBs** Banksia serrata dry woodland
- **WdEb** Eucalyptus gunnifera dry woodland
- **WdEsEg** Eucalyptus sclerophylla - E. gunnifera dry woodland
- **WdEsEg** Eucalyptus sieberi - E. gunnifera dry mallee
- **WmAm** Avicennia marina mangrove woodland
- **WmJl** Melaleuca linariifolia swamp woodland
- **MdEg** Eucalyptus gunnifera dry mallee
- **MdEpC** Eucalyptus paniculata dry mallee
- **SsLp** Leptospermum polygalifolium swamp shrubland
- **SsMc** Melaleuca capitata swamp shrubland
- **SsM** Melaleuca ericifolia swamp shrubland
- **SsMs** Melaleuca squarrosa swamp shrubland
- **HcBi** Baeckea imbricata coastal heath
- **HdAd** Allocasuarina distyla dry heath
- **HiBr** Banksia ericifolia intermediate heath
- **HiSi** Sprengelia incarnata intermediate heath
- **HwLj** Wet heath
- **HkAd** Allocasuarina distyla rocky heath
- **ScAsLI** Acacia sophorae - Leptospermum laevigatum coastal shrubland
- **ScLI** Leptospermum laevigatum coastal shrubland
- **SdAd** Allocasuarina distyla dry shrubland
- **SdAv** Allocasuarina ericillata dry shrubland
- **SdAdMc** Allocasuarina distyla - Melaleuca capitata rocky shrubland
- **VwGc** Galyma calkii wet sedgeland
- **VgIn** Isotopes nodosa grassy sedgeland
- **VsBa** Baumea arborescita swamp sedgeland
- **VsEs** Elaeocarpus spinaceus swamp sedgeland
- **VsSb** Schoenus brevisulius swamp sedgeland
- **VwLi** Lepidosperma forsythii wet sedgeland
- **Jalk** Juncus kraussii salmarsh rushland
- **JLI** Lomandra longifolia tussock rushland
- **GsSh** Spinifex bursarius coastal grassland
- **GsSg** Sporobolus virginicus coastal grassland
- **K** Kikuyu grassland
- **PeP** Former pine plantation
- **PeE** Eucalyptus plantation
- **Q** Water
- **D** Disturbed areas

**RIAF** Litoral rainforest
- **RdB** Backhousia myrtifolia dry rainforest
- **RpCg** Ceratopetalum apiculatum warm temperate rainforest
Appendix

Adaptive Management of biological systems: a review

Heleioporus australiacus
Abstract

Adaptive Management (AM) is widely considered to be the best available approach for managing biological systems in the presence of uncertainty. But AM has arguably only rarely succeeded in improving biodiversity outcomes. There is therefore an urgent need for reflection regarding how practitioners might overcome key problems hindering greater implementation of AM. In this paper, we present the first structured review of the AM literature that relates to biodiversity and ecosystem management, with the aim of quantifying how rare AM projects actually are. We also investigated whether AM practitioners in terrestrial and aquatic systems described the same problems; the degree of consistency in how the term ‘adaptive management’ was applied; the extent to which AM projects were sustained over time; and whether articles describing AM projects were more highly cited than comparable non-AM articles. We found that despite the large number of articles identified through the ISI web of knowledge (n=1336), only 61 articles (<5%) explicitly claimed to enact AM. These 61 articles cumulatively described 54 separate projects, but only 13 projects were supported by published monitoring data. The extent to which these 13 projects applied key aspects of the AM philosophy – such as referring to an underlying conceptual model, enacting ongoing monitoring, and comparing alternative management actions – varied enormously. Further, most AM projects were of short duration; terrestrial studies discussed biodiversity conservation significantly more frequently than aquatic studies; and empirical studies were no more highly cited than qualitative articles. Our review highlights that excessive use of the term ‘adaptive management’ is rife in the peer-reviewed literature. However, a small but increasing number of projects have been able to effectively apply AM to complex problems. We suggest that attempts to apply AM may be improved by: (1) Better collaboration between scientists and representatives from resource-extracting industries. (2) Better communication of the risks of not doing AM. (3) Ensuring AM projects “pass the test of management relevance.”
1. Introduction

It is widely accepted that biodiversity is in rapid and global decline as a result of human alteration of natural systems (Kingsford et al. 2009; Millenium Ecosystem Assessment 2005; Sala et al. 2000), a situation sometimes called the ‘sixth mass extinction’ (Wake and Vredenburg 2008). Many biologists believe there is a critical need to conserve biodiversity more effectively (Sodhi et al. 2010), and that this can occur through scientifically informed management of populations, species, landscapes and ecosystems (Lindenmayer et al. 2008; Nichols 2012; Pullin and Knight 2009). However, human effects on natural systems take many forms including habitat loss, alteration and fragmentation (Collinge 2009; Fahrig 2003; Lindenmayer and Fischer 2006), spread of invasive plants and animals (Simberloff 2010; Vitousek et al. 1997), and climate change (Lawler et al. 2010; Thomas et al. 2004). In any given ecosystem, it is often difficult to identify which are the most important stressors underpinning environmental change, and therefore driving population declines (Caughley and Gunn 1996). Anthropogenic changes to ecosystems are complex, and hence it may be unclear what actions by landscape managers will reduce impacts on biodiversity, or how to prioritize potential impact-mitigation efforts (Nicholson and Possingham 2007).

Adaptive Management (AM) can be thought of as ‘learning by doing’ (Walters and Holling 1990) and it aims to combine the need for immediate action with a plan for learning (Gunderson and Holling 2002; Van Wilgen and Biggs 2011). But like any approach to evidence-based ecosystem management, it faces a number of challenges. For example, Theberge et al. (2006) highlight that variability within natural systems makes it difficult to plan and implement studies that reliably differentiate between management options, or between alternative models of ecosystem processes (see also Sutherland 2006). Further, AM should ideally involve compromise between groups with different motivating values, but this may lead to a stalemate where controversial management interventions are suggested to improve knowledge of the system (Gregory et al. 2006; Hughes et al. 2007). Finally, AM is dependent on well-designed
monitoring programs (Nichols and Williams 2006), but such programs are notoriously difficult to implement and maintain (Lindenmayer and Likens 2010a). Therefore, considerable barriers exist which can limit the implementation of AM (Lindenmayer et al. 2008; Stankey et al. 2003), and these barriers in turn curtail its usefulness as a tool for improving biodiversity outcomes.

Despite these difficulties, the use of AM has been widely advocated, largely because of the intuitive appeal of evidence-based systems for environmental and biodiversity management (Gregory et al. 2006; Sutherland et al. 2004). Therefore, a valuable question is: How rare are effective AM projects, and how might practitioners overcome key problems hindering greater implementation? While successful AM projects – in which monitoring provides feedback that improves understanding of the system and guides future management decisions – are generally considered to be rare (Walters 2007), we are unaware of any review that provides a comprehensive, literature-wide search for examples of the AM process being applied to biological systems. Such a review would highlight the range of activities currently being described as AM in the literature, and demonstrate the extent to which collaborations between scientists and management practitioners can achieve meaningful outcomes for biodiversity conservation. Such partnerships are often difficult to achieve and maintain (Caudron et al. 2012; Knight et al. 2008), but remain a vital component of applied ecological research (Gibbons et al. 2008; Russell-Smith et al. 2003). Demonstrating the applicability of theoretical concepts using real-world examples is a valuable means of translating ideas into action (Hall and Fleishman 2010).

As a means of providing both direction and inspiration, we conducted a review designed to evaluate the degree of empirical support for AM in the ecological literature. This is a slightly different aim from thematically describing the entire literature, which is a more common method for conducting a review (e.g. Driscoll et al. 2010; Sutherland 2006). Nor was it our aim to describe the taxonomic and geographic bias of AM research, issues that are well understood for the ecological literature in general (e.g. Fazey et al. 2005; Felton et al. 2009; Teague et al. 2011). Instead, our overall goals in this study were to: highlight the major issues and
misunderstandings of what the term ‘adaptive management’ means; quantify the degree of empirical support for AM in the literature; discuss some reasons why AM might be so difficult to achieve; and provide some ways to overcome these difficulties. Such a systematic, quantitative approach has not been applied to the AM literature before, despite a number of qualitative reviews or essays (Fessehazion et al. 2011; Heinimann 2010; Keith et al. 2011; Loeb et al. 1998; Lyons et al. 2008; Medema et al. 2008; Pahl-Wostl et al. 2007; Shea et al. 2002; Thom 2000; Wilhere 2002). Our work therefore builds upon, and is complementary to, a number of articles that provide advice on those situations in which AM is appropriate (e.g. Gregory et al. 2006; McCarthy and Possingham 2007; McDonald et al. 2007; McDonald-Madden et al. 2010a; Rout et al. 2009).

In addition to the overall goals listed above, we wished to address a number of important questions regarding the extent to which AM has been applied to real-world problems. Our questions were: (1) What kinds of problems are authors in the AM literature attempting to address? (2) How rare are examples of AM in the ecological literature? (3) Is there confusion regarding what AM is and how to do it? (4) Has AM been limited by difficulties associated with long-term monitoring? (5) Is there a lack of incentives for ecologists to overcome the above barriers? Despite the importance of these questions, we don’t know of any attempt to find quantitative evidence to resolve them in the literature.

Given that AM is often difficult to enact, but could be highly beneficial for enhanced ecosystem management, there is a need for retrospection and guidance on how AM can be implemented to improve biodiversity conservation outcomes. We hope that the approach that we use to summarize the literature on AM will assist those who, despite the array of ‘bad news’ papers on this topic, still wish to undertake AM projects.

2. Defining Adaptive Management

Before moving on to a methodology for reviewing the AM literature, it is necessary to define what AM is, as well as what it is not. Providing a clear definition is necessary because there
appears to be both confusion and genuine disagreement about what AM is (Allen et al. 2011). Therefore, in this section, we highlight some of the subtleties and complexities of the language in the AM literature.

Management of biological systems universally involves some form of intervention aimed at maintaining or improving the state of the system ('system state' is a common term in the literature to which we will refer again; see Nichols and Williams 2006; Walters and Hilborn 1978; Williams 2011a). Unfortunately, there are many potential management actions, and it is often unclear what actions will improve system state most effectively. This means that managers have to make a trade-off between actions that are expected to improve the system state, and actions designed to improve knowledge. This is the 'dual control problem' (Walters and Hilborn 1978), which AM addresses by combining the need for action with a plan for learning (hence the commonly-used phrase 'learning by doing'; Walters and Holling 1990). The clearest and most succinct definition that we are aware of is given by Williams et al. (2009, page 1), although note that these authors also provide a more thorough definition:

"Adaptive management is a systematic approach for improving resource management by learning from management outcomes."

This general goal can be implemented using a range of methods, as appropriate to each study system. Although different authors provide different advice for how to implement AM, there is general agreement that the process typically involves several steps (this list is modified from Duncan and Wintle 2008; Keith et al. 2011; Williams et al. 2009):

1. Identification of management goals in collaboration with stakeholders.
2. Specification of multiple management options, one of which can be 'do nothing'.
3. Creation of a rigorous statistical process for interpreting how the system responds to management interventions. This stage typically involves creation of quantitative conceptual models and/or a rigorous experimental design (see Section 2.2).
4. Implementation of management action(s).
5. Monitoring of system response to management interventions (preferably on a regular basis).

6. Adjust management practice in response to results from monitoring.

It is these criteria that we use to classify articles in the remainder of our review.

2.1. Active versus passive AM

The dichotomy between active and passive AM has been discussed widely in relation to ecosystem management, although not without some confusion. Walters and Holling (1990) describe passive AM as an approach that takes a single conceptual model of system function and improves it over time, while active AM tests multiple competing models simultaneously (for an implementation of the latter approach see Nichols et al. 2007). Williams (2011b) gives a more general definition, stating that both passive and active AM include management interventions to improve system state, but that active AM has the additional aim of using management actions to reduce uncertainty in the underlying conceptual model(s) (see also Rout et al. 2009). In both definitions, active AM is intended to increase the rate of learning.

We favour Williams’ (2011b) definition, because it emphasizes that passive and active AM can be thought of as different solutions to the dual-control problem. Both approaches can be appropriate in certain circumstances, depending on the extent to which learning will improve management effectiveness (McDonald-Madden et al. 2011). According to Williams’ definition, it is overly simplistic to argue that active AM should always be the preferred approach. In particular, active AM can be controversial in cases where management interventions are used to improve knowledge of the system state, but which are not necessarily advantageous to all parts of the system (e.g. Hughes et al. 2007). Further, passive AM is the logical choice when little improvement in management outcomes could be achieved by collecting further information (Walters 1986). Passive AM can typically be more readily implemented than active AM, and may provide useful information for lower financial cost in certain circumstances (McCarthy and Possingham 2007).
2.2. Learning from management experiments

In practice, different AM projects can have very different experimental designs, and this variety is potentially confusing for new practitioners. Some AM projects concurrently test multiple management treatments in spatially distinct trials. Such methods provide useful results in some applications (e.g. Lindenmayer et al. 2010a; Waterhouse et al. 2010; Whitehead et al. 2008), but not others. For example, ecological responses to AM of the middle Colorado River are predominantly influenced by a single type of management treatment, namely release of water from the Glen Canyon Dam (situated in northern Arizona, USA; see Meretsky et al. 2000; Stevens et al. 2001; Walters et al. 2000). Further, this treatment can only be implemented at a single location (i.e. the Colorado River), rather than with strict controls (multiple dams) that would enable separation of the effects of treatment and location (Likens 1985). Therefore, the influence of management is ascertained by creating several competing models of system function (Johnson et al. 2002; Probert et al. 2011), and determining which model best explains change in the system following management interventions (Nichols et al. 1995; Rout et al. 2009).

Without an underlying conceptual model (or models), studies lacking spatially replicated treatments are at risk of becoming exercises in trial-and-error management (Duncan and Wintle 2008; Keith et al. 2011; Walters and Holling 1990), a process also described as ‘reactive’ management (Sutherland 2006). However, we remain agnostic on the extent to which projects must include both quantitative conceptual models and multiple management interventions to be classified as AM. Our approach in this review was to identify how studies were conducted, without arguing that they are (or are not) AM on the basis of these distinctions.

3. Methods

3.1 Review structure

We used a multi-stage process to empirically review the AM literature (see Fig. 1). Our first stage involved using the ISI ‘web of science’ to search for articles that included either the
phrase ‘adaptive management’ in the topic (i.e. keywords or abstract), or included both of the words ‘adaptive’ and ‘management’ in the title (at this stage, articles did not have to linearly combine the two words, e.g. ‘adaptive ecosystem management’). The web of science groups articles into categories and we used this feature to exclude articles from non-relevant fields, retaining articles with a focus on ecology, fisheries, forestry or biodiversity conservation. We then restricted our search to articles or reviews (excluding conference proceedings) that were published in English. Although we did not restrict our search to a subset of years, the earliest article that we found was from 1978 (Walters and Hilborn 1978). We ran our search on 25th October 2011, which identified a total of 1336 papers that met our search criteria.

[Fig. 1]

For the second stage of our review, we used an automated approach to classify identified articles, by searching for selected words in the titles, abstracts and keywords of each article (see Table A1) using the R statistical language (R Core Development Team 2011). We chose words that were indicative of three topics of interest: applications of AM to biodiversity conservation (see McCarthy and Possingham 2007; McDonald-Madden et al. 2010b), the importance of social engagement (e.g. Armitage et al. 2009), and methodological issues (e.g. Williams 2011a). We then supplemented these results by manually classifying each article into one of three categories: those that described studies specific to either terrestrial or aquatic systems, or those articles that were location non-specific (i.e. that aimed to be generally relevant to AM projects).

Our first and second analysis stages described the AM literature in its broadest sense, using AM articles from the ‘web of knowledge’ identified using ‘or’ commands to give a general representation of the work in this field. Although such an overview was important, we wished for our next section to refine our selection to only those articles whose primary focus was enacting AM projects. Therefore, our third stage was to apply supplementary filters to our automatic search, so as to identify those articles that most strongly emphasized AM. To be included in subsequent analysis (i.e. stage 3 onwards), each article had to meet one of the
following criteria: include both of the words ‘adaptive’ and ‘management’ in the title; include the phrase ‘adaptive management’ in the keywords; or include both of the words ‘adaptive’ and ‘management’ in the same sentence in the abstract. This left us with 316 articles that strongly emphasized AM in their searchable information.

For the fourth stage of our work, we read the remaining articles to identify those that claimed to describe actual AM projects, either as part of a review or as a case study. Many authors classified their work as relevant to the AM literature without presenting case studies; but it was case studies only that were the focus of our review. We used the information from these articles to create a dataset of projects that authors described as being examples of AM. This stage (moving from discussion of articles to discussion of projects) was necessary because multiple articles described the same project, while some single articles described multiple projects.

Our final stage was to categorize projects according to the definitions set out in Section 2 (above). However, we limited this stage of our analysis to those projects that included quantitative summaries in the articles we reviewed. Although there were a number of useful qualitative case studies, demonstrating that a project has been able to determine the effects of management actions requires quantitative evidence, even if only in a heavily condensed form. More pragmatically, it is difficult to evaluate the statistical design of a project that is only discussed in general terms, and this was necessary to address some of the criteria that we outlined in our definitions section. Further, projects lacking adequate description would be difficult to emulate in new situations. For those articles that provided quantitative information, we assessed the extent to which the project included the six core elements of AM that we outlined in Section 2.

3.2 Addressing research questions

We used data generated using our search methodology to address the five questions of interest that we had previously identified (see Introduction). Below we outline the data and methods used to address these questions in detail.
3.2.1 What kinds of problems are authors in the AM literature attempting to address?

We addressed our first question by using data from our second stage analysis stage (i.e. automatic and manual classification of identified articles) to discuss broad trends in the AM literature. We used logistic regression (Generalized Linear Models (GLMs) with a logit link; see McCullagh and Nelder 1989) to test for significant differences in the proportion of articles emphasizing biodiversity conservation between three different categories (aquatic, terrestrial, or neither). We then repeated our analysis to test for differences between categories in relation to emphasis on social context (model 2) or statistics (model 3). For each of our three models, we used Tukey post-hoc tests to determine whether differences in occurrence of relevant keywords were significantly different between categories.

3.2.2 How rare are examples of AM in the ecological literature?

The rarity of AM articles can be classified in several ways, depending on which criteria are used, and the stringency with which those criteria are applied. To highlight the diversity of possible views, we reported the proportion of articles that were retained as we applied increasingly stringent criteria through sequential methodological stages. We calculated our final value for the rarity of AM projects as the number of articles containing AM projects (stage 5) as a proportion of the total dataset (stage 1).

3.2.3 Is there confusion regarding what AM is and how to do it?

Our remaining questions attempted to investigate trends in the opinions and motivations of authors contributing to the AM literature. In most cases, these aspects of ecological research are difficult to quantify from a review of the existing literature, leading to a reliance on indirect surrogates to address our questions. Consequently, we addressed our third question using two lines of evidence. First, we anecdotally identified any articles that misinterpreted the term AM in our reading of AM articles (stage 3). Second, and more thoroughly, we investigated the extent to which articles matched multiple AM criteria (stage 5). Although not directly indicative
of ‘confusion’ by practitioners, the latter approach effectively demonstrated the breadth of opinion regarding how AM should be practiced.

3.2.4 Has AM been limited by difficulties associated with long-term monitoring?

Our fourth question was difficult to address, as authors rarely publish incomplete studies, and those that do rarely give detailed reasons for project cessation. None-the-less, we considered it useful to classify two sources of information on the longevity of AM projects. First, we identified the proportion of articles that described the start-up stage of AM projects as a proportion of all articles that emphasized AM in their searchable information (stage 3). Second, we determined the longevity of ongoing or completed AM projects (stage 5), as well as the frequency with which they enacted monitoring while active. In combination, these sources of evidence give information regarding the longevity of AM projects in the literature.

3.2.5 Is there a lack of incentives for ecologists to overcome the above barriers?

Our final question was the most complex one to address using data from a literature review. Although it is difficult to measure motivations and incentives in a meaningful way, citation rates are a widely-used measure of success in academia. Therefore, we created two separate models to investigate different trends in citation rates in relation to AM articles.

First, tested whether AM articles were more highly cited than non-AM articles. We achieved this by taking each article that claimed to enact AM in our review (stage 5), and comparing its number of citations against the number of citations of the article that immediately preceded it in the same journal (using citations recorded on 27th July 2012). Where the preceding article also discussed AM, we chose increasingly earlier articles from that journal until we found an article on a different topic. We then used a generalized linear mixed model (GLMM; Pinheiro and Bates 2000) from the nlme R package (Pinheiro et al. 2011) to compare ‘source’ articles against their paired ‘comparison’ article, using ‘article type’ (source or comparison) as a fixed effect. We included ‘source article ID’ as a random factorial variable to account for the paired design of our dataset. We also log-transformed citations for normality and included the number of
years since publication as a covariate to account for accrual of citations over time. Finally, we allowed interactions between ‘article type’ and ‘years since publication’ to test whether AM articles accrue citations more quickly than non-AM articles.

Second, we were interested in whether projects that we described in quantitative terms were more highly cited than projects that were described only qualitatively. We tested this by taking all articles identified in stage 5 and then using Generalized Linear Models (GLMs) to test for differences in the citation rate between qualitative and quantitative articles. We tested for linear effects of ‘article type’ (qualitative vs quantitative), ‘years since publication’, and the interaction between the two.

4. Results

Our search for articles that discussed AM yielded 6962 articles. Restricting our search to relevant subject areas reduced this to 1336 articles. These articles were from a total of 184 sources, including conference proceedings and technical research papers as well as peer-reviewed journals. The majority of sources contained only a small number of articles discussing AM, with 67 sources (36%) publishing only one article each on this topic in the period between 1978 and 2011. Seventeen journals published ≥20 articles on adaptive management during the same period, cumulatively accounting for 765 articles, or 57% of the total number of abstracts that we read. The vast majority of AM articles were from the 10 years preceding our search in October 2011 (n=2011-2011=1124, 84%), corresponding to a massive increase in the AM literature since early work by Walters and Hilborn (1976) and Holling (1978).

4.1. What kinds of problems are authors in the AM literature attempting to address?

We found that, of the three categories of article content that we investigated, biodiversity conservation was most commonly addressed in articles mentioning AM (n=625, 47%), followed by social context (n=367, 27%), and finally statistical issues (n=321, 24%). A total of 380 articles (28%) did not discuss any of these three topics, while of those that did, 40 (4%) discussed all three (Fig. 2). Most articles primarily discussed terrestrial systems (692 articles,
52%), while 402 articles (30%) described aquatic systems and 242 articles (18%) described problems that were general to the field of ecology (i.e. both aquatic and terrestrial systems).

[Fig. 2]

Biodiversity conservation was discussed in a significantly higher proportion of articles describing terrestrial systems (50%) than in aquatic systems (42%, $\beta_{\text{terrestrial}} = 0.32 \pm 0.13$, $P = 0.013$; see Fig. 3). Studies in aquatic systems also emphasized statistical issues significantly less often than either articles from terrestrial ecosystems ($\beta_{\text{terrestrial}} = 0.41 \pm 0.15$, $P = 0.008$) or location non-specific articles ($\beta_{\text{other}} = 0.53 \pm 0.19$, $P = 0.005$). However, there was no difference in the proportion of terrestrial or aquatic studies that described the social context of AM ($\beta_{\text{terrestrial}} = 0.06 \pm 0.15$, $P = 0.67$). Instead, a high proportion articles on this topic were essays that did not give a specific study system ($\beta_{\text{other}} = 0.71 \pm 0.18$, $P < 0.001$).

[Fig. 3]

4.2. How rare are examples of AM in the ecological literature?

Of our original 1336 articles, 137 (10%) included ‘adaptive’ and ‘management’ in the title; a further 179 (13%) either mentioned AM more than once in the abstract, or mentioned AM once and included AM as a keyword, giving a total of 316 articles (24%). Despite finding a relatively high number of articles that emphasized AM, only 61 articles explicitly claimed to enact AM (19% of read articles; 5% of all articles). These 61 contained a total of 54 descriptions of separate AM projects. In total, quantitative results were provided for only 27 projects, while only 13 projects referred to an underlying conceptual model against which results from management experiments were compared (see Table 1).

[Table 1]

4.3. Is there confusion regarding what AM is and how to do it?

Our first stage in identifying confusion regarding AM in theory and practice involved identifying unusual applications of the term ‘adaptive management’ during stage 3 of our
review process. These findings were largely anecdotal; however, it appeared that only a small number of authors believed they were enacting AM when in fact they weren’t (according to the operation definition of AM that we adopted for this review; see Section 2). For example, two agricultural articles (Fessehazion et al. 2011; Teague et al. 2011) used monitoring data to continually adjust the rate of nutrient application to crops, and described this process as AM. Where a similar definition occurred in other industries (e.g. forestry; see Gong 1998), this was referred to an ‘adaptive’ approach, but not ‘adaptive management’. Fortunately, it was more common for authors to explicitly acknowledge cases where their work only partially matched a more complete definition of AM (e.g. Hansen and Jones 2008).

Although few authors fundamentally misinterpreted AM principles, the extent to which authors articulated their application of key AM criteria varied enormously (Table 1). Some tested a single management hypothesis (Whitehead et al. 2008); others articulated contrasting hypotheses and tested them (Innes et al. 1999), while the strongest studies developed a range of quantitative models of system function and compared their performance over time (Rumpff et al. 2011; Williams and Nichols 2001). All projects included management interventions of some kind, although few claimed to be implementing active AM. Although five of the 13 projects were primarily industry-based (with eight primarily focusing on conservation), we found no examples of fisheries projects that claimed to be enacting AM.

4.4. Has AM been limited by difficulties associated with long-term monitoring?

During our review, we found no published examples of authors stating that a requirement to monitor system state over time caused the cessation of an AM project. However, our data suggested two trends regarding longevity in the AM projects. First, during our reading of 316 articles (stage 3), we found 58 articles (18%) that claimed to be in the initial or set-up stages of AM projects. This is almost as many as claimed to describe in-progress or completed AM projects (n= 61), suggesting either a massive increase in project start-ups in recent times, or that most projects never progress beyond the early planning stages. We found some evidence for the
former, since many ‘start-up’ articles were recent (mean age = 4.8 years). This result suggests that the number of AM projects currently underway could be larger than a review of existing articles would imply.

Second, few projects were long-lasting. Of the 13 projects identified as likely AM examples, only four lasted longer than 10 years. Moreover, although all projects mentioned some form of monitoring, some chose occasional revisits to managed sites after a long interval (e.g. Rumpff et al. 2011), rather than regularly timed, ongoing monitoring (e.g. annual or biannual measurements). Nine projects explicitly stated that they involved regular monitoring at fixed intervals. However, some projects were very short (n<sub>(≤3 years)</sub> = 3, n<sub>(4-10 years)</sub> = 8), and it was unclear whether that frequency of monitoring effort could be sustained.

4.5. **Is there a lack of incentives for ecologists to overcome barriers to implementation of AM?**

Our analysis showed no significant difference between the number of citations of AM vs non-AM articles (\(\beta_{(article\ type)} = 0.27 \pm 0.23, P=0.26, n=61\) in each class), nor a difference in the rate at which AM and non-AM article accrued citations over time (\(\beta_{(article\ type:time)} = -0.036 \pm 0.033, P=0.28\); see Fig. 4a). Similarly, AM projects supported by empirical results (n=27, 50%) were cited marginally less often than were qualitative articles (after time since publication was taken into account), although this difference was not statistically significant (\(\beta_{(quantitative\ articles)} = -0.54 \pm 0.43, P=0.23\)). Further, both qualitative and quantitative articles accrued citations at a similar rate with increasing time (\(\beta_{(article\ type:time)} = 0.063 \pm 0.075, P=0.41\); Fig. 4b). This suggests that during the process of writing articles for peer-review, ecologists do not value AM studies more highly than the wider literature, and place roughly equal value on quantitative and qualitative information from existing AM studies.

[Fig. 4]
5. Discussion

5.1. Why is AM so hard to do?

Our review has indicated that despite the extensive literature on AM, there are surprisingly few practical, on-ground examples of adaptive management (as defined for this review). Evidence from other authors (e.g. Muir 2010) suggests that this is a real trend in environmental and biodiversity management, rather than the result of difficulty in publishing articles that describe AM projects (although see Bormann et al. 2007). A key question then is: Why is AM so difficult to do? In this section of our paper, we review and reflect on the key reasons that have been suggested to contribute to the paucity of practical, on-ground examples of AM.

5.1.1. What kinds of problems are authors in the AM literature attempting to address?

We found that research emphasizing biodiversity conservation was common in the AM literature, with 47% of articles emphasizing this topic. This concentration of research effort appears to reflect legitimate difficulties in applying AM to some of the kinds of problems that policy-makers and resource managers want addressed. For example, AM projects involving extremely rare and/or endangered species can be very difficult if not impossible (Bakker and Doak 2009). Although some examples exist (e.g. Mackenzie and Keith 2009), limited numbers of populations often cause in difficulties in designing robust experiments such as establishing replicates of multiple treatments (e.g. Baw Baw Frog Philoria frosti in south-eastern Australia, see Hollis (2004)). What is less clear is why attempts to apply AM to biodiversity conservation are significantly more common in terrestrial systems than aquatic systems, both in absolute and relative terms (Fig. 3). It is possible that this result reflects that marine reserves are generally more recent and contested than terrestrial reserves as tools for ameliorating biodiversity loss (e.g. see Hughes et al. 2007). Fortunately, it appears that the prolonged research effort focused on applying AM to biodiversity conservation is paying dividends, with a small but growing number of examples appearing in the literature (Table 1).
In other cases, our review suggests that AM may not be well suited to testing management options associated with some large-scale ecological phenomena or factors that are important at multiple spatial scales or across multiple land tenures. It was particularly telling that only three projects in our final list (Waterfowl management (Williams et al. 1996), the Northwest Forest Plan (Stankey et al. 2003), and wolf management in the Yukon (Hayes et al. 2003)) involved truly large-scale problems. All three projects were from continental North America, which has a long history of research in this field. At these large scales, conflict between resource users can be exacerbated where the range of potential management interventions is limited, such as in large hydrological systems (Roe and van Eeten 2002). An example in an Australian context is the coordinated, multi-landscape-scale poison baiting control of feral predators (Parkes et al. 2006) that, to be effective, often needs to occur across areas under different tenures and managed by different organizations and/or private individuals with different management priorities, goals, values and reward systems.

Unfortunately, our results showed that a significantly higher proportion of articles discussed the social context of ecological problems in general terms, rather than describing specific tools for conservation in terrestrial or aquatic systems (Fig. 3). Clearly, more work is required to enable extension of AM to truly ‘wicked’ problems that occur at large spatial scales and across multiple land tenures.

Although the above points may appear discouraging, there are important counter-arguments to the problems that we have raised. Decision theory provides a mechanism for evaluating the usefulness of information gained by taking risks (see McDonald-Madden et al. 2010b; Rout et al. 2009), and AM can provide useful information even when one or more parts of the project are unsuccessful (e.g. reintroductions of endangered birds in New Zealand; see Armstrong et al. 2007). Further, our results showed that most articles that discussed statistics in the AM literature related to specific study systems, rather than attempting to develop statistical approaches that are generally applicable across AM projects.
As well as highlighting the high level of thought that has gone into developing AM projects – a number of which have been successful (Table 1) – our results suggest that attempts to interpret the outcomes of management experiments remain an area of active research. Finally, it is important to state that no other approach is clearly superior to AM. Approaches such as trial-and-error management can only provide an impression of superiority by masking the sources of uncertainty inherent in any environmental management problem.

5.1.2. How rare are examples of AM in the ecological literature?

Perhaps the most important result of our review has been to quantify how rare AM projects are in the AM literature. Articles claiming to enact AM constitute <5% of all articles on the topic, between them encompassing a total of 54 potential projects. Although some of these projects are very large in scale (e.g. Nichols et al. 2007), overall, our review supports the widely-held view that AM projects are very rare indeed (Allen et al. 2011; Keith et al. 2011; Stankey et al. 2003; Walters 2007; Williams et al. 2009).

Although our finding reflects genuine difficulties in enacting AM, the appearance of rarity may be reinforced by two processes. First, the scale of the literature hinders effective synthesis. We studied 1336 articles for this review, and it is highly likely that we missed some key papers. This could occur because: 1) articles were mistakenly excluded from our automated search; 2) we misinterpreted some of the content of articles during manual evaluation; or 3) the authors of articles themselves did not identify their research as AM despite implementing management experiments. Such issues are inevitable in a literature review of this size, and clearly the same difficulty in identifying AM examples exists for any would-be AM practitioners searching for motivating examples. Second, the grey literature of books and technical reports is likely to contain some laudable examples of AM projects. In particular, we speculate that the grey literature is likely to contain some useful studies in fisheries. This may explain why we found few articles claiming to enact AM in fisheries, despite the large amount of early work on AM that focused on that industry (e.g. Hilborn and Sibert 1988; Smith and Walters 1981; Walters...
and Hilborn 1976; Walters 1986). Unfortunately, grey literature is often unavailable to most practitioners. In addition to reviews such as ours, the development of websites that aim to share the results of management experiments (e.g. Jenkinson et al. 2006; Sutherland 2011) is a useful vehicle for reducing information barriers to further AM practice in future.

5.1.3. Is there confusion regarding what AM is and how to do it?

One reason why AM projects appear to be rare may be associated with the myriad of different kinds of investigations that are claimed under the banner of AM (Table 1). Although our results suggest that researchers who publish on this topic generally have a clear understanding of AM principles, there is a risk that the diversity of ways in which AM is applied may lead to confusion for those less familiar with the concept. This might explain why – in our experience of the broader NRM community – there appears to be a lot of confusion and arguments at cross-purposes about what AM actually is (see section 2; Allen et al. 2011). The concept of AM appears to be differently understood by researchers, policy makers and resource managers, with many agencies claiming they are doing AM but in fact are using *ad hoc* approaches (trial and error management (Duncan & Wintle 2008) or reactive management (Sutherland 2006)). Thus, robust experimental studies underpinned by well-designed comparisons of different management options may be deemed unnecessary by policy makers and resource managers when they (incorrectly) believe that existing approaches – such as reactively adjusting their management in the light of new information – constitute ‘adaptive’ management.

5.1.4. Has AM been limited by difficulties associated with long-term monitoring?

A central tenet of the AM paradigm is that monitoring has to be adequate to detect change resulting from management experiments. It therefore follows that where management effects accrue over long time periods, monitoring will also have to occur over a long period of time (Lindenmayer and Likens 2010a). For example, testing the predictions of competing models that aim to quantify population sizes of migratory birds requires annual monitoring over a number of years (Williams and Nichols 2001), while comparable studies regarding the
distribution of wildfires could span decades (Andersen et al. 2005). Unfortunately, long-term investigations are notoriously difficult to establish and maintain (Lindenmayer and Likens 2010b). This was exemplified when, during our review, we noted a number of articles (n=58) describing experimental designs for then-incomplete AM projects (e.g. Ascoli et al. 2009; Campbell et al. 2001), or advocating indicators to measure change resulting from future management actions (discussed by Lindenmayer and Likens 2011). However, comparatively few articles described the results of such projects. While not conclusive that a requirement for long-term monitoring is hindering AM, our results suggest either that a number of AM projects have been established recently (and so are yet to report their results), or that considerable barriers exist to the establishment of long-term AM projects.

Once established, proposed long-term projects are vulnerable to further problems, such as: (1) Funding cuts (Likens 1989; Lindenmayer and Likens 2010a). (2) Policy changes that leave them struggling for management relevance (Russell-Smith et al. 2003). (3) Events like fires and floods that can destroy the design of an experiment (Lindenmayer et al. 2010b). (4) Changes in personnel, leading to the loss of a project champion within an organization and in turn, the erosion of the partnerships necessary to keep AM projects going (Williams et al. 2009; see also below). These difficulties may dissuade researchers from establishing long-term AM projects, despite the ample opportunities such research would provide for investigation into novel, highly relevant and interesting problems.

5.1.5. Is there a lack of incentives for ecologists to overcome barriers to implementation of AM?

Although determining the motivations of AM practitioners from a literature review is inherently difficult, we reasoned that citation rates are a surrogate for the extent to which ecologists value a given piece of research. They are also a metric of academic ‘success’ used by universities. We therefore expected that academic ecologists might take citation rates into account when making decisions about the kinds of research in which to engage. In this context, we were surprised to find that AM articles were no more highly cited than paired, randomly-selected articles (Fig.
4a), despite the need for better evidence-based approaches to biodiversity management (Pullin and Knight 2009; Sutherland et al. 2004). This lack of an incentive to publish AM research adds to a number of other known disincentives to academic engagement in the AM process. For example, academic input is often not valued by industry partners in the early stages of AM projects (Molina et al. 2006; Stankey et al. 2003). Fortunately, it appears that ecologists are aware of these issues, and are seeking ways to improve future engagement (e.g. Susskind et al. 2012). This was shown in our study by the lack of a difference in citation rates between quantitative and qualitative AM articles (Fig. 4b), implying that qualitative insights into the successes and failures of AM projects are equally of interest to academics as methodological or statistical aspects of the AM process. But overall, our results imply that reward systems in universities may not encourage academics to overcome the difficulties that we have outlined above, providing little incentive for academics to engage in AM experiments.

Although we have focused here on academic incentives to engagement in the AM process, we are acutely aware there may be many other reasons why combining management and research is rare in biological systems (e.g. see Gray 2000; Jacobson et al. 2006; Norton 1998). One of these is the culture and psyche of some natural resource management institutions. First, the personnel in many agencies may be threatened by the risks posed by admitting they do not have complete knowledge about a given issue (Lindenmayer and Franklin 2002). This, in turn, may be threatening for senior staff in that organization or for politicians whom are inherently risk-averse. Second, some policy makers and resource managers do not see the need for the science which underpins AM as being relevant and nor do they understand how it may help good decision making. They also may believe that key scientific parts of the design of adaptive management projects (e.g. replicated alternative treatments) will lead to projects being “over-engineered” – a criticism of a recent temperate woodland stewardship project in south-eastern Australia (Lindenmayer, personal observation). Third, AM projects may demand that strongly contrasting treatments be tested – but this can require management activities outside the normal prescriptions to be employed (e.g. more frequent burning or higher intensity logging than...
usual). Legislative, philosophical and cultural barriers may preclude such treatments from being implemented (see Hughes et al. 2007 for an example in the establishment of AM in the Great Barrier Reef). Fourth, successful AM projects typically require partnerships among people with scientific, policy making and resource management expertise. However, many organizations lack the range of staff with this suite of skills. To overcome this, there may be a need to foster partnerships among people from different institutions with different expertise and sets of skills but who have different reward systems (Gibbons et al. 2008).

5.2. Potential approaches to overcome the impediments to establishing AM

Despite the many difficulties in implementing AM projects, there presently appears to be no alternative, viable, or clearly superior framework. Given this, there is value in seeking to identify ways in which to reduce the barriers to increasing the adoption of AM projects. We argue that three approaches may be important in this regard.

First, the often considerable costs of AM projects might be reduced (making such projects more likely to be maintained, and hence more likely to be successful) if they are “piggy-backed” on existing management and/or resource extraction practices wherever possible (Walters 1992). In cases where the AM process is truly collaborative, management activities and research are integrated, potentially reducing management costs in the long-term (Zhou et al. 2008). For example, the costs of a recent AM project investigating logging practices were minimized by building a blocked and replicated experiment around ongoing timber harvesting operations (Lindenmayer et al. 2010a). A similar approach was followed during investigation of alternative silvicultural systems in western British Columbia (Bunnell and Dunsworth 2009). Our review highlighted several more examples of successful AM in industries responsible for extraction of renewable resources (Table 1), suggesting that ‘piggy-backing’ has been a successful approach, despite problems in some specific industries (e.g. fisheries; Walters 2007). Such projects require scientists to establish working partnerships with policy makers, resource managers and become more aware of the social dimensions of AM (Davis et al. 2001). These include the reality that
policy makers, resource managers and scientists have different cultures and reward systems and are motivated by different kinds of questions and conceptual models (Gibbons et al. 2008).

Second, scientists need to better communicate the benefits of doing AM for cost-efficient and more effective resource management. For example, the U.S. waterfowl management project has generated information capable of answering questions that could not be answered except through an AM process, greatly improving management effectiveness. Similarly, Armstrong et al. (2007) were able to use the AM process to provide valuable information despite failure of their first attempted reintroduction. A related point is that scientists need to communicate the risks of not doing AM, such as the problems associated with negative ecological “surprises” that are difficult or impossible to reverse once they have manifested (see Lindenmayer et al. 2010b). Such communication may need to be couched within a framework of risk-aversion, and highlight why evidence-based approaches are important for informed resource management and conservation efforts (Pullin et al. 2004).

Third, more AM projects are likely to be established and maintained if they “pass the test of management relevance” (sensu Russell-Smith et al. 2003). Although this would appear obvious, it was clear from our review that many locations which have been the focus of extensive research efforts are not necessarily effectively managed. For example, the Florida Everglades is a location where much ecological research is done – Redfield (2000) estimated that there had been 1500 articles published on this location, while a search conducted for our review in January 2012 (using ISI web of knowledge, for the topic ‘Florida Everglades’) yielded a further 724 articles published since 2001. Some of this research has evaluated relative support for different models of landscape function (e.g. Hagerthe y et al. 2008), but integration of this research into an AM plan for the Everglades has taken a huge amount of time and effort (Brown 2005; Sklar et al. 2005). Given the potential for a mismatch between publication output and management effectiveness, ecologists should acknowledge that management-relevant research is primarily useful when it is (or can be) applied by management agencies (Russell-Smith et al. 2003). In addition to maintaining publication output, ecologists should also consider
sustainable management of natural resources, and meeting of pre-defined goals to be valid and important measures of successful ecological research (see e.g. McDonald-Madden et al. 2009).

6. Conclusions

We have presented the first structured review of the AM literature that relates to biodiversity and ecosystem management. We found that despite the enormous literature on AM, articles describing AM projects are extremely rare, consisting of <5% of all reviewed articles. One important consequence of the lack of AM has been inappropriate evaluation of the outcomes of past interventions, and therefore of corresponding future research needs. Application and monitoring of management interventions has been inadequate, limiting our understanding of important ecological processes necessary for effectively managing biological systems. The key goal for future practitioners should not only be to improve their methodologies to allow identification of cause and effect in biological systems (which can be achieved by AM projects), but more importantly to find ways to enact the iterative improvement of management and research questions though time (which is far rarer).

Acknowledgements

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References


management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications 21, 2016-2033.


Table 1: Properties of identified AM Projects (see text for details of selection methodology). Key to AM criteria: 1) Identification of management goals. 2) Specification of ≥2 management options. 3) Discussion of a rigorous statistical process for interpreting how the system responds to management interventions (quantitative conceptual models and/or a rigorous experimental design). 4) Number of management actions implemented (ideally ≥2). 5) Regular monitoring of system response to management interventions. 6) Adjust management practice in response to results from monitoring. Stars show cases where a criterion has been attained, while question marks show that information is not available in the identified sources.

<table>
<thead>
<tr>
<th>Project</th>
<th>Country</th>
<th>Duration (years)</th>
<th>AM Criteria</th>
<th>References</th>
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<tr>
<td>Waterfowl Management</td>
<td>United States</td>
<td>25</td>
<td>** * many</td>
<td>Conn &amp; Kendall (2004); Lyons et al. (2008); Johnson et al. (2002); Williams et al. (1996); Williams &amp; Nichols (2001)</td>
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<tr>
<td>Colorado River, Glen Canyon</td>
<td>United States</td>
<td>13</td>
<td>* 1</td>
<td>Cross et al. (2011); Hughes et al. (2007); Walters et al. (2000)</td>
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<td>Northwest Forest Plan</td>
<td>United States</td>
<td>10</td>
<td>** ? many</td>
<td>Bormann et al. (2007); Gray (2000); McAlpine et al. (2007); Molina et al. (2006); Stankey et al. (2003)</td>
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<td>Reintroduction of Hiihi (Mokoia Island)</td>
<td>New Zealand</td>
<td>8</td>
<td>** 4</td>
<td>Armstrong et al. (2007)</td>
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<td>Predator control - Kokako (North Island)</td>
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<td>8</td>
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<td>- Whio (Fiord-land NP)</td>
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<td>** 6</td>
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<td>** 2</td>
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Figure 1: Flowchart describing the article evaluation process undertaken for this review.
Figure 2: Venn diagram showing the overlap in topics discussed by articles, as identified during stage two of our review. Percentages are based on the 956 articles that occurred in at least one category, which accounted for 72% of the 1336 articles identified for this review.
Figure 3: Proportions of articles describing each of three topics (conservation, statistics, and social context) between three different article categories (terrestrial, aquatic or neither). Values give predicted proportions from a GLM unique to each topic. Error bars give 95% confidence intervals. Unlike letters show significant pairwise differences between contexts for a given topic.
Figure 4: Total number of article citations as a function of years since publication. a) Comparison of AM (dark circles) versus non-AM articles (light circles). Solid lines give slopes of regression line fit to AM article citations, while dashed lines show line for non-AM articles. Shaded regions show 95% confidence intervals, with darker regions showing overlap between 95% CIs of each line. b) Comparison of quantitative AM articles (dark circles) versus qualitative AM articles (light circles). Lines and shaded regions calculated as for (a).
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