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Interactive effects of climate change and fire on metapopulation viability of a forest-dependent frog in south-eastern Australia

Running head: Fire and climate change influence population viability

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Abstract

Climate change directly affects the suitability of habitats for species, but also indirectly alters natural disturbances such as fire, which can negatively impact species' persistence. Developing accurate predictions of climate change impacts requires estimates of the interactive effects of climate and disturbance regimes at both population and landscape scales. Here we couple a habitat suitability model with a population viability model to examine the interactive effects of climate change and altered fire regimes on a fire-responsive frog species across its geographic range in south-eastern Australia. By 2100, we predict expected minimum abundances (EMA) to decline by 66% (under GFDL-CM2 A1FI climate projections) or 87% (CSIRO Mk3.5 A1FI) in the absence of fire. Increased frequency of low-intensity fires reduced EMA by less than 5%, whereas increased frequency of high-intensity fires reduced EMA by up to 40% compared with the no-fire scenario. While shifts in fire regimes are predicted to impact metapopulation viability, these indirect effects of fire are far less severe than the direct impact of climate change on habitat suitability. Exploring the interactive impacts of climate change and altered disturbance regimes can help managers prioritize threats across space and time.

Keywords

amphibian; fire regime; ecological niche model; matrix population model; niche-population model; Maxent; population viability analysis; RAMAS; habitat suitability model

Introduction

Climate change is one of the most significant challenges for the conservation of biodiversity in the 21st century (Heller and Zavaleta 2009). Even small shifts in climate can directly affect survival (Chamaille-Jammes et al. 2006), reproductive output (Forchhammer 1998; Crick and Sparks 1999; Winkler et al. 2002), resource availability (Visser 2005) and habitat use (Telemeco et al. 2009). Climate change may also alter biotic interactions that affect the suitability of habitat for interacting species (Meynecke 2004; Cahill et al. 2013; Moritz and Agudo 2013). A relatively small number of native species are predicted to benefit by extending their distributions into previously unoccupied areas (Thuiller et al. 2005; Hamann and Wang 2006; Van der Putten et al. 2010). However, for most taxa, currently suitable habitat is predicted to decrease in spatial extent, and undergo considerable fragmentation (Meynecke 2004; Thuiller et al. 2005; Penman et al. 2010). Under such circumstances, persistence will depend on an ability to maintain viable populations in remaining pockets of habitat, or an ability to colonise and persist in newly available habitat.

Climate change is also likely to impact species indirectly through altered disturbance regimes. The severity, frequency and seasonality of drought, flood and wildfire are all predicted to change under future climate scenarios (Palmer et al. 2008; Allen et al. 2010; Bradstock et al. 2012). Species are adapted to specific disturbance regimes, and the alteration of these regimes may affect habitat suitability or key population processes (Whelan 1995; Keith 1996; Wardell-Johnson 2000). However, integrating shifts in disturbance regimes into projections of climate change impacts is difficult due to a poor understanding of the link between climate and most forms of disturbance (Bradstock et al. 2014).

Predicted changes in fire regimes, for example, are extremely uncertain due to the interactive effects of the key drivers of fire in different landscapes. Most studies have predicted that wildfires will increase in frequency and intensity under climate change, but most of these predictions are based solely on predicted increases in the frequency and severity of fire weather (Bergeron and Flannigan 1995; Fried et al. 2004; Hennessy et al. 2005; Pitman et al. 2007; Westerling and Bryant 2008; Clarke et al. 2011). Annual area burnt is one spatial expression of fire regimes, and is a function of four switches – weather, biomass, fuel moisture, and ignitions (Archibald et al. 2009; Bradstock 2010). Several opposing forces influence fire regimes under future climates. Firstly, severity of fire weather has been predicted to increase globally (Westerling et al. 2006; Matthews et al. 2012; Clarke et al. 2013), although average wind speed, a key predictor of fire behaviour, is predicted to decrease (McVicar et al. 2008). Secondly, leaf litter, a major component of biomass, is predicted to decrease in many forests and woodlands due to decreased moisture and increased temperature (Penman and York 2010; Matthews et al. 2012; Thomas et al. 2014). Decreases in biomass may in turn result in a decrease in fire intensity and spread. However, these changes may be offset by increases in the concentration of carbon dioxide. Elevated carbon dioxide concentration increases the structural complexity of fuels by thickening woody vegetation and increasing foliage cover (Eamus and Palmer 2007; Donohue et al. 2013), thereby increasing fuel loads. Thirdly, fuel moisture is likely to decrease with increasing temperature and seasonal reductions in rainfall (Matthews et al. 2012). Fourthly, ignitions are expected to increase under future climate scenarios (Price and Rind 1994; Syphard et al. 2007; Penman et al. 2013b; Romps et al. 2014), potentially increasing fire frequency and extent. However, the relative importance of each these variables, as well as their feedbacks and the influence of humans on ignition patterns and frequencies, are extremely uncertain, making definitive statements about future fire regimes difficult.

Accurate predictions of climate change impacts on species require estimates of the interactive effects of climate and disturbance regimes at population and landscape scales. Correlative habitat suitability models (HSMs) (Elith and Leathwick 2009) are commonly used to infer the impact of climate change (Meynecke 2004; Araújo and New 2007). However, these models typically use coarse estimates of dispersal to estimate realised distributions (e.g., no dispersal vs. unlimited dispersal) , and do not explicitly incorporate demographic parameters that influence extinction risk (Pearson and Dawson 2003; Fordham et al. 2012). Recently, these limitations have been addressed by coupling HSMs with population viability analyses (PVAs) (Keith et al. 2008; Brook et al. 2009; Dullinger et al. 2012; Fordham et al. 2012). PVAs use key demographic variables to estimate a populations' risk of decline, often simulating various alternative management scenarios. Coupling HSMs with PVAs allows for spatially explicit predictions of metapopulation extinction risk while accounting for dispersal between the temporally dynamic locations of suitable habitat patches (Keith et al. 2008; Conlisk et al. 2012; Fordham et al. 2012; Swab et al. 2012; Bonebrake et al. 2014). Few studies, however, have examined the interactive effects of climate change and disturbance regimes on metapopulation viability (but see Keith et al. 2008; Swab et al. 2012).

Frogs are considered extinction-prone globally (Houlahan et al. 2000; Stuart et al. 2004) and are likely to be extremely susceptible to future climatic changes (Pounds et al. 2006; Lemckert and Penman 2012). Species that occur predominantly in fire-prone vegetation will be further impacted by climate-driven shifts in fire regimes. The impacts of different fire regimes on frog species are poorly understood (Penman et al. 2006b) but are likely to vary with fire intensity, species' life history traits, and the exposed life stages (Bamford 1992; Driscoll and Roberts 1997; Pilliod et al. 2003; Woinarski et al. 2004; Penman et al. 2006b; Penman and Towerton 2007).

Given the uncertainties about the impacts of climate change on fire regimes, it is important to examine the response of extinction-prone biota across the potential spectrum of fire frequency and intensity combinations that may occur in the future. Results of such studies will help identify fire regimes associated with high extinction risk and clarify whether these vary depending on future climate (Keith et al. 2008; Swab et al. 2012). Once high-risk fire regimes are identified, we may be able to develop management strategies that reduce the probability of such regimes arising under future climates. In this study, we couple a HSM and a PVA to examine the interactive effects of climate change and fire regime on a fire-responsive frog species. Many studies have examined shifts in predicted suitable habitat under climate change without explicitly considering dispersal or impacts of other threats such as fire. Here we overcome these limitations by explicitly considering dispersal and shifts in habitat suitability under changing climates and a range of fire regimes. This coupled modelling approach brings several advantages. First, it allows us to explicitly test effects of fire regimes on the species under changing climates, and the interaction between these threats on the viability of the species over a 100-year period. Second, this approach estimates the viability of the species directly by integrating demographic data, rather than inferring viability based on habitat suitability alone. As a result, we are able to estimate the relative threat to persistence due to fire and to climate change, which we would not have been able to do if we did not have a coupled model. Finally, the landscape-level impacts of fire on metapopulation viability would not be captured in either a standalone HSM approach or a static PVA. In undertaking this analysis, we specifically aimed to assess whether the fire regimes that are most detrimental to this species under current climates are also detrimental under future climates, and explore whether we can develop management strategies to mitigate the risk of extinction under such regimes.

Materials and methods

Study species

The study focused on the Giant Burrowing Frog, *Heleioporus australiacus,* as this species is restricted to fire-prone native vegetation throughout its range, primarily dry forest and heathland (Penman et al. 2004). *Heleioporus australiacus* is a large myobatrachid species found in native vegetation along the coast and adjacent ranges of south-eastern Australia (Figure 1). Climate strongly influences the species' current distribution (Penman et al. 2005b, 2007b) and behaviour (Penman et al. 2006a). Longer-term climatic variation has also shaped the species' distributional extent. There are currently six species within the *Heleioporus* genus, with all other species occurring in south-western Australia (Cogger 2000). Molecular evidence indicates that *H. australiacus* evolved from a west to east migration five million years ago and has subsequently been isolated due to changing climates that caused loss of forest cover in southern Australia (Maxson and Roberts 1984; Roberts and Watson 1993).

The species spends most of its time at depths of 1-30 cm below the soil surface (Lemckert and Brassil 2003; Penman et al. 2008c). It is most active after rainfall, when it forages above ground (Penman et al. 2006a). After summer or autumn rains, the species moves to breeding sites such as hanging swamps, small creeks and wet heath (Littlejohn and Martin 1967; Daly 1996; Penman et al. 2006c). *Heleioporus australiacus* is currently listed as *vulnerable* on the IUCN Red List, and under Australian Commonwealth and State legislation.

FIGURE 1 APPROXIMATELY HERE

The impact of fire is likely to be greatest on adult *H. australiacus* (Penman et al. 2008b). During the adult phase, individuals spend >99% of their time in the forest away from breeding areas (Penman et al. 2008c) and it is these areas that are more likely to burn during a low or high intensity fire (Penman et al. 2007a; Collins et al. 2013). Low-intensity fires are likely to result in low mortality of adult frogs, due to the fossorial nature of the species, and the patchiness (Penman et al. 2007a) and low soil heating associated with low-intensity fires (Penman et al. 2006b; Penman and Towerton 2008). Conversely, high-intensity fires tend to result in greater adult mortality (Penman et al. 2004), as such fires are more homogenous (Bradstock et al. 2010) and result in higher soil heating (Humphreys and Craig 1981; Bradstock et al. 1992). To a lesser extent, fire may affect tadpole mortality. Breeding occurs immediately after the fire season for this species, and increased sedimentation of the streams following a fire has been postulated to increase tadpole mortality (Penman et al. 2004). This effect is likely to be greater after high-intensity fires, which are expected to burn more of the riparian zone (Penman et al. 2007a; Collins et al. 2013).

Predictive modelling

Estimating the extinction risk of *H. australiacus* under future climate and fire regime scenarios involved four main steps. First, we built a predictive HSM that related the current distribution of the species to environmental covariates. Second, we used this HSM and projections of future climatic conditions to predict future habitat suitability. Third, we used published and unpublished data and expert knowledge on *H. australiacus* vital rates and dispersal to build a stage-structured, stochastic matrix population model. Finally, this matrix model was coupled with the HSM in order to perform a spatially-explicit PVA under future climate and fire scenarios. Fire scenarios were not spatially explicit, but incorporated a range of probabilistic fire return intervals and intensities as catastrophes in the PVA. We describe each of these steps in detail below.

Habitat suitability model

Locality data for the HSM were compiled from survey and museum records held by the New South Wales Office of Environment and Heritage, the Victorian Department of Environment and Primary Industries, and the Australian Museum. Records were carefully checked by experts on the species by viewing the records overlaid on Google Earth satellite images and with other GIS data, and zooming in to consider locational accuracy. Erroneous and unreliable records were removed. Records were thinned so that locations were separated by a minimum distance of 1 km to reduce pseudo-replication and survey bias, with preference given to the most recent records. This resulted in a set of 250 presence records across the species’ range. The experts judged the resulting dataset to be a reasonable and unbiased sample of the species distribution. A set of 9120 background points (a sample representing conditions throughout the region of interest; Elith et al. 2011) was sampled from within a region defined by the four bioregions in which the species occurs (Sydney Basin, South Eastern Highlands, South East Corner, South East Coastal Plain) (Environment Australia 2000).

Spatial environmental data layers (resolution of 9 arc-seconds, approximately 281 m) were selected as potential predictors of suitable habitat based on previous studies of the species (Penman et al. 2004; Penman et al. 2007b) (Table 1). HSMs containing different subsets of predictors were then fitted using the Maximum Entropy algorithm of Phillips *et al.* (2006) , an appropriate method for modelling presence-background data that also performs well for prediction (Elith et al. 2006). Models used hinge features with a regularization multiplier of 1.5 to create models with smoothed responses that would extrapolate in a biologically realistic manner (Elith et al. 2010). An iterative model fitting approach was taken. Each model was initially evaluated by experts to ensure realism of response curves and predictions. In models accepted by experts, variables providing small contributions (<1%) were removed and the models refitted and rechecked by the experts. We primarily relied on expert opinion for model evaluation, but also checked that model fit was reasonable using the area under the receiver-operating characteristic curve (AUC) on training data.

TABLE 1 APPROXIMATELY HERE

Future habitat suitability was estimated by projecting HSMs to future environmental conditions predicted by two global climate models (GCMs). All climatic variables were predicted to change in the future; we assumed temporally static vegetation extent and topographic characteristics of the landscape. We used GCMs appropriate to the study region – CSIRO Mk 3.5 and GFDL-CM2 (Perkins et al. 2007; Suppiah et al. 2007) – and we assumed the A1FI (fossil fuel intensive) emissions scenario, which predicts a large temperature increase and most closely resembles the realized trajectory (Working group 3 2000; Peters et al. 2013). Individual projections of spatial climate data were made for the years 2030, 2050, 2070 and 2100 using the algorithms supplied in ANUCLIM v6.1 (http://fennerschool.anu.edu.au/files/anuclim61.pdf) and the CSIRO OZCLIM (www.**csiro**.au/**ozclim**/) climate change grids, and these were linearly interpolated to create projections for each year for the 100 year period from 2000 to 2099 (Keith et al. 2008).

Demographic model

A spatially-explicit, stochastic matrix population model based on annual time steps was constructed in RAMAS GIS v5 (Akçakaya and Root 2005). We considered three distinct life history stages (tadpoles, juveniles and adults) and only modelled females as males were considered non-limiting. Tadpoles metamorphosed after either one or two seasons (Daly 1996; Penman et al. 2004). Based on field observations of growth rates across the species' range, we assumed individuals were juveniles for three years before joining the breeding population. Demographic rates were estimated from published information (Daly 1996; Anstis 2002; Lemckert and Brassil 2003; Penman 2005; Penman et al. 2006a; Penman and Lemckert 2007; Penman et al. 2008b; Penman et al. 2008c), unpublished data, and expert knowledge.

Vital rates varied between life stages, and annually due to environmental and demographic stochasticity. Environmental stochasticity was assumed to follow a lognormal distribution and demographic stochasticity was modelled by sampling the number of survivors from a binomial distribution and the number of offspring (fecundity) from a Poisson distribution. Survival rates were lowest and most variable in tadpole stages, and were greatest and least variable in the large adult stage (Table 2). Fecundity varied between years with a CV of 20%. Variation in survival and fecundity were assumed to be correlated within populations. Elasticities for the model are presented in Table 3 and demonstrate that the model is most sensitive to adult survival. Spatial autocorrelation in environmental stochasticity (i.e. temporal fluctuation in vital rates) was based on a correlation-distance function derived from annual rainfall data from meteorological stations in the region (Fordham et al. 2012). Breeding and non-breeding behaviour of the species is strongly linked to rainfall (Penman et al. 2006a; Penman et al. 2008b; Penman and Brassil 2010).

A contest model (Akçakaya and Root 2005) was adopted to represent density dependence of vital rates, given the species' relatively long generation length and evidence of territorial behaviour in breeding (Penman et al. 2004) and non-breeding habitats (Penman et al. 2008c). The carrying capacity of each population was estimated from relative habitat suitability values predicted by the HSM (see Model integration below).

TABLE 2 APPROXIMATELY HERE

Annual dispersal rates between populations (defined as grid cells; see below) were estimated from radio-telemetry (Penman et al. 2008c) and capture-recapture data from unpublished pitfall-trapping studies. Most recorded movements of the species involve distances less than 300 m (Penman et al. 2008c). Dispersal was assumed to predominantly occur in the juvenile stage, particularly in the first year, and movement was only possible between four neighbouring cells in the cardinal directions. Juveniles were modelled as being 20 times more likely to disperse than other terrestrial stages Based on grid geometry, the average annual probability of dispersal to a neighbouring grid cell was 0.0044. Dispersal rates varied annually with a CV of 5%.

Low- and high-intensity fires were included separately in models as stochastic "catastrophes" that reduced abundances of all life stages (Table 2). Fires were not spatially correlated, i.e. fires in one cell did not affect adjacent cells. However, as explained below, the PVA was run on an aggregated grid with cell size approximately 10 km x 10 km. This resolution exceeds the areal extent of all low-intensity fires and many of the wildfires in the region. Due to uncertainty about future fire regimes, we considered probabilistic fire return intervals of 10, 20, 30 and 40 years. The 20-year return interval approximates the current fire regime in the north of the species' range (Bradstock et al. 2012), while the 30-year interval is more representative of that experienced in the south.

Model integration

The HSM and demographic model were coupled following the procedures described by Keith *et al.* (2014). HSM prediction grids were transformed to an equal-area projection (Australian Albers) with a resolution of 281 m. Cells with predicted habitat suitability less than the fifth percentile of suitability at training occurrence points were considered unsuitable and set to a value of 0. The 281 m cells were then aggregated (by summing suitability scores) to 9,835 m cells. Subsequently, aggregated grid cells with values less than the first percentile of the values at training occurrence points were excluded, as they represented very small and potentially diffuse areas of suitable habitat. Each cell formed a population unit or patch for modelling purposes. Carrying capacity of each patch was calculated as a linear function of the habitat suitability of that patch multiplied by the number of individuals that would occur in optimal habitat. Field data suggest *H. australiacus* has an approximately 1:1 sex ratio (Penman *unpublished data*). Individuals have non-overlapping home ranges of 0.04 ha, with no difference between the sexes (Penman et al. 2008c). Within a 281 m cell, we assumed one breeding site was present. Outside breeding events, the species shelters at sites that are generally at least 75 m from the nearest stream. Using these data, we estimated that optimal habitat would support approximately 10 females per hectare, which translates to 73 females per 281 m grid cell. For each time step, carrying capacity of each patch was estimated as HS*73, where HS is the aggregated habitat suitability value from the HSM at each 9,835 m cell.

For patches associated with known occurrences, the initial abundance was assumed to be at carrying capacity and at a stable age distribution. All other patches were assumed to be unoccupied. The model was then run for a burn-in period long enough to ensure the metapopulation occupancy reached equilibrium. One thousand iterations were subsequently run for each combination of fire scenario and climate model for the 100-year period from 2000 to 2099. For comparison purposes, we also ran 1,000 iterations under stable climatic conditions. Outputs were compared with respect to estimates of expected minimum abundance (EMA), calculated as the mean, across simulations, of the 100-year population size trajectories' minima (McCarthy and Thompson 2001).

Sensitivity of the model was tested by independently increasing or decreasing each of the transition probabilities and the effect of fire on survival by 20%. Values were altered for the 20-year fire return interval scenario with climatic changes predicted by the CSIRO Mk 3.5 model. These sensitivity analyses were conducted for both low- and high-intensity fire scenarios. Model sensitivity was measured using the change in the Expected Minimum Abundance (EMA), with models considered sensitive to a parameter if the EMA changed by more than 20%.

Results

The final HSM included six variables, five of which represent aspects of climate (Table 4). Summer rainfall, extant vegetation, rainfall seasonality and annual mean temperature were the primary drivers in the model (see supplementary material for the full Maxent output). The model was judged as sensible by the experts, and had high discrimination capacity, with an AUC of 0.897 on training data. Under current climatic conditions, the model predicted higher suitability in northern areas where there were substantially more species observations. Under the projections of both GCMs, the HSM predicted considerable contraction of suitable habitat to the south of the species' range and into higher elevation sites (Figure 2; Figure 3). The CSIRO Mk3.5 model predicted a marginally smaller future distribution than the GFDL-CM2 model.

TABLE 4 APPROXIMATELY HERE

Regardless of GCM, temporal changes in habitat suitability due to climate change were more influential than fire regimes in determining EMA. When using CSIRO Mk3.5 projections of future climate, EMA decreased by approximately 87% relative to the no climate change scenario for a given fire scenario (Figure 4). Similarly, GFDL-CM2 projections led to a reduction in EMA of approximately 66% (Figure 4). The influence of fire regime on abundance was consistent across future climate scenarios. Low-intensity fire regimes resulted in very small reductions (<5%) in EMA relative to an equivalent scenario without fire and the result was consistent regardless of the inter-fire interval. In contrast, high-intensity fire regimes resulted in large reductions in EMA that increased as fire interval decreased. At a 40-year interval, EMA was reduced by approximately 10% compared to a no-fire scenario, whereas at a 10-year interval it was reduced by approximately 40% (Figure 4). The worst-case scenario was a regime of frequent high-intensity fires (10-year intervals) which reduced the EMA to 7.8% (CSIRO Mk3.5) or 21.1% (GFDL-CM2) of the scenario lacking fire and climate change.

The model was not considered sensitive to any of the vital rates in the model (Table 5).

FIGURES 2, 3, 4 APPROXIMATELY HERE

TABLE 5 APPROXIMATELY HERE

Discussion

Habitat suitability models estimate direct effects of climate change on habitat suitability, but often ignore synergies between spatial threats. We have shown that interactions between climate change and disturbance regimes can be important when considering the impacts of climate change. Species are adapted to specific fire regimes, which are likely to shift as a result of climatic change. Our results suggest that for *H. australiacus*, the direct impact of climate change on habitat suitability will far outweigh any potential shifts in fire regimes throughout the species' range. However, avoiding frequent, high-intensity fires could still produce benefits to the viability of the metapopulation. These results can assist conservation managers in developing plans to mitigate the direct impacts of climate change on habitat suitability.

Impacts of fire on metapopulation viability

Changes in fire regimes were predicted to impact the viability of the *H. australiacus* metapopulation under both current and future climates, but the magnitude of this impact varied according to the combination of fire interval and fire intensity. Specifically, our results indicate that fire frequency affects metapopulation viability only when fires are of high intensity. Interestingly, the effect of fire was consistent under a stable and changing climate. Modelled low-intensity fires were based on observations of prescribed fire that were patchy and resulted in low adult mortality (Penman et al. 2007a). Soil temperatures experienced in such fires are not sufficient to result in mortality for the majority of individuals in the fire area (Penman et al. 2006b; Penman and Towerton 2008). In contrast, high-intensity fires result in greater heating of the soil (Humphreys and Craig 1981; Bradstock et al. 1992), causing higher mortality in the adult population. The effects of high-intensity fires are exacerbated by the timing of fires, which occur immediately prior to the breeding season and are thus expected to reduce reproduction capacity within the population. The overall reduction in metapopulation abundance associated with frequent, high-intensity fires therefore reflects the inability of populations to recover from larval mortality, but particularly from high adult mortality between successive fires (Table 3).

TABLE 3 APPROXIMATELY HERE

Our models simulated impacts of fire on survival, but did not include indirect effects of a changed fire regime. The two most likely indirect impacts are changes in the structural suitability of habitat and alterations to food resources. Altering fire frequency can result in significant shifts in floristic diversity and vegetation structure (Cary and Morrison 1995; Lunt and Morgan 1999; Gent and Morgan 2007; Keith et al. 2007; Penman et al. 2011a). Increased fire frequency generally increases the diversity and extent of ground cover species (Keith 1996; Andersen et al. 2005; Penman et al. 2008a), which decreases habitat suitability for this and other burrowing frog species (Jansen et al. 2001; Penman et al. 2005a). Furthermore, invertebrate diversity is closely linked with floristic diversity and vegetation structure (Andersen et al. 2009; Wittkuhn et al. 2011). Fire frequency also directly impacts invertebrates by altering composition and abundance (York 2000; Andersen et al. 2005). Invertebrates dominate the diet of *H. australiacus* and changes in invertebrate communities may reduce nutritional intake for the species (Penman et al. 2006b), potentially reducing survival and reproductive output. The species may therefore be more susceptible to high frequency, low-intensity fire regimes than suggested by our results. Hence the indirect effects of changes in fire regimes on *H. australiacus* under future climates warrants further examination.

Implications for fire management

Our results suggest that fire management actions that reduce the risk of frequent high-intensity fires would be beneficial to *H. australiacus* both now and under possible future climates. Prescribed fire (i.e., controlled, low-intensity fire), is often proposed as a tool to reduce the extent of future fires (Fernandes and Botelho 2003; Penman et al. 2011b). However, there does not appear to be a direct trade-off between high- and low-intensity fires. Several studies have found that to reduce the extent of wildfire in Eucalypt forests by one hectare, three to four hectares of land must be treated with prescribed fire (Boer et al. 2009; Price and Bradstock 2011). That is, for every 1% decrease in the average annual area burned by wildfire, managers must increase the annual prescribed burning effort by 3-4% (Bradstock et al. 2012). The net effect is a 2-3% increase in the total area affected by fire in the landscape each year. The combined impact of increased prescribed fire and wildfires would exceed critical thresholds for a number of flora species (Kenny et al. 2004), resulting in significant shifts in community composition and structure, potentially impacting *H. australiacus* through processes described above. Additionally, although empirical analysis of fire severity patterns in Eucalypt forests have shown that the probability of high-intensity fires is lower in young fuels (< 5 years old), this is dependent on fire weather (Bradstock et al. 2010; Price and Bradstock 2012; Collins et al. 2013), with the effect of prescribed fire either reduced or lost under extreme fire weather. The majority of area burned by wildfire in the study area occurs under extreme fire weather (Bradstock et al. 2009), suggesting prescribed fire is unlikely to reduce the occurrence, extent or severity of high-intensity fires.

Clearly, alternate fire management strategies that mitigate the risk of more frequent high-intensity fires are required. One potential solution is the management of ignitions, which has been shown to significantly reduce the extent and impact of wildfires (Cary et al. 2009; Wintle et al. 2011). In the study area, the majority of ignitions are anthropogenic (Penman et al. 2013a). However, to date there are no known successful management approaches that effectively reduce the occurrence of anthropogenic ignitions (Bryant 2008). If successful ignition abatement strategies can be developed and implemented, they offer a means of ameliorating the cumulative impacts of two semi-independent threats. Slower rates of decline that result from such strategies may allow more time for climate mitigation policies to take effect. Regan et al. (2011) similarly showed that appropriate fire management strategies were crucial to limiting the combined impacts of fire and disease on a fire-prone plant species.

Climate change impacts on metapopulation viability

While changes in the frequency of high-intensity fires under climate change will impact the viability of *H. australiacus*, the effect is predicted to be small relative to the direct impact of changes in habitat suitability due to climate change (Figure 4). Our models predict climate change will reduce metapopulation viability through an extensive reduction in climatically suitable habitat by 2100 (Figure 2; Figure 3). By that time, suitable habitat is predicted to be confined to a small area in the southern portion of the species' range, where there are few recent records of the species.

The loss of the northern populations would represent a significant conservation issue for this species. *Heleioporus australiacus* is thought to be composed of two genetically distinct taxa (Penman et al. 2008b), with a geographic division between the two taxa at the current disjunction in the distributional records (Penman et al. 2005b) (Figure 1). Our study suggests that under future climates we might expect the complete extinction of the northern populations, with only the southern populations persisting. Even if the two groups of populations are found to represent a single species, there will be significant losses in its genetic diversity, as well as that of other species that occupy similar ranges. Collection and storage of genetic samples from these populations should be undertaken in an attempt to conserve their genetic diversity.

Conservation management

Managing biodiversity through rapid climatic change poses great challenges to conservation managers globally (Heller and Zavaleta 2009). Models such as ours can help scientists and conservation managers identify key management strategies that could be implemented to protect the species. In the case of *H. australiacus*, the key actions we propose based on the results of the study are:

1. Identification of new populations at the southern end of the species' range (potentially guided by predictions of our HSM) and the protection of habitats predicted as suitable by 2100. Our models suggest these areas may be climatic

refuges for the species. It is therefore vital to locate and conserve these populations to promote the long term survival of the species. If necessary, assisted migration may also be a viable strategy (McDonald-Madden et al. 2011).

2. Monitoring northern populations to detect an early warning of expected responses to climate change. These populations are predicted to disappear in a relatively short period of time (20-40 years). Identifying declines in these populations will allow managers to decide when to increase their investment in the conservation of the species in these areas. Data from monitoring could be used to validate and revise the model, particularly if a range of fire histories are considered.
3. Collection and storage of genetic material to conserve genetic diversity (see above).
4. Investigate and develop strategies for reducing human ignitions during extreme fire weather as a means of minimising population declines related to climate change.

Model limitations

Our modelling approach was selected to provide an assessment of the relative influence of the direct impacts of climate change on habitat suitability and the indirect effects of changing fire regimes. However, there are three major limitations to our modelling approach. Firstly, we did not model spatial autocorrelation in fire (i.e. fire in one grid cell did not affect the probability of fire in adjacent cells). As a result, though there was some probability of fires occurring simultaneously in adjacent or nearby cells, large wildfires (i.e. > 10 000 ha) were not explicitly included. In reality, there is spatial and temporal clustering in the probability of a fire occurring (Boer et al. 2008; Bradstock et al. 2009; Penman et al. 2013b) that we did not incorporate, and the fire impacts we detected may have been over-estimated unless suitable habitat was similarly autocorrelated. Alternatively, we may have under-estimated the impact of fire as the model did not include extremely large wildfires that have the potential to simultaneously impact a large number of populations or isolated populations in fragmented landscapes. In reality, however, such events are extremely rare.

Secondly, the model was not capable of incorporating the interactive effects of low and high intensity fires in a meaningful way. Disturbance events in the RAMAS software are treated as independent with a probability of occurrence. In reality, low intensity planned fires will not occur for a given period after a wildfire due to ecological concerns (Kenny et al. 2004). Furthermore, the impact of high intensity wildfire on populations of this species may be altered by previous low intensity fires (Penman et al. 2006b). RAMAS is also incapable of capturing this interaction. Addressing this issue would require a fire regime model coupled with the HSM and PVA.

Thirdly, our model assumes that land use and vegetation are static over the study period. As human populations continue to grow, urban areas will continue to encroach on native vegetation (Syphard et al. 2007), thereby decreasing the extent of habitat and shifting vegetation boundaries (Cramer et al. 2001). Climate change is also likely to lead to spatial dynamics in the distribution of vegetation. Our assumption of static land cover is therefore an optimistic scenario and the magnitude of the change may in fact be much greater.

Despite these limitations, the aim of our study was to examine the relative contribution of climate change and fire to metapopulation viability. A thorough examination of all the potentially interacting factors would require far more untested assumptions regarding fire regimes and vegetation dynamics, and a more complex modelling framework.

Conclusion

Simulating environmental change and management actions by coupling models of habitat suitability with spatial models of population dynamics provides a means of assessing the relative importance of threats to species, as well as their potential interactions. Our results support the notion that climate change is likely to be the major threat to biodiversity in the coming century. While shifts in fire regimes are predicted to impact the viability of *H. australiacus*, the effect is far less severe than direct impacts of climate change. These results are consistent with some studies (Lawson et al. 2010), but contrast with others that found shifts in fire regimes were a greater threat to other species (Swab et al. 2012). Exploring the interactive impacts of climate change and disturbance regimes allows managers to prioritize threats across space and time. In turn, managers can identify conservation actions that increase species' ability to persist in future climates.

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References

Akçakaya, H.R., Root, W.R., 2005. RAMAS Metapop. Applied Biomathematics, Setauket.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259, 660-684.

Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J., Woinarski, J.C.Z., 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecology 30, 155-167.

Andersen, A.N., Penman, T.D., Debas, N., Houadria, M., 2009. Ant community responses to experimental fire and logging in a eucalypt forest of south-eastern Australia. Forest Ecology and Management 258, 188-197.

Anstis, M., 2002. Tadpoles of South-eastern Australia. New Holland Publishers, Sydney, Australia.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22, 42-47.

Archibald, S., Roy, D.P., Van Wilgen, B.W., Scholes, R.J., 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. Global Change Biology 15, 613-630.

Bamford, M.J., 1992. The impact of fire and increasing time after fire upon Heleioporus eyrei, Limnodynastes dorsalis and Myobatrachus gouldii (Anura, Leptodactylidae) in Banksia woodland near Perth, Western Australia. Wildlife Research 19, 169-178.

Bergeron, Y., Flannigan, M.D., 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air, & Soil Pollution 82, 437-444.

Boer, M., Sadler, R., Bradstock, R., Gill, A., Grierson, P., 2008. Spatial scale invariance of southern Australian forest fires mirrors the scaling behaviour of fire-driving weather events. Landscape Ecology 23, 899-913.

Boer, M.M., Sadler, R.J., Wittkuhn, R., McCaw, L., Grierson, P.F., 2009. Long-term impacts of prescribed burning on regional extent and incidence of wildfires – evidence from fifty years of active fire management in SW Australian forests. Forest Ecology and Management 259, 132-142.

Bonebrake, T.C., Syphard, A.D., Franklin, J., Anderson, K.E., AkÇAkaya, H.R., Mizerek, T., Winchell, C., Regan, H.M., 2014. Fire Management, Managed Relocation, and Land Conservation Options for Long-Lived Obligate Seeding Plants under Global Changes in Climate, Urbanization, and Fire Regime. Conservation Biology, n/a-n/a.

Bradstock, R., Hammill, K., Collins, L., Price, O., 2010. Effects of weather, fuel and terrain on fire severity in topographically diverse landscapes of south-eastern Australia. Landscape Ecology 25, 607-619.

Bradstock, R., Penman, T., Boer, M., Price, O., Clarke, H., 2014. Divergent responses of fire to recent warming and drying across south-eastern Australia. Global Change Biology 20, 1412-1428.

Bradstock, R.A., 2010. A biogeographic model of fire regimes in Australia: current and future implications. Global Ecology & Biogeography 19, 145-158.

Bradstock, R.A., Auld, T.D., Ellis, M.E., Cohn, J.S., 1992. Soil temperatures during bushfires in semi-arid, mallee shrublands. Australian Journal of Ecology 17, 433-440.

Bradstock, R.A., Cary, G.J., Davies, I., Lindenmayer, D.B., Price, O.F., Williams, R.J., 2012. Wildfires, fuel treatment and risk mitigation in Australian eucalypt forests: Insights from landscape-scale simulation. Journal of Environmental Management 105, 66-75.

Bradstock, R.A., Cohn, J.S., Gill, A.M., Bedward, M., Lucas, C., 2009. Prediction of the probability of large fires in the Sydney region of south-eastern Australia using fire weather. International Journal of Wildland Fire 18, 932-943.

Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G., Araújo, M.B., 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. Biology Letters 5, 723-725.

Bryant, C., 2008. Understanding bushfire: trends in deliberate vegetation fires in Australia. Australian Institute of Criminology.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280.

Cary, G.J., Flannigan, M.D., Keane, R.E., Bradstock, R.A., Davies, I.D., Lenihan, J.M., Li, C., Logan, K.A., Parsons, R.A., 2009. Relative importance of fuel management, ignition management and weather for area burned: Evidence from five landscape-fire-succession models. International Journal of Wildland Fire 18, 147-156.

Cary, G.J., Morrison, D.A., 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Combinations of inter-fire intervals. Australian Journal of Ecology 20, 418-426.

Chamaille-Jammes, S., Massot, M., Aragon, P., Clobert, J., 2006. Global warming and positive fitness response in mountain populations of common lizards Lacerta vivipara. Global Change Biology 12, 392-402.

Clarke, H., Lucas, C., Smith, P., 2013. Changes in Australian fire weather between 1973 and 2010. International Journal of Climatology 33, 931-944.

Clarke, H.G., Smith, P.L., Pitman, A.J., 2011. Regional signatures of future fire weather over eastern Australia from global climate models. International Journal of Wildland Fire 20, 550-562.

Cogger, H.A., 2000. Reptiles and amphibians of Australia. Reed Books Australia, Melbourne.

Collins, L., Bradstock, R.A., Penman, T.D., 2013. Can precipitation influence landscape controls on wildfire severity? A case study within temperate eucalypt forests of south-eastern Australia. International Journal of Wildland Fire Accepted April 3rd 2013.

Conlisk, E., Lawson, D., Syphard, A.D., Franklin, J., Flint, L., Flint, A., Regan, H.M., 2012. The Roles of Dispersal, Fecundity, and Predation in the Population Persistence of an Oak (*Quercus engelmannii*) under Global Change. PLoS ONE 7, e36391.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., Young-Molling, C., 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7, 357-373.

Crick, H.Q.P., Sparks, T.H., 1999. Climate change related to egg-laying trends. Nature 399, 423-424.

Daly, G., 1996. Observations of the eastern owl frog Heleioporus australiacus (Anura, Myobatrachidae) in Southern New South Wales. Herpetofauna 26, 33-42.

Donohue, R.J., Roderick, M.L., McVicar, T.R., Farquhar, G.D., 2013. Impact of CO2 fertilization on maximum foliage cover across the globe's warm, arid environments. Geophysical Research Letters 40, 3031-3035.

Driscoll, D.A., Roberts, J.D., 1997. Impact of fuel reduction burning on the frog Geocrinia lutea in south west Western Australia Australian Journal of Ecology 22, 334-339.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnbock, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D.R., Silc, U., Vittoz, P., Hulber, K., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Clim. Change 2, 619-622.

Eamus, D., Palmer, A.R., 2007. Is Climate Change a Possible Explanation for Woody Thickening in Arid and Semi-Arid Regions? Research Letters in Ecology 2007.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129-151.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1, 330-342.

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics 40, 677-697.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17, 43-57.

Environment Australia, 2000. Revision of the Interim Biogeographic Regionalisation of Australia (IBRA) and the Development of Version 5.1. - Summary Report. Department of Environment and Heritage, Canberra.

Fernandes, P.M., Botelho, H., S., 2003. A review of prescribed burning effectiveness in fire hazard reduction. International Journal of Wildland Fire 12, 117-128.

Forchhammer, M.C., E. Post, and N. C. Stenseth, 1998. Breeding phenology and climate change. Nature 391, 29-30.

Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C., Brook, B.W., 2012. Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? Global Change Biology 18, 1357-1371.

Fried, J., Torn, M., Mills, E., 2004. The Impact of Climate Change on Wildfire Severity: A Regional Forecast for Northern California. Climatic Change 64, 169-191.

Gent, M.L., Morgan, J.W., 2007. Changes in the stand structure (1975-2000) of coastal *Banksia* forest in the long absence of fire. Austral Ecology 32, 239-244.

Hamann, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in Bristish Columbia. Ecology 87, 2773-2786.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142, 14-32.

Hennessy, K.J., Lucas, C., Nicholls, N., Bathols, J., Suppiah, R., Ricketts, J., 2005. Climate change impacts on fire-weather in south-east Australia. CSIRO Marine and Atmospheric Research, Melbourne, Australia.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S., 2000. Quantitative evidence for global amphibian population declines. Nature 404, 752-755.

Humphreys, F.R., Craig, F.G., 1981. Effects of fire on soil chemical, structural and hydrological properties, In Fire and the Australian Biota. eds A.M. Gill, R.H. Groves, I.R. Noble, pp. 177-200. Australian Academy of Science, Canberra.

Jansen, K.P., Summers, A.P., Delis, P.R., 2001. Spadefoot Toads (*Scaphiopus holbrookii holbrookii*) in an Urban Landscape, Effects of Non-natural Substrates on Burrowing in Adults and Juveniles. Journal of Herpetology 35, 141-145.

Keith, D.A., 1996. Fire-driven extinction of plant populations: A synthesis of theory and review of evidence from Australian vegetation. Proceedings of the Linnean Society of New South Wales 116, 37-78.

Keith, D.A., 2011. Relationships between geodiversity and vegetation in south-eastern Australia. Proceedings of the Linnean Society of New South Wales 132, 5-26.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B., Rebelo, T.G., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4, 560-563.

Keith, D.A., Holman, L., Rodoreda, S., Lemmon, J., Bedward, M., 2007. Plant functional types can predict decade-scale changes in fire-prone vegetation. Journal of Ecology 95, 1324-1337.

Keith, D.A., Mahony, M., Hines, H., Elith, J., Regan, T.J., Baumgartner, J.B., Hunter, D., Heard, G.W., Mitchell, N.J., Parris, K.M., Penman, T.D., Scheele, B., Simpson, C.C., Tingley, R., Tracy, C.R., West, M., Akcakaya, H.R., 2014. Detecting extinction risk from climate change by IUCN Red List criteria. Conservation Biology 28, 810-819.

Kenny, B., Sutherland, E., Tasker, E., Bradstock, R., 2004. Guidelines for Ecologically Sustainable Fire Management. NSW National Parks and Wildlife Service, Hurstville.

Lawson, D.M., Regan, H.M., Zedler, P.H., Franklin, J., 2010. Cumulative effects of land use, altered fire regime and climate change on persistence of Ceanothus verrucosus, a rare, fire-dependent plant species. Global Change Biology 16, 2518-2529.

Lemckert, F., Brassil, T., 2003. Movements and habitat use by the giant burrowing frog, Heleioporus australiacus. Amphibia-Reptilia 24, 207-211.

Lemckert, F., Penman, T., 2012. Climate Change and Australia's frogs: how much do we need to worry?, In Wildlife & Climate Change: Towards robust conservation strategies for Australian fauna. eds D. Lunney, P. Hutchings, pp. 92-98. Surrey Beatty, Sydney, Australia.

Littlejohn, M.J., Martin, A.A., 1967. The rediscovery of Heleioporus australiacus in eastern Victoria. Proceedings of the Royal Society of Victoria 80, 31-35.

Lunt, I.D., Morgan, J.W., 1999. Effect of fire frequency on plant composition at the Laverton North Grassland Reserve, Victoria. Victorian Naturalist 116, 84-90.

Matthews, S., Sullivan, A.L., Watson, P., Williams, R.J., 2012. Climate change, fuel and fire behaviour in a eucalypt forest. Global Change Biology 18, 3212-3223.

Maxson, L.R., Roberts, J.D., 1984. Albumin and Australian Frogs: Molecular Data a Challenge to Speciation Model. Science 225, 957-958.

McCarthy, M.A., Thompson, C., 2001. Expected minimum population size as a measure of threat. Animal Conservation 4, 351-355.

McDonald-Madden, E., Runge, M.C., Possingham, H.P., Martin, T.G., 2011. Optimal timing for managed relocation of species faced with climate change. Nature Clim. Change 1, 261-265.

McVicar, T.R., Van Niel, T.G., Li, L.T., Roderick, M.L., Rayner, D.P., Ricciardulli, L., Donohue, R.J., 2008. Wind speed climatology and trends for Australia, 1975–2006: Capturing the stilling phenomenon and comparison with near-surface reanalysis output. Geophysical Research Letters 35, L20403.

Meynecke, J.-O., 2004. Effects of global climate change on geographic distributions of vertebrates in North Queensland. Ecological Modelling 174, 347-357.

Moritz, C., Agudo, R., 2013. The Future of Species Under Climate Change: Resilience or Decline? Science 341, 504-508.

Palmer, M.A., Reidy Liermann, C.A., Nilsson, C., Flörke, M., Alcamo, J., Lake, P.S., Bond, N., 2008. Climate change and the world's river basins: anticipating management options. Frontiers in Ecology and the Environment 6, 81-89.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12, 361-371.

Penman, T., Lemckert, F., Mahony, M., 2004. Two hundred and ten years looking for the Giant Burrowing Frog. Australian Zoologist 32, 597-604.

Penman, T., Lemckert, F., Slade, C., Mahony, M., 2005a. Non-breeding habitat requirements of the giant burrowing frog, Heleioporus australiacus (Anura: Myobatrachidae) in south-eastern Australia. Australian Zoologist 33, 251-257.

Penman, T.D., 2005. Applied conservation biology of a threatened forest dependent frog, *Heleioporus australiacus*. University of Newcastle.

Penman, T.D., Binns, D.L., Shiels, R.J., Allen, R.M., Kavanagh, R.P., 2008a. Changes in understorey plant species richness following logging and prescribed burning in shrubby dry sclerophyll forests of south-eastern Australia. Austral Ecology 33, 197-210.

Penman, T.D., Binns, D.L., Shiels, R.J., Allen, R.M., Penman, S.H., 2011a. Hidden effects of forest management practices: Responses of a soil stored seed bank to logging and repeated prescribed fire. Austral Ecology 36, 571-580.

Penman, T.D., Bradstock, R.A., Price, O., 2013a. Modelling the determinants of ignition in the Sydney Basin, Australia: implications for future management. International Journal of Wildland Fire 22, 469-478.

Penman, T.D., Brassil, T.E., 2010. Management of Amphibian Populations in Booderee National Park, South-Eastern Australia. Herpetological Conservation and Biology 5, 73-79.

Penman, T.D., Christie, F.J., Andersen, A.N., Bradstock, R.A., Cary, G.J., Henderson, M.K., Price, O., Tran, C., Wardle, G.M., Williams, R.J., York, A., 2011b. Prescribed burning: How can it work to conserve the things we value? International Journal of Wildland Fire 20, 721-733.

Penman, T.D., Kavanagh, R.P., Binns, D.L., Melick, D.R., 2007a. Patchiness of prescribed burns in dry sclerophyll eucalypt forests in South-eastern Australia. Forest Ecology and Management 252, 24-32.

Penman, T.D., Lemckert, F.L., 2007. *Heleioporus australiacus* predation. Herpetological Review 38, 185-186.

Penman, T.D., Lemckert, F.L., Mahony, M.J., 2006a. Meteorological effects on the activity of the giant burrowing frog (Heleioporus australiacus) in south-eastern Australia. Wildlife Research 33, 35-40.

Penman, T.D., Lemckert, F.L., Mahony, M.J., 2006b. A preliminary investigation into the potential impacts of fire on a forest dependent burrowing frog species. Pacific Conservation Biology 12, 78-83.

Penman, T.D., Lemckert, F.L., Mahony, M.J., 2008b. Applied Conservation Management of a Threatened Forest Dependent Frog, *Heleioporus australiacus*. Endangered Species Research 5, 45-53.

Penman, T.D., Lemckert, F.L., Mahony, M.J., 2008c. Spatial ecology of the giant burrowing frog (Heleioporus australiacus): implications for conservation prescriptions. Australian Journal of Zoology 56, 179-186.

Penman, T.D., Lemckert, F.L., Slade, C.P., Mahony, M.J., 2006c. Description of breeding sites of the giant burrowing frog *Heleioporus australiacus* in south-eastern NSW. Herpetofauna 36, 102-105.

Penman, T.D., Mahony, M.J., Towerton, A.L., Lemckert, F.L., 2005b. Bioclimatic analysis of disjunct populations of the giant burrowing frog, Heleioporus australiacus. Journal of Biogeography 32, 397-405.

Penman, T.D., Mahony, M.J., Towerton, A.L., Lemckert, F.L., 2007b. Spatial models of giant burrowing frog distributions. Endangered Species Research 3, 115-124.

Penman, T.D., Pike, D.A., Webb, J.K., Shine, R., 2010. Predicting the impact of climate change on Australia's most endangered snake, *Hoplocephalus bungaroides*. Diversity & Distributions 16, 109-118.

Penman, T.D., Price, O., Bradstock, R.A., 2013b. Modelling the determinants of ignition in the Sydney Basin, Australia: implications for future management. International Journal of Wildland Fire in press.

Penman, T.D., Towerton, A.L., 2007. Observations of responses to a prescribed burn in the frog *Litoria verreauxii* (Dumeril, 1853). Herpetofauna 37, 83-84.

Penman, T.D., Towerton, A.L., 2008. Are soil temperatures during autumn prescribed burning sufficient to trigger germination in fire responsive species? International Journal of Wildland Fire 17, 572-578.

Penman, T.D., York, A., 2010. Climate and recent fire history affect fuel loads in Eucalyptus forests: Implications for fire management in a changing climate. Forest Ecology and Management 260, 1791-1797.

Perkins, S.E., Pitman, A.J., Holbrook, N.J., McAneney, J., 2007. Evaluation of the AR4 Climate Models' Simulated Daily Maximum Temperature, Minimum Temperature, and Precipitation over Australia Using Probability Density Functions. Journal of Climate 20, 4356-4376.

Peters, G.P., Andrew, R.M., Boden, T., Canadell, J.G., Ciais, P., Le Quere, C., Marland, G., Raupach, M.R., Wilson, C., 2013. The challenge to keep global warming below 2 [deg]C. Nature Clim. Change 3, 4-6.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231-259.

Pilliod, D.S., Bury, R.B., Hyde, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. Forest Ecology & Management 178, 163-181.

Pitman, A., Narisma, G., McAneney, J., 2007. The impact of climate change on the risk of forest and grassland fires in Australia. Climatic Change 84, 383-401.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161-167.

Price, C., Rind, D., 1994. Possible implications of global climate change on global lightning distributions and frequencies. Journal of Geophysical Research 99, 10,823–810,831.

Price, O.F., Bradstock, R.A., 2011. The influence of weather and fuel management on the annual extent of unplanned fires in the Sydney region of Australia. International Journal of Wildland Fire 20, 142-151.

Price, O.F., Bradstock, R.A., 2012. The efficacy of fuel treatment in mitigating property loss during wildfires: Insights from analysis of the severity of the catastrophic fires in 2009 in Victoria, Australia. Journal of Environmental Management 113, 146-157.

Regan, H., Keith, D., Regan, T., Tozer, M., Tootell, N., 2011. Fire management to combat disease: turning interactions between threats into conservation management. Oecologia 167, 873-882.

Roberts, J.D., Watson, G.F., 1993. Biogeography and phylogeny of the anura, In Fauna of Australia Volume 2A – Amphibia and Reptilia. eds G. Glasby, G.J.B. Ross, P.L. Beesley, pp. 35-40. Australian Government Publishing Service, Canberra, Australia.

Romps, D.M., Seeley, J.T., Vollaro, D., Molinari, J., 2014. Projected increase in lightning strikes in the United States due to global warming. Science 346, 851-854.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodriguez, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and Trends of Amphibian Declines and Extinctions Worldwide. Science 306, 1783-1786.

Suppiah, R., Hennessy, K.J., Whetton, P.H., McInnes, K., Macadam, I., Bathols, J., Ricketts, J., Page, C.M., 2007. Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. Australian Meteorological Magazine 56, 131-152.

Swab, R.M., Regan, H.M., Keith, D.A., Regan, T.J., Ooi, M.K.J., 2012. Niche models tell half the story: spatial context and life-history traits influence species responses to global change. Journal of Biogeography 39, 1266-1277.

Syphard, A.D., Radeloff, V.C., Keeley, J.E., Hawbaker, T.J., Clayton, M.K., Stewart, S.I., Hammer, R.B., 2007. Human influence on California fire regimes. Ecological Applications 17, 1388-1402.

Telemeco, R.S., Elphick, M.J., Shine, R., 2009. Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. Ecology 90, 17-22.

Thomas, P.B., Watson, P.J., Bradstock, R.A., Penman, T.D., Price, O.F., 2014. Modelling surface fine fuel dynamics across climate gradients in eucalypt forests of south-eastern Australia. Ecography 37, 827-837.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102, 8245-8250.

Van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2025-2034.

Visser, M.E., and C. Both, 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society of London Series B-Biological Sciences 272, 2561-2569.

Wardell-Johnson, G.W., 2000. Responses of forest eucalypts to moderate and high intensity fire in the Tingle Mosaic, south-western Australia: comparisons between locally endemic and regionally distributed species. Austral Ecology 25, 409-421.

Westerling, A., Bryant, B., 2008. Climate change and wildfire in California. Climatic Change 87, 231-249.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313, 940-943.

Whelan, R.J., 1995. Fire Ecology. Cambridge University Press, Melbourne.

Winkler, D.W., Dunn, P.O., McCulloch, C.E., 2002. Predicting the effects of climate change on avian life-history traits Proceedings of the National Academy of Science, USA 99, 13595-13599.

Wintle, B.A., Bekessy, S.A., Keith, D.A., van Wilgen, B.W., Cabeza, M., Schroder, B., Carvalho, S.B., Falcucci, A., Maiorano, L., Regan, T.J., Rondinini, C., Boitani, L., Possingham, H.P., 2011. Ecological-economic optimization of biodiversity conservation under climate change. Nature Clim. Change 1, 355-359.

Wittkuhn, R.S., McCaw, L., Wills, A.J., Robinson, R., Andersen, A.N., Van Heurck, P., Farr, J., Liddelow, G., Cranfield, R., 2011. Variation in fire interval sequences has minimal effects on species richness and composition in fire-prone landscapes of south-west Western Australia. Forest Ecology and Management 261, 965-978.

Woinarski, J.C.Z., Armstrong, M., Price, O., McCartney, J., Griffiths, A.D., Fisher, A., 2004. The terrestrial vertebrate fauna of Litchfield National Park, Northern Territory: monitoring over a 6-year period and response to fire history. Wildlife Research 31, 587-596.

Working group 3, 2000. Special report on emissions scenarios: a special report of working group III of the Intergovernmental Panel on Climate Change. Cambridge University Press.

York, A., 2000. Long-term effects of frequent low-intensity burning on ant communities in coastal blackbutt forests of southeastern Australia. Austral Ecology 25, 83-98.

Tables

Table 1: Potential predictors for the habitat suitability modelling process

Variable	Definition	Source
Annual mean moisture index	Mean of weekly moisture index values 0 to 1	Bioclim v 6.0
Annual mean temperature	Mean of weekly temperatures in degrees Celsius	Bioclim v 6.0
Annual precipitation	Mean annual precipitation in mm/year	Bioclim v 6.0
Extant vegetation	Binary distribution of extant native vegetation (0 = absent, 1 = present)	(Keith 2011)
Highest period radiation	Largest weekly solar radiation estimate	Bioclim v 6.0
Max temp. of the warmest period	The highest maximum temperature in all weeks of the year in degrees Celsius	Bioclim v 6.0
Mean diurnal temperature range	The mean of the weekly diurnal temperature ranges in degrees Celsius.	Bioclim v 6.0
Mean moisture of the lowest quarter	Average moisture index (0 to 1) of the quarter with the lowest moisture index	Bioclim v 6.0
Mean moisture of the highest quarter	Average moisture index (0 to 1) of the quarter with the highest moisture index	Bioclim v 6.0
Min temp. of the coldest period	Average moisture index (0 to 1) of the quarter with the lowest temperature	Bioclim v 6.0
Precipitation of the driest period	Precipitation of the driest month (mm)	Bioclim v 6.0
Rainfall seasonality	SD of the weekly rainfall	Bioclim v 6.0
Slope	Slope of the ground (degrees)	(Keith 2011)
Substrate	A coarse measure of soil type	(Keith 2011)
Summer rainfall	Precipitation falling in summer months	Bioclim v 6.0
Temperature seasonality	SD of the weekly temperature	Bioclim v 6.0
Winter rainfall	Precipitation falling in winter months	Bioclim v 6.0

Table 2: Mean transition rates (and standard deviations) included in the population model (Y = year). Cell values indicate the rate of transition from the stage indicated by the column's header, to the stage indicated by the row's name, with the exception of the first row, which shows the fecundity of each stage. The last two rows show the survival multipliers in years of low and high intensity fires, respectively.

	Tadpole Y1	Tadpole Y2	Juvenile Y1	Juvenile Y2	Juvenile Y3	Small adult	Large adult
Tadpole Y1	0	0	0	0	0	50 (10)	150 (30)
Tadpole Y2	0.01 (0.002)	0	0	0	0	0	0
Juvenile Y1	0.1 (0.02)	0.1 (0.02)	0	0	0	0	0
Juvenile Y2	0	0	0.25 (0.025)	0	0	0	0
Juvenile Y3	0	0	0	0.25 (0.025)	0	0	0
Small adult	0	0	0	0	0.5 (0.05)	0.25 (0.025)	0
Large adult	0	0	0	0	0	0.5 (0.05)	0.75 (0.025)
Low intensity	0.75	0.75	0.90	0.95	0.95	0.95	0.95
High intensity	0	0.05	0.20	0.40	0.50	0.50	0.50

Table 3: Elasticities in the PVA model based on the stage matrix.

	Tadpole Y1	Tadpole Y2	Juvenile Y1	Juvenile Y2	Juvenile Y3	Small adult	Large adult
Tadpole Y1	0	0	0	0	0	0.0198	0.1012
Tadpole Y2	0.0011	0	0	0	0	0	0
Juvenile Y1	0.1199	0.0012	0	0	0	0	0
Juvenile Y2	0	0	0.121	0	0	0	0
Juvenile Y3	0	0	0	0.1208	0	0	0
Small adult	0	0	0	0	0.1208	0.0377	0
Large adult	0	0	0	0	0	0.1004	0.256

Table 4: Variable importance as estimated by Maxent.

Variable	Percent Contribution	Permutation importance
Summer rainfall	68	11.8
Extant vegetation	9.2	4.2
Rainfall seasonality	8.8	44.5
Annual mean temperature	8.5	17.5
Annual mean moisture index	4	20.7
Max temp. of the warmest period	1.5	1.3

Table 5: PVA model sensitivity to input parameters using the 20 year fire interval for the CSIRO Mk3.5 climate prediction. Each parameter is varied individually while all others are held constant. Missing values represent cases where the change in parameter results in a transition rate that exceeds 100%. Values represent the percentage change in the Expected Minimum Abundance.

Parameter	Stage	Decrease 20%	Increase 20%
Survival	All tadpoles	0.89	0.31
	Tadpole year 1	1.73	1.65
	Tadpole year 2	0.73	0.08
	Year 1 juvenile	0.67	2.12
	Year 2 juvenile	1.09	1.25
	Year 3 juvenile	1.08	0.01
	Small adult a	1.23	0.23
	Small adult b	3.01	0.17
	Big adult	1.00	1.21
Fecundity	Small adult	1.43	0.95
	Big adult	1.05	1.70
High intensity fire survival	Tadpole year 1	1.41	
	Tadpole year 2	1.47	0.66
	Year 1 juvenile	0.19	1.16
	Year 2 juvenile	1.09	0.98
	Year 3 juvenile	0.44	1.28
	Small adult	0.24	2.35
	Big adult	3.93	3.43
Low intensity fire survival	Tadpole year 1	0.55	0.72
	Tadpole year 2	0.71	0.32
	Year 1 juvenile	0.15	
	Year 2 juvenile	0.80	
	Year 3 juvenile	1.66	
	Small adult	1.68	
	Big adult	2.46	

Figure captions

Figure 1: Maxent prediction of habitat suitability for *H. australiacus* under current climatic conditions. White circles indicate locations where the species has been observed.

Figure 2: Future predictions of habitat suitability for *H. australiacus*, assuming climate changes according to projections of the CSIRO Mk 3.5 model, with emissions following the A1FI scenario. Suitability scale is equivalent to that in Figure 1.

Figure 3: Future predictions of habitat suitability for *H. australiacus*, assuming climate changes according to projections of the GFDL-CM2 model, with emissions following the A1FI scenario. Suitability scale is equivalent to that in Figure 1.

Figure 4: Proportional change in the expected minimum abundance of *H. australiacus* from 1000 simulations covering the period 2000–2100 under varying fire return intervals for: a) stable climate; b) climate change scenario based on the CSIRO Mk3.5 model; and c) climate change scenario based on the GFDL-CM2 model. Change is measured relative to a base scenario with no fire and constant climate. Note the y-axis scales differ between plots. Confidence intervals are not shown as they are not visible at the resolution of the graph due to the large sample size (n=1000) in the simulations.