Decline of an endangered amphibian during an extreme climatic event

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Abstract.   Climate change is a poorly understood, emerging threat to many amphibian species. One of the ways climate change is likely to affect amphibians is through increased recruitment failure associated with more frequent climatic extremes. To understand the risk posed by this threat, we combined 13 years of annual monitoring and multi-scaled habitat modelling at the site ($n = 60$), pool ($n = 105$) and nest ($n = 170$) levels to investigate the decline of the endangered northern corroboree frog (*Pseudophryne pengilleyi*), during the most severe drought on record in southern Australia. We documented the local extinction of 42% of *P. pengilleyi* breeding sites during the climatic extreme. Using logistic regression we investigated habitat variables associated with extinction sites. We found that locally extinct sites now resemble historically absent sites, with fewer pools, less water, and drying-related tree invasion. Extended periods of limited water availability at extinction sites is likely to have restricted breeding, contributing to localised extinctions. Habitat variables recorded at the pool and nest level did not significantly influence *P. pengilleyi* presence/absence, indicating that site level wetness had an overriding effect. We anticipate that increasing climate variability is likely to disproportionately threaten seasonal pool-breeding amphibian species, exacerbating the global amphibian biodiversity crisis. However, our work with *P. pengilleyi* suggests there are a range of simple habitat manipulations that could help to ameliorate the impacts.

Key words: *Batrachochytrium dendrobatidis*; chytridiomycosis; climate change; climate extreme; drought; frog; landscape drying; *Pseudophryne pengilleyi*; southern Australia.

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INTRODUCTION

Amphibian declines are occurring at an alarming rate (Stuart et al. 2004), and are a prominent component of the contemporary biodiversity crisis (Wake and Vredenburg 2008). Globally, 32% of amphibian species are threatened with extinction, more than in any other vertebrate class (Stuart et al. 2004, Hof et al. 2011). Established causes of decline include habitat loss (Cushman 2006), introduced predators (Kats and

Ferrer 2003) and pollution (Relyea and Diecks 2008). In addition, the emerging infectious disease chytridiomycosis, caused by the fungus *Batrachochytrium dendrobatidis* (Berger et al. 1998, Vredenburg et al. 2010) and climate change (McMenamin et al. 2008, Mac Nally et al. 2009) have been implicated in widespread declines, often occurring within protected environments.

Although amphibian populations are widely recognized to experience significant natural fluctuations in response to climate variability

(Semlitsch 1987, Pechmann et al. 1991, Stewart 1995), the impacts of unprecedented climate extremes and climate change are far less well understood. Climate change may affect amphibians directly through altering behaviour, disease interactions, reproduction, body condition, and survivorship (McCaffery and Maxell 2010, Todd et al. 2011), and indirectly through altering habitat (McMenamin et al. 2008). Predicted climate change and associated increases in the frequency and intensity of extreme climatic events are likely to pose a major threat to amphibian species with specific requirements or small ranges (Sodhi et al. 2008, Lawler et al. 2010). Investigating how species respond to variations in climate may provide a valuable first step in understanding and predicting the effects of long-term climate change (Debinski et al. 2006). This knowledge can then be used to develop tangible management responses such as habitat enhancement (Shoo et al. 2011).

Climate extremes and climate change are likely to affect different amphibian species at various spatial scales (Shoo et al. 2011). In Central America, amphibian declines have been connected with climate-driven reductions in leaf-litter microhabitat (Whitfield et al. 2007), while in Europe, amphibian persistence during a climate extreme was related to landscape heterogeneity (Piha et al. 2007). Understanding the spatial scale at which climate-associated threats affect amphibians is crucial for developing and effectively implementing management responses.

Here, we use a long-term dataset to investigate the impact of an extreme climatic event on the endangered Australian northern corroboree frog (*Pseudophryne pengilleyi*) (IUCN 2011). From 1997 to 2009, south-eastern Australia was in the grip of a severe drought, with unprecedented reductions in precipitation and increased temperatures (Timbal et al. 2010). During this drought, precipitation deficiencies were 45% more severe than during the previous driest period (Timbal et al. 2010), and a recent multi-proxy precipitation reconstruction concluded that there was a 97% probability that it was the worst drought since European settlement in 1788 (Gergis et al. 2012). We hypothesised that *P. pengilleyi* would be severely affected by these conditions because populations already have been reduced by chytridiomycosis (Hunter et al. 2010) and the

species has a highly restricted geographic range, low fecundity and is dependent on seasonal pools (Osborne 1989). Globally, restricted geographic range, low fecundity and the presence of multiple threatening processes are characteristics often associated with declining amphibian species (Cooper et al. 2008, Murray et al. 2011).

To study the effects of this climatic extreme on populations of *P. pengilleyi*, we combined the results of an annual long-term monitoring program established in 1997 with multi-scaled habitat modelling. We investigated whether population persistence during the climatic extreme was related to breeding habitat characteristics. Specifically, we asked: Do nest, pool or site level characteristics drive population extinctions? To answer this question we examined habitat variables measured at each spatial scale at extant sites, locally extinct sites and nearby sites where the species does not occur. We focused on variables related to site wetness because suppressed breeding, egg desiccation (Pengilley 1973) and tadpole mortality from early pool drying (Osborne 1989) have been identified as potential factors affecting recruitment.

Globally, climate extremes are a poorly understood, emerging threat. Our study quantified the spatial scale at which this threat impacted on a seasonal-pool breeding amphibian. In the context of the ongoing amphibian decline crisis (Hof et al. 2011), our study provides a rare insight into the likely additional stressors that amphibians breeding in seasonal pools will face under increasing climate variability.

METHODS

Study species

Pseudophryne pengilleyi is a small (23–27 mm), terrestrial frog with a restricted distribution occurring largely in protected environments in the montane and sub-alpine forests of south-eastern New South Wales, Australia. From early January to mid-March adult *P. pengilleyi* enter bogs and seepages from the surrounding forest to breed (Pengilley 1971, 1973). Males construct, territorially defend, and call from terrestrial nests, which are several centimetres deep and located in loose vegetation around the edges of small seasonal pools that are typically dry during breeding (Pengilley 1971, 1973). Breeding occurs

within the nest where females deposit an average of 25 eggs (Pengilley 1973). Fertilised eggs develop through to hatching stage and then enter diapause. Given sufficient precipitation in autumn and winter, nests flood, allowing the eggs to hatch and tadpoles to enter adjacent pools. Tadpoles are then free swimming and feeding until metamorphosis begins in November (Pengilley 1992). The closely related *P. corroboree* reaches sexual maturity after four years, can live for up to nine years and exhibits a high level of breeding site fidelity (Hunter 2000).

Since the late 1980s there has been considerable concern surrounding the decline of *P. pengilleyi* (Osborne 1989, Hunter et al. 2010). Retrospective analysis has implicated chytrid fungus in initial declines during the 1980s (Hunter et al. 2010). Real-time sampling and monitoring indicates that sub-alpine *P. pengilleyi* populations (at altitudes of approximately 1400 to 1750 m above sea level) have exhibited an epidemiological pattern of progressive decline to extinction (Osborne et al. 1999, Hunter et al. 2010). In contrast, montane populations (at lower altitudes, 800 to 1400 m) have exhibited an epidemiological pattern of initial decline, followed by stabilisation at lower densities with endemic chytridiomycosis in the surviving populations (Osborne et al. 1999, Hunter et al. 2010). The long-term persistence of montane populations despite the ongoing presence of chytrid fungus is consistent with patterns of chytridiomycosis outbreaks observed for other Australian (McDonald et al. 2005), European (Walker et al. 2010) and Central American (Lips et al. 2008) amphibian species.

Study area

All survey sites were located in Kosciuszko and Brindabella National Parks in New South Wales, Australia (Fig. 1). The topography of the region is undulating to mountainous, ranging from 800–1,600 m above sea level. Mean annual precipitation is 1,200 mm, falling predominantly in winter and spring. The vegetation of the region is dominated by dry and wet sclerophyll *Eucalyptus* forest with frost hollow grasslands. Breeding sites are generally isolated and occur along narrow seepage lines or in open bogs that support shallow seasonal pools from late autumn

through to late spring. These areas are generally treeless and are characterised by moist vegetation associations including sphagnum, wet heath, wet grassland and wet herbfield (Costin 1954, Pengilley 1971). Co-occurring frog species include *Crinia signifera* and *P. bibronii*.

Study design

A hierarchical experimental design was used to assess possible ecological effects at multiple scales (Meentemeyer and Box 1987). Four levels of experimental unit were specified within the hierarchy: (1) region ($n = 2$), (2) site ($n = 60$), (3) pool ($n = 105$), and (4) nest ($n = 170$) (Fig. 1). At the region level, *P. pengilleyi* populations were separated by approximately 20 km and were genetically distinct (Morgan et al. 2008).

At the site level habitat variables were measured at three different site types. *Extant* ($n = 26$) and *locally extinct* ($n = 19$) sites were randomly selected from sites monitored by the New South Wales Office of Environment and Heritage since 1997. Extant sites were defined as those with one or more calling males in 2010. To ensure the extinction estimates were conservative, we defined an extinction site as one where no frogs were recorded during annual surveys from 2007–2010; but all extinction sites had males recorded in the period 1997–2006. Habitat variables were also collected at *absence sites* ($n = 15$). Absence sites were assumed to have never supported *P. pengilleyi* populations despite occurring within the range of the species and containing vegetation associated with bog habitat. These sites were located within the same region that had been monitored extensively by the New South Wales Office of Environment and Heritage since 1997, and hence it was very likely that frogs would have been recorded at some stage if they had been present. Absence sites were included to gain further insight into habitat characteristics associated with *P. pengilleyi* occupancy. All sites were defined as an area of continuous potential breeding habitat separated from other sites by >500 m (straight line) and/or 1,000 m of riparian distance. One exception (straight line distance = 420 m) was made to include an additional extant site in Brindabella National Park where few sites with frogs were available.

At the pool level habitat variables were measured at pools with and without frogs. At
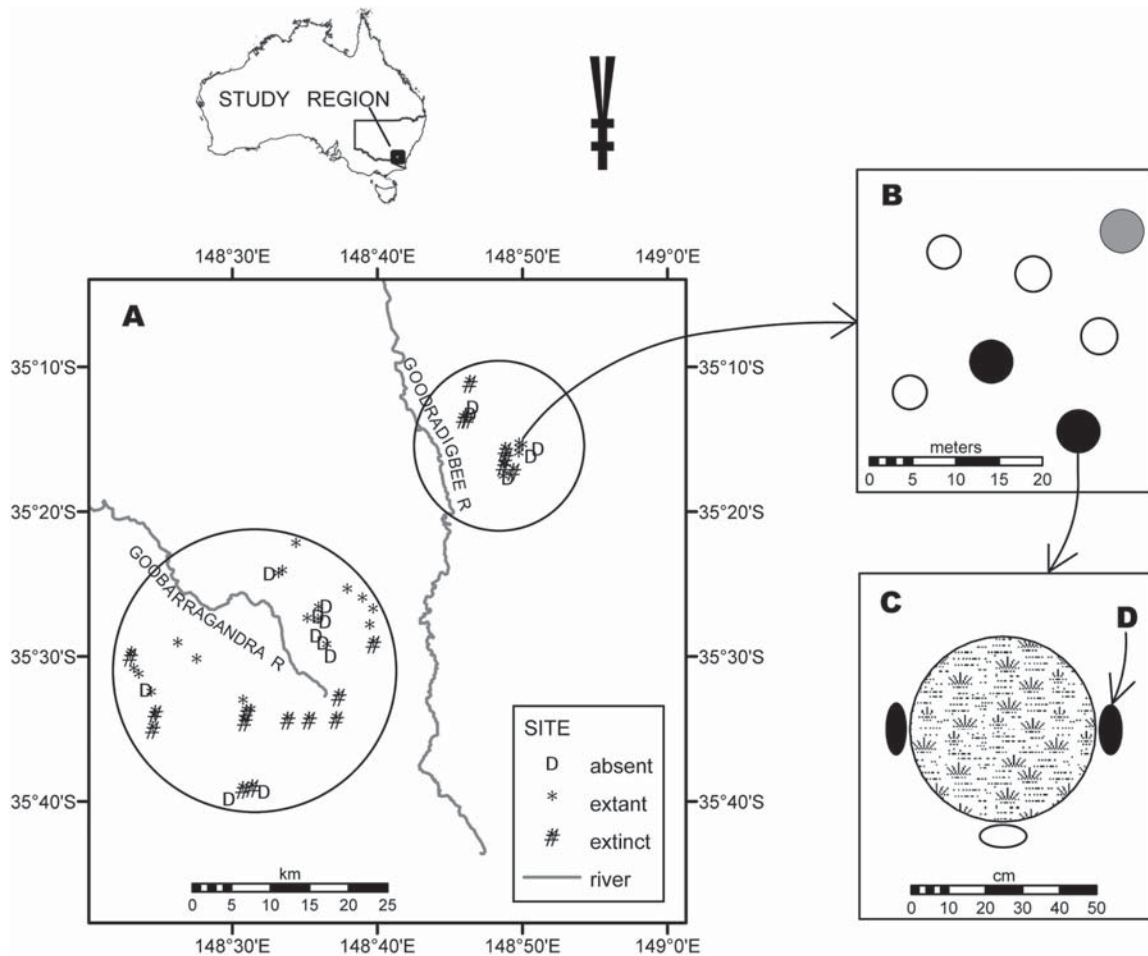
Fig. 1. Location of study sites in south-eastern New South Wales, Australia. Insets show (A) the spatial distribution of study sites, (B) an example of frog pools (black), a random pool (grey) and non-measured pools (white) within an extant site, and (C) a frog pool, with (D) actual nests (black) and a potential nest (white).

extant sites there were two pool types; frog pools ($n = 45$) and random non-frog pools ($n = 26$). If more than two frog pools occurred at a site, two were chosen at random. Habitat variables were also measured at random pools in extinction sites ($n = 19$) and frog absence sites ($n = 15$) to enable a comparison with random pools in extant sites.

At the nest level habitat variables were measured at nests and potential nest sites. At extant sites there were three nest level locations; frog nests ($n = 65$) and random locations on the banks of frog pools ($n = 45$) and non-frog pools ($n = 26$). If more than two nests occurred at a site, two were chosen at random. The randomly selected nests were potential nest locations and

were identified from a randomly generated compass bearing taken from the middle of the pool. Habitat variables were also measured at random locations on the banks of pools in extinction sites ($n = 19$) and frog absence sites ($n = 15$) to enable a comparison with random nest locations in extant sites.

Frog surveys

Occupied breeding pools and nest sites were identified by locating males during February and early March 2010. Males were located using the shout-response technique (Osborne 1989). This technique involves a person shouting loudly into an area of potential breeding habitat/pool, to

which males respond with their threat call. Surveys involved two people systematically walking through each site, and shouting twice at all possible breeding habitat/pools, with an interval of 20 s between each shout, which resulted in a consistent sampling effort per unit area across all sites. The position of responding males was then determined by two people using triangulation. The first time a pool and nest containing a calling male was located it was individually marked with flagging tape. The presence or absence of males at marked nests was recorded on subsequent surveys. All study sites were surveyed three times during the day or evening. Osborne (1989) has shown that there is little variation between day to day calling activity during the breeding season provided seasonal conditions are suitable. During the 2010 breeding season conditions were favourable with average precipitation. Annual monitoring from 1997–2009 used the same method but consisted of only a single visit by the New South Wales Office of Environment and Heritage in February, during which the number of calling males at each site was recorded.

Habitat measurements

All habitat measurements were completed during March 2010 except water-related variables, which were measured within three days of the first significant autumn rain following breeding. Variables measured at the site, pool and nest levels were chosen because they may relate to site wetness, the suitability of the site for tadpoles (Osborne 1990), or indicate reduced moisture availability.

The following information was collected at all sites: area, elevation, number of potential pools, geology, slope, number of trees under 5 cm diameter at breast height (recent tree invasion indicative of site drying) and the number of pools with water. Sites were defined as an area of discrete potential habitat along a seepage line or the entire area within a bog. Surface area measurements were taken by multiplying the longest axis by the mean of two evenly spaced measurements perpendicular to the longest axis. Geology was identified from surface rock samples taken during field measurements, and was broadly classified as sedimentary, volcanic or granitic. The slope between the highest and lowest points at a site was measured using a clinometer.

At all pools within a site, we measured potential pool area, water surface area, percentage bare substrate, percentage canopy cover, pool side vegetation height, and water depth. Both surface area measurements were taken by multiplying the longest axis by the mean of three evenly spaced measurements perpendicular to the longest axis. The percentage of bare ground and percentage of canopy cover directly above the pool was assessed visually. Pool side vegetation height was measured by averaging four measurements taken at bearings of 0°, 90°, 180° and 270°. Pool water depth and water surface area were highly correlated; therefore only water surface area was used. Canopy cover and pool side vegetation were measured because they are known to influence pool temperature (Skelly et al. 2002).

At the nest level, we quantified aspect, vegetation depth to substrate and vegetation type. Aspect of the nest was measured using a compass and was grouped into eight classes defined by 45° arcs. Vegetation depth was measured by inserting a ruler through the vegetation until the ground was reached. Potential nest vegetation types were; grass, sphagnum moss, forbs and leaf litter. Vegetation depth was measured because it may influence the capacity for males to establish nest sites (Hunter et al. 2009).

Climate and stream flow data

Monthly precipitation and temperature data (1970–2008) were interpolated from the climatic surfaces of Kesteven et al. (2003). The climate surfaces were created using the ANUSPLIN package developed by Hutchinson (2004). Annual flow volumes (1958–2008) for the Goodradigbee and Goobragandra Rivers, which drain the study region, were obtained through the New South Wales Office of Water Information. This data was included to demonstrate the hydrological impact of the drought.

Statistical analysis

Generalised linear mixed modelling (GLMM) (Breslow and Clayton 1993) was initially used to estimate the probability of occurrence of *P. pengilleyi* at the site, pool and nest levels as a

function of habitat variables. A binomial distribution was used for all presence/absence data. GLMM was appropriate to account for the physical structure of experimental units. However, random effects were shown to account for an inconsequential amount of variation (with variance components <0.1% of the residual variance) and therefore generalised linear models (GLM) were adequate (Zuur et al. 2009). The model selection process involved non-automated backward selection which commenced with a full model (containing all explanatory variables) followed by the step-by-step deletion of non-significant variables ($P > 0.05$) until only statistically significant variables remained (Zuur et al. 2009). Scatterplots were used prior to data analysis to assess potential collinearity between habitat variables. When two explanatory variables were highly correlated only one variable was analysed. All analyses were completed using R 2.10.0 (R Development Core Team 2009), including the package lme4 (Bates and Maechler 2010).

Four separate GLMs were constructed, with *P. pengilleyi* presence/absence as the response variable. (1) The first model was at the site level ($n = 45$), with the binomial response denoting extant versus extinction sites. Potential explanatory variables were region, elevation, number of potential pools, number of water-filled pools, slope, geology and presence of tree invasion. The number of trees under 5 cm diameter at breast height and the number of pools with water were converted to binary data due to the large number of zero values. The number of potential pools was natural log + 1 transformed to ensure that variance of the residuals was constant across the range of fitted values (Quinn and Keough 2002). (2) A second site level model included the same potential explanatory variables, but with data from extant versus absence sites ($n = 41$). (3) The third model was at the pool level, comparing pools with and without frogs in extant sites ($n = 71$). The potential explanatory variables were pool area, bare substrate, poolside vegetation height, percentage canopy cover and water presence. Pool area was log transformed because it was highly skewed. (4) The fourth model focused at the nest level, and compared potential nest locations with actual nest locations in occupied pools ($n = 110$). Potential explanatory

variables were depth, aspect and vegetation type. Nest depth was log + 1 transformed because it was skewed.

At the pool and nest levels we tested for significant differences between habitat variables at randomly selected pools and randomly selected nests, comparing pools or nests located in extant ($n = 26$), extinction ($n = 19$) and absence ($n = 15$) sites. For continuously distributed variables (bare substrate, poolside vegetation height, dry pool surface area and nest depth) we used analysis of variance (ANOVA). Variables with a large number of zeros (pool canopy cover and water depth) were converted to binary data and GLM with binomial error distribution was used to test for differences with or without canopy cover or water, respectively.

Finally, we were interested in the adequacy of the survey effort to reliably detect frog presence/absence at the site, pool and nest levels. First, we calculated the probability of detecting all individuals recorded at a site during any single visit. Second, we constructed detectability curves to assess the probability of all individuals being detected after three visits (Wintle et al. 2005). Detectability curves were calculated as the sum of all the binomial probabilities of detection across each of the visits. We used the 'unmarked' package (Fiske and Chandler 2010) in R 2.10.0 (R Development Core Team 2009) for all detectability analyses.

RESULTS

Detection and decline

At extant sites surveyed in 2010, the number of individuals detected during the first survey was similar to the numbers detected during the two subsequent surveys. Of the total number of frogs detected after three surveys in 2010, 91%, 90% and 89% were detected during the first survey, at the site, pool, and nest levels respectively. The probability of detecting all males at a site after three surveys was 0.99 (SE = 0.0004). Given the very high level of male detectability following three surveys, we reasoned the chance of false absences at extinction or absence sites during the study was low. Combining the results of the surveys with the long-term monitoring data, 19 of the 45 sites that contained frogs in the period 1997–2006 did not support frogs during the

period 2007–2010.

Climate and hydrological change

In our study region the recent drought was characterised by a significant reduction in precipitation and increased temperatures (Fig. 2). From 1997 to 2008, annual and autumn precipitation declined by 20% and 38% respectively compared to the long term averages (1970–2008) (Fig. 2). Mean annual temperature also increased sharply (Fig. 2). Reduced precipitation and increased temperatures resulted in substantial changes to the hydrology of the region. Flow records for the Goodradigbee and Goobragandra Rivers, which drain the study region, show an approximate 40% decline in annual run-off for the period 1997 to 2008 compared to the long term average (1958–2008).

Occupancy modelling

The probability of *P. pengilleyi* occurrence, at extant sites compared with extinction sites, was positively related to the number of potential pools and presence of surface water, and negatively related to tree invasion and elevation (Table 1, Fig. 3). Compared with absence sites, the probability of *P. pengilleyi* occurrence at a site was positively related to the number of potential pools, and negatively related to slope and elevation (Table 1, Fig. 4). At the pool level, the probability of *P. pengilleyi* occurrence (occupied pools compared with random pools) within extant sites was not related to any of the variables measured. However, there was a non-significant ($P = 0.07$) trend towards increased occupancy with increasing pool area (Table 1). At the nest level, the probability of *P. pengilleyi* occurrence (actual nests compared with random locations) within the same pool was positively related to vegetation depth (Table 1).

Variation between random pools and nests

Random pools in extant sites had a significantly higher probability (P (Chi) $= 0.0004$, df $= 57$) of water presence than random pools in extinction and absence sites (Fig. 5). There were no significant differences between any of the other habitat variables measured at random pools in extant, extinction and absences sites. There were also no significant differences between any of the nest habitat variables measured at random locations in random pools in extant, extinction and absence sites.

Discussion

During the recent unprecedented drought, *P. pengilleyi* experienced significant declines, with 42% of breeding sites becoming locally extinct. In comparison to historical droughts, this drought was characterised by a sustained reduction in precipitation (Timbal et al. 2010) and record high temperature anomalies (Nicholls 2004, Timbal et al. 2010), which exacerbated dry conditions resulting in record low soil moisture and stream flow values (Cai et al. 2009, Potter et al. 2010). Notably, the changes we observed are not restricted to the study region but are part of a larger, global pattern of increasingly frequent and severe climatic extremes (Frich et al. 2002). Climate predictions for the coming century indicate that southern Australia is likely to experience further climate drying and increasingly frequent and intense droughts (Nicholls 2004, Shi et al. 2008). Similar changes have been predicted for several regions around the world (IPCC 2007). Amphibians are one of the groups severely affected by such climate extremes because their habitats are highly vulnerable to desiccation (McMenamin et al. 2008).

In our study, local extinctions appear to be driven by site level habitat characteristics, with positive relationships between extant sites and the presence of water and number of pools (Fig. 3, Fig. 4). We also found a higher level of tree invasion at extinction sites compared to extant sites (Fig. 3C). In wetland environments tree invasion occurs as a result of increased dryness (Bren 1992, Berg et al. 2009), indicating that extinction sites have experienced prolonged periods of desiccation. At the pool and nest level there were no significant relationships between habitat variables measured at randomly selected pool and randomly selected nest locations at the three different site types, with the exception of presence of water (Fig. 5).

In combination, these results indicate that the recent climate extreme primarily affected *P. pengilleyi* through habitat desiccation at the site level. Previous droughts, typically one to two years in duration, reduced *P. pengilleyi* reproductive success; however, they have not been
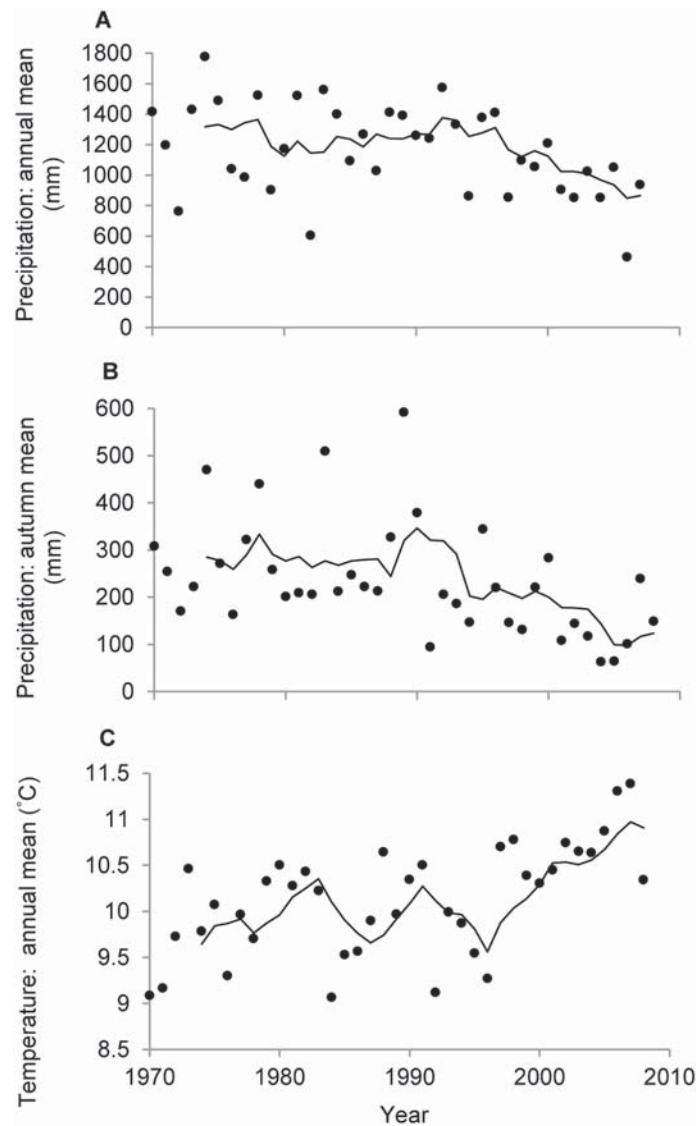
Fig. 2. Mean five year moving averages of precipitation for the region for (A) annual precipitation, (B) autumn (March-May), and (C) mean annual temperature.

observed to result in local extinction (Pengilley 1973, Osborne 1989). Record mosture deficiencies that developed during the 2002–2003 El Niño event (Timbal et al. 2010) are likely to have caused successive years of catastrophic reproduction failure by limiting breeding activity and increasing egg desiccation and tadpole mortality (Pengilley 1973, Osborne 1989). Because the duration of the drought exceeded the lifespan (nine years) of *P. pengilleyi*, the gradual attrition of adults without the recruitment of juveniles is likely to have caused local extinctions. Furthermore, because the four year period of absence at extinction sites exceeded the time taken for *P. pengilleyi* to reach sexual maturity, the presence of sexually immature individuals at extinction sites is unlikely.

Increased recruitment failure associated with climatic extremes and climate drying is a major threat to amphibian species worldwide (Don-

Table 1. Logistic regression models for *Pseudophryne pengilleyi* presence/absence at the site-level, pool-level and nest-level.

Response	Term	Coefficient	SE	P	Graphical summary
Site					
Presence/absence (extinction vs. extant)	(Intercept)	7.2821	5.2418	0.1647	Fig. 3
	Number of pools	2.1457	0.8544	0.0120	Fig. 3
	Presence of water	2.7275	1.0057	0.0066	Fig. 3
	Tree invasion	−2.3527	1.0515	0.0252	Fig. 3
	Elevation	−0.0104	0.0050	0.0382	Fig. 3
Presence/absence (absence vs. extant)	(Intercept)	10.1697	7.3388	0.1658	Fig. 4
	Slope	−0.8631	0.3614	0.0169	Fig. 4
	Number of pools	4.7234	1.7490	0.0069	Fig. 4
	Elevation	−0.01435	0.0071	0.0433	Fig. 4
Pool					
Presence/absence	(Intercept)	−2.8263	1.8815	0.1330	Not shown
	Surface area	0.3914	0.2163	0.0704	Not shown
Nest					
Presence/absence	(Intercept)	−3.9179	0.9249	<0.0001	Not shown
	Vegetation depth	2.7361	0.5717	<0.0001	Not shown

nelly and Crump 1998, Blaustein et al. 2010). For example, in western North America McMenamin et al. (2008) documented the decline of four previously common amphibian species as a result of wetland desiccation associated with climatic drying. Similarly, in a long term study from eastern North America a drying trend reduced pool hydroperiod and resulted in reproductive failure and the decline of several amphibian species (Daszak et al. 2005). In southern Australia, decreased autumn and winter precipitation associated with prolonged drought have reduced the number of sites supporting common frog species, and have greatly lowered the densities of calling males at remaining sites (Mac Nally et al. 2009).

Although our research was restricted to a single species, for which long term monitoring data was available, our results are likely to be applicable to other amphibian species. Because of the generality of the underlying mechanism, the association between habitat drying and local extinctions we documented may foreshadow comparative impacts in other regions predicted to, or already experiencing, climate drying. Seasonal pool breeding amphibian species are likely to be disproportionately affected because their breeding habitats are highly susceptible to desiccation during drought (McMenamin et al. 2008, Blaustein et al. 2010). Amphibian reproduction in the Neotropics, a diversity hotspot (Wake and Vredenburg 2008, Hof et al. 2011), may be particularly vulnerable. Central America and the Amazon Basin are predicted to suffer

substantial precipitation declines and increased precipitation variability and dry season length (Hulme and Viner 1998, Neelin et al. 2006). This landscape desiccation is likely to reduce pool hydroperiod and soil moisture, increasing the frequency of premature pool drying (Donnelly and Crump 1998) and egg desiccation (Touchon and Warkentin 2010). Similarly, climate drying predicted for south-east Asia (Neelin et al. 2006, Allan and Soden 2008) is likely to affect direct and aquatic developing species through increased egg and larvae desiccation (Bickford et al. 2010).

Despite the important role of chytridiomycosis in causing *P. pengilleyi* declines in the sub-alpine region (Osborne et al. 1999, Hunter et al. 2010), its contribution to the recent declines that we document in the montane region is likely to be secondary to drought for several reasons. First, *B. dendrobatidis* sampling conducted at several of our study sites in 2006 found low (6%) infection prevalence (Hunter et al. 2010). Second, after an initial decline associated with the emergence of *B. dendrobatidis* in the mid to late 1980s, montane populations were relatively stable during the 1990s, coinciding with favourable climatic conditions (Osborne et al. 1999). Similar decline patterns have been observed in Far North Queensland, where both *Litoria nannotis* and *L. rheocola* disappeared during the early 1990s in areas above 400 m elevation, while persisting at lower elevations with endemic *B. dendrobatidis* (McDonald et al. 2005). Furthermore, because climate conditions during the period of decline
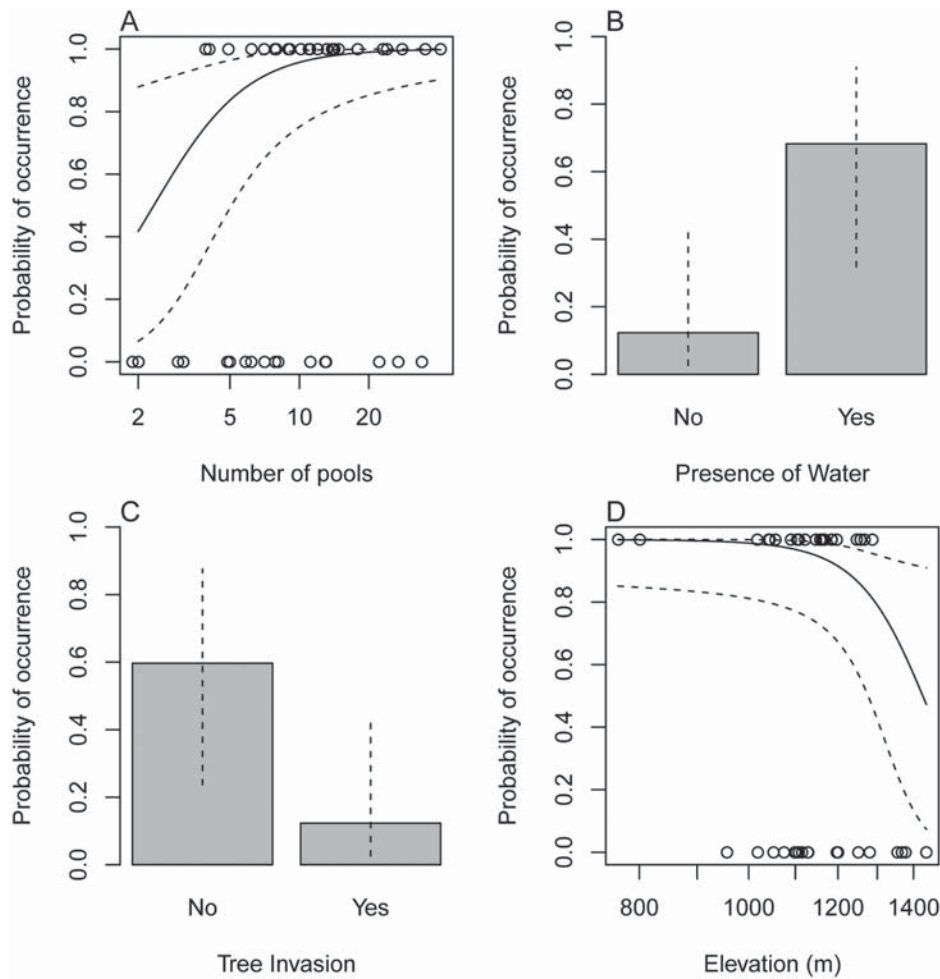
Fig. 3. Predicted values of the probability of occurrence of *Pseudophryne pengilleyi* as a function of (A) the number of potential pools, (B) surface water presence, (C) tree invasion and (D) elevation at extant versus extinction sites. Solid lines indicate model predictions; dashed lines indicate 95% confidence intervals. Actual presences and absences are shown as small circles.

were unfavourable to *B. dendrobatidis* growth, it is unlikely that the prevalence of chytridiomycosis would have increased during the drought (Kriger 2009). However, we cannot exclude the possibility that the presence of *B. dendrobatidis* may have decreased adult survivorship (cf. Murray et al. 2009), reducing the buffering capacity provided by long lived individuals (up to nine years) and contributing to the unprecedented impact of the recent prolonged drought.

Management implications

We provide evidence that unprecedented drought has contributed to the decline of *P. pengilleyi* within protected areas, highlighting the inability of reserves to protect species against climate-associated threats. Since 2010, seasonal conditions have improved; however, annual monitoring has shown that populations are continuing to decline (B. Scheele, *personal observation*). Because *P. pengilleyi* takes four years to reach sexual maturity from egg (Pengilley 1992), reduced recruitment during the recent drought is likely to have an ongoing effect on extant populations. The low fecundity and high breeding site fidelity of *P. pengilleyi*, combined with the
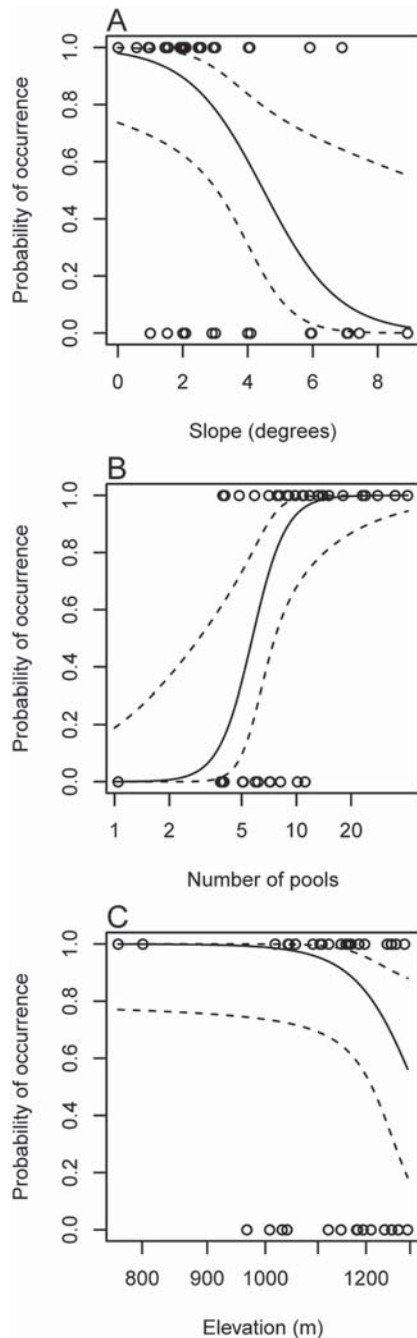
Fig. 4. Predicted values of the probability of occurrence of *Pseudophryne pengilleyi* as a function of (A) slope, (B) number of potential pools and (C) elevation at extant versus absence sites. Solid lines indicate model predictions; dashed lines indicate 95% confidence intervals. Actual presences and absences are shown as small circles.
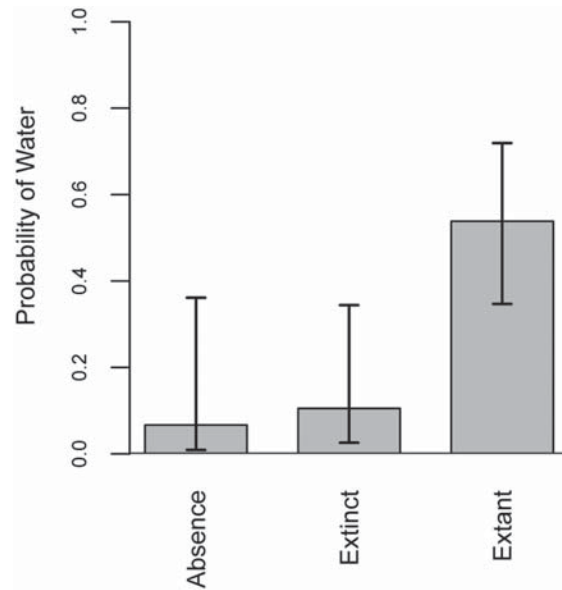

Fig. 5. Predicted probability of water at random pools in absence, extinction and extant sites. Error bars indicate 95% confidence intervals.

small size of many populations suggests that occasional wet years will be unable to compensate for the predicted increase in the frequency of dry years.

Given the results of our study and the predicted increase in the frequency of climatic extremes in south-eastern Australia over the coming decades (Nicholls 2004, Shi et al. 2008) *P. pengilleyi* faces an uncertain future. Actively mitigating the impact of habitat drying, through manipulating breeding habitat, may be critical for the future persistence of this species (cf. Shoo et al. 2011). In North America and Europe habitat creation has been successfully used to increase abundance in threatened (Rannap et al. 2009) and non-threatened amphibians (Vasconcelos and Calhoun 2006). To succeed, newly created pools must provide suitable habitat and have high levels of connectivity (Lesbarreres et al. 2010). Based on our results, increasing the density and depth of pools within a site is likely to reduce the risk of tadpole mortality from premature pool drying. However, due to a lack of water at extinction sites, successful habitat manipulation may be restricted to increasing the resilience of extant sites. The potential value of pool creation is underlined by the anecdotal observation of

breeding activity in pools created by wombat (*Vombatus ursinus*) and roadwork excavations. Interestingly, these recently created pools were generally deeper and supported higher breeding densities than existing pools (B. Scheele, *personal observation*).

Conclusions

Our study highlights the emerging threat posed by climate extremes to amphibians. With many regions worldwide predicted to experience increasingly frequent and severe droughts (IPCC 2007), there is an urgent need to identify which species are at most risk and the potential suitability of methods such as habitat manipulation to ameliorate impacts. For *P. pengilleyi* this could involve remediation at the site level rather than at finer scales. We anticipate that increasingly intense droughts are likely to disproportionately threaten seasonal pool-breeding amphibian species, exacerbating the global amphibian biodiversity crisis. The severe decline of *P. pengilleyi* within protected environments demonstrates the profound impact unprecedented climate extremes are already having on amphibians.

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