

Anuran responses to pressures from high-amplitude drought–flood–drought sequences under climate change

Ralph Mac Nally¹ · Gregory F. B. Horrocks¹ ·
Hania Lada¹

Received: 3 May 2016 / Accepted: 21 December 2016 / Published online: 6 January 2017
© Springer Science+Business Media Dordrecht 2017

Abstract We measured changes in the occurrence, abundances and evidence of breeding of frogs to a sequence of severe drought–extreme wet–drought in south-eastern Australia, which is projected to characterize the regional climate in the coming decades. We collected data on anuran abundances, species richness and breeding by using aural surveys and visual searches in 80 waterbodies in 10 landscapes. We surveyed six times during the austral winter–springs of 2006 and 2007 (9–10 years into the 13-year ‘Big Dry’ drought), six times in the corresponding seasons of 2011 and 2012 (the ‘Big Wet’) and another six times in 2014 and 2015, which had lapsed into another intense dry period (‘post-Big Wet’). The relatively small gains in species occupancy rates and evidence of breeding achieved during the Big Wet following the Big Dry were eroded and reversed in the years after the Big Wet period, with several biotic measures falling substantially below the values for the Big Dry. The global prognosis is for long-term drying and warming, notwithstanding much geographic variation in the degree and temporal patterns of drying. Longer droughts with short periods of wet/benign conditions are projected for many parts of the world. For water-dependent fauna such as most amphibians, our results signal widespread declines in lowland regions experiencing such patterns. If droughts exceed lifespans of frogs, then resistance to drought will be so low that populations will plunge to levels from which the short periods of more benign conditions will be insufficient to enable substantial recovery.

1 Introduction

Weather and climate variability—extreme climatic events—are predicted to be more common and more severe, and there already is evidence that these expectations are occurring (Coumou

Electronic supplementary material The online version of this article (doi:10.1007/s10584-016-1890-z) contains supplementary material, which is available to authorized users.

✉ Ralph Mac Nally
Ralph.MacNally@gmail.com

¹ Institute for Applied Ecology, The University of Canberra, Bruce, ACT 2617, Australia

and Rahmstorf 2012). The effects of increasingly marked climate variability on the demography of plants and animals are on par with those of land-use change (Selwood et al. 2015), which previously had been regarded as the most severe adverse effect on non-marine biodiversity (Foley et al. 2005). Measuring biotic responses to climate extremes is a first step in constructing effective management actions for maintaining biodiversity in the face of this growing pressure (Mantyka-Pringle et al. 2012).

There are several models for attempting to represent the trajectory for the biota exposed to pressures arising from direct (e.g. harvesting) or indirect (e.g. climate change) human actions. The resistance–resilience framework measures the relative importance of two stages to the persistence of populations or even of species (Nimmo et al. 2015). The resistance stage is the degree to which a biotic measure (e.g. abundance, natal or mortality rate) is maintained in the face of a sustained pressure, such as drought. The second stage is the resilience stage, which measures the recovery of the biotic measure once the pressure is relieved (e.g. cessation of drought). When there are successions of pressures applied and relieved, the relative magnitudes of the resistance and resilience responses dictate whether the population or species can persist (Nimmo et al. 2015).

The pressure we consider is profound variation in precipitation in south-eastern Australia in recent decades. Since 1997, there has been the deepest drought on record (the ‘Big Dry’, 1997 to mid-2010) (Verdon-Kidd and Kiem 2009; Chiew et al. 2011), followed by a ‘Big Wet’ (mid-2010 to 2012), which was the wettest 2-year period in Australia’s records (Leblanc et al. 2012). Since the end of the Big Wet, rainfall returned to the levels seen in the Big Dry (<http://www.bom.gov.au/climate/enso/>; accessed 31 December 2015), apparently at least partially driven by the intense El Niño event starting in 2015 (Schiermeier 2015). The Australian Bureau of Meteorology (BoM) uses a baseline from 1961 to 1990 to assess climate trends. Relative to means for this baseline, the rainfall over the Big Dry in the region we consider was below average for 13 years relative to this baseline (Fig. 1a), and the accumulated deficit was almost 2.5 years worth of average baseline rainfall (Fig. 1b). The Big Wet replenished about a year of the baseline rainfall deficit from the Big Dry (Fig. 1b), but the post-Big Wet dry already has reversed the reductions of the deficit of the Big Wet (Fig. 1b). An alternation between extended very dry conditions punctuated by short, sharp wet periods is expected using Coupled Model Intercomparison Project Phase 5 (CMIP5) of the World Climate Research Programme (WCRP) when applied to the Murray–Darling basin region of south-eastern Australia (Timbal 2015).

This alternation between dry and wet phases offers a global bellwether example of the kinds of imposition and relaxation of rainfall extremes that many biotic populations will experience in the near and medium future. We previously reported on responses by anuran amphibians to the Big Dry (Mac Nally et al. 2009b) and to the Big Wet (Mac Nally et al. 2014). Most frogs depend on water, especially for breeding, and species with aquatic larvae are overrepresented in IUCN-threatened lists (Hero et al. 2005). Moreover, there have been major conservation concerns for frogs arising from diverse factors (Mendelson et al. 2006). While many anuran amphibians are adapted to drought–flood climates, the patterns of rainfall variation may now be so different that amphibians will be unable to cope (Walls et al. 2013a). A very wet period is not an adverse pressure for the species of anuran amphibians considered here (Mac Nally 1985), so we regard drought as the pressure for these animals and Big Wet-like periods as being the release of the pressure.

We were concerned that the relatively small gains in species’ occupancy and evidence of breeding seen in response to the Big Wet (Mac Nally et al. 2014) may have been due to the short time available after the rains. Therefore, the current study originally was intended to

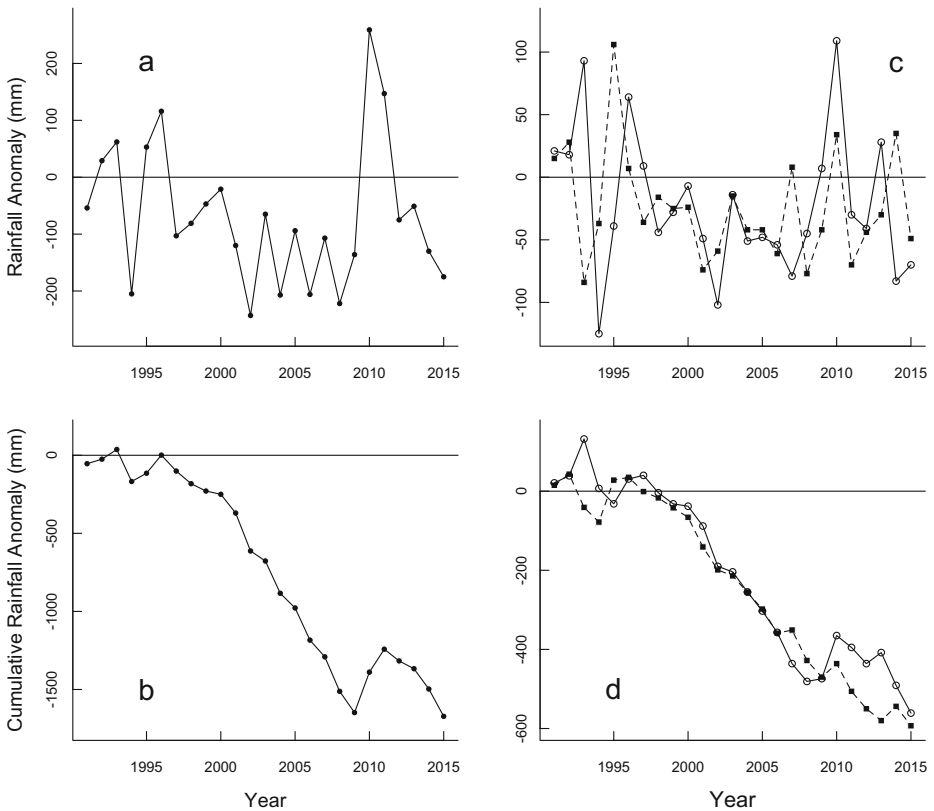


Fig. 1 Annual rainfall anomalies (mm) and cumulative annual rainfall anomalies (mm) (**a** and **b**, respectively) for 1991–2015 relative to the 1961–1990 baselines used by the Australian Bureau of Meteorology. **c**, **d** The data are for anomalies within the catchment-wetting period (April–June, *solid squares*) and for the survey periods (July–September, *open circles*) in each year. Data are means from six representative stations in central Victoria, Australia (Australian Bureau of Meteorology station numbers: 81085, 81003, 81123, 81053, 88043, 88019)

monitor longer-term responses to the Big Wet, but, given the return to xeric conditions, the data now provided an evaluation of the impact of a succession on droughts separated by an intense wet period. The study involved a strict emulation of the anuran survey programme first conducted in 2006–2007 (Big Dry), repeated in 2011–2012 (Big Wet) and then in 2014–2015 (post-Big Wet). The same locations were used, and the protocols for surveys within waterbodies and among landscapes were repeated diligently so that the results were comparable. We estimated species-specific resistance (Big Dry, post-Big Wet) and resilience (Big Wet) (Harrison 1979) to these large fluctuations in rainfall.

2 Methods

2.1 Rainfall patterns

We assembled data from six weather stations that were representative of the region (<http://www.bom.gov.au/climate/data/>, accessed December 31, 2015). We pooled data for the

stations and computed mean monthly rainfall estimates for the region from these figures. We report on anomalies for the whole year and for two parts of the year. The first part, the ‘wetting’ period of autumn and early winter (April–June), rewets the soil after the arid summers and prepares the waterbodies for filling if dry. Wetting-period rainfall stimulates breeding (Lemckert and Penman 2012; Walls et al. 2013a). The second part was the July–September ‘survey’ period, in which there is the highest calling activity for these anurans in this region (Mac Nally 1984). We calculated the cumulative anomalies to assess the cumulative deficit or surplus rainfall experienced from 1991, which was our starting point here given the baseline finished in 1990.

2.2 Region, landscapes and waterbodies

The 30,000 km² region is a forest-agricultural mosaic with 17% of the original vegetation cover and is characterized by box and ironbark eucalypt forests and woodlands at low elevations (150–400 m). There were five pairs of agricultural and forested landscapes distributed in the region, with each landscape in a pair being similar to most respects apart from forest cover (Supplementary Information, Fig. S1). Average cover of forest in the agricultural landscapes was 3% ± 1 (SD) and was 86% ± 14 (SD) in forested landscapes. All waterbodies were delineated on GIS using a Victorian Government map layer (<http://www.land.vic.gov.au/vicmap>; accessed May 2006). The waterbodies were farm dams, forest fire dams, culverts and natural ponds. Ten candidate waterbodies within a 2.5-km radius (19.6 km²) were identified for each landscape, from which eight were selected based on on-site inspections (total waterbodies 10 landscapes × 8 waterbodies landscape⁻¹).

2.3 Waterbody attributes

We measured variables for landscape, morphology and water characteristics of waterbodies (Table S1). Most attributes did not change during the 9 years and were measured in 2006. Dynamic variables (e.g. overbank flooded or completely drying) were measured for each year.

2.4 Anuran surveys

Methods and waterbodies were the same for each survey. Three surveys were conducted during the austral winter-springs in 2006 and 2007 (Big Dry), 2011 and 2012 (Big Wet) and 2014 and 2015 (post-Big Wet), making six surveys per ‘phase’. The 2 years of surveys per phase were samples of each phase, and we did not distinguish between years within phases. Waterbodies were surveyed at day and at night (Mac Nally et al. 2014). One landscape within a pair (either forested or agricultural) was surveyed during the day and its pair at night in a given survey round; the order was reversed in the subsequent survey round. The five landscape pairs were visited in a different random order in each survey round, and waterbodies within landscapes were visited in a random order.

Diurnal surveys facilitated (1) completing three visits to each of the 80 waterbodies during the 4 months and (2) conducting visual surveys for evidence of breeding (see below). Males of all species call during the day. Diurnal surveys commenced at c. 1400 h and ceased at dusk, while nocturnal surveys began after the last light and continued until c. 0100 h (Hazell et al. 2001).

We used a 25-min survey. The first 5 min was spent standing quietly recording calling males. The next 15 min was spent monitoring calls while searching for eggs and tadpoles. The

final 5 min was spent searching for reproductive outputs eggs and tadpoles alone. We visually inspected the perimeter of each water body 1 m from the water's edge for egg masses and tadpoles.

Weather conditions were measured because these influence calling activity (Mac Nally et al. 2009b). Cloud [0–8 (clear–completely overcast)], wind (0 calm; 1 light, leaves rustle; 2 moderate, moves branches; 3 strong, impedes progress) and air temperature (near the water body out of wind or direct sunlight) were measured.

3 Statistical analyses

3.1 Spatial autocorrelation

We used the mantel function in vegan package (Oksanen et al. 2006) to evaluate spatial autocorrelations with a Gower-index (accommodates all-0 s assemblage data recorded on some occasions) community dissimilarity matrix and a distance-between-site matrix. Data for the former were the number of surveys (of 18) in which each of the frog species was recorded at a waterbody. The mantel function allows within-strata permutations, which allowed us to explore whether there were larger scale patterns than within landscapes, which are handled in our model by using random effects (Supplementary Information).

3.2 Analyses of survey data

3.2.1 Counts: species richness and calling males

There were eight response variables (R_{ij} at waterbody i in survey round j ; $i = 1–80$, $j = 1–18$): (1) species richness, (2) the total number of calling males pooled for species and the abundances of (3) *Crinia parinsignifera*, (4) *Crinia signifera*, (5) *Limnodynastes tasmaniensis*, (6) *Limnodynastes dumerilii*, (7) *Litoria ewingi* and (8) *Litoria peroni*. No other species were recorded within 5 m from any waterbody.

We used a Poisson-errors model with a log-link function because the response variables were counts ≥ 0 (McCullagh and Nelder 1989). A response variable was modelled as a function of phase (Big Dry, Big Wet, post-Big Wet), landscape type (Agricultural vs Forested), waterbody characteristics, survey weather conditions and random effects for landscape, waterbody and year. The weather conditions were ‘forced’ into the model (i.e. were always included in the model) as conditioning covariates. Posterior $\Pr(\text{parameter} \geq 0) > 0.90$ or < 0.10 provides strong evidence of a parameter's importance for forced predictors (Kass and Raftery 1995).

Bayesian variable selection was used to quantify the evidence for the effects of phase, landscape type and waterbody attributes (Supplementary Information). We used reversible jump MCMC (Lunn et al. 2009) to estimate posterior model probabilities for all possible combinations of predictors and the posterior probabilities that waterbody attributes were important for understanding patterns (Thomson et al. 2010). Variable selection generally uses a posterior probability of inclusion in the best ensemble of models ≥ 0.75 (Thomson et al. 2010). The arithmetic differences in parameters among phases translate to proportional differences given the log-link function for Poisson-errors models.

Model fits were measured by using posterior predictive assessment (PPfit) (Supporting Information). A good model has $0.05 \leq \text{PPfit} \leq 0.95$, indicating plausible explanations of the data given the model and the fitted parameter values and uncertainties (Gelman et al. 1996).

3.2.2 Analysis of evidence of breeding

We could not distinguish egg masses or tadpoles by species given the survey programme (no egg masses or tadpoles could be collected given the conditions of our ethics approvals) so data were pooled for species. The binary (present/absent) data were used in the above model (Supplementary Information), apart from using a logit link and Bernoulli errors that apply for binary responses.

3.2.3 Retrospective reporting rate analysis

We used reporting rates (RRs = number of sites with positive detections divided by the number of surveyed sites) to determine changes in occurrences of anuran species since 1991. Data were from the Atlas of Victorian Wildlife (DNRE 2003) and were coupled with our results for the Big Dry, Big Wet and post-Big Wet. The atlas data were occurrences in general, multi-species survey lists as a proportion of the total numbers of lists conducted in the study region in a given phase and during July–September (Mac Nally et al. 2009b). Atlas data were blocked into two phases to produce sample sizes large enough to facilitate comparisons: 1990–1996 ($N = 43$) and 1997–2003 ($N = 28$). Mean rainfall in the 1990–1996 phase was $525 \text{ mm} \pm 138 \text{ SD}$ but fell to $436 \text{ mm} \pm 96 \text{ SD}$ for the 1997–2003 phase (early Big Dry). The latter Big Dry (2004–2009; $397 \text{ mm} \pm 67$) was drier again, while the Big Wet mean (2010–2012: $693 \text{ mm} \pm 233$) was wettest. The post-Big Wet mean rainfall was similar to the later Big Dry (2013–2015: $401 \text{ mm} \pm 69$).

We randomly sampled from the six waterbody visits in the Big Dry, Big Wet and post-Big Wet phases to emulate the atlas data, where waterbodies were visited only once. We calculated the number of waterbodies in which a species was recorded as present from these random samples. We repeated the random sampling 100 times for each species and calculated the mean single-visit number of positives for the three phases.

A binomial model was used to compare the estimated proportions of surveys in which each species was reported in each phase:

$$O_{ij} \sim \text{Binomial}(\rho_{ij}, N_j); \rho_{ij} \sim \text{Beta}(1, 1),$$

where O_{ij} is the observed number of occurrence of species i in phase j , N_j is the number of surveys (1990–2003 phases) or waterbodies (Big Dry, Big Wet and post-Big Wet) in phase j and ρ_{ij} is the estimated proportion for species i in phase j . Uninformative beta priors were used for each proportion. The ρ_{ij} were used to produce differences and corresponding uncertainties among all pairs of phases for each species (Mac Nally et al. 2009a).

3.3 Model estimation

All estimations were done using WinBUGS (Lunn et al. 2000), with three chains of 100,000 iterations, with the first 20,000 iterations discarded. Convergence of Markov chains was checked using Gelman–Rubin statistics and chain convergence (Gelman and Rubin 1992).

4 Results

4.1 Rainfall

Annual rainfall for the region in 2006–2015 was less than the baseline for every year apart from 2010 to 2011 (Fig. 1a). Patterns generally were similar to the wetting and survey periods in each year (Fig. 1c). The cumulative annual deficit since 1991 reached −1648 mm by 2009 but was reduced to −1242 by the end of 2011 (Fig. 1b). The post-Big Wet period increased the cumulative deficit to −1672 by the end of 2015. The temporal pattern for the wetting and survey periods mirrored the annual patterns (Fig. 1d).

4.2 Spatial autocorrelation

The compositions of anuran assemblages were not correlated with geographic separations among waterbodies when permutations were within landscapes (Fig. S2, $r_{\text{Mantel}} = 0.09$, permutation P value = 0.25), so that the species recorded in waterbodies did not change much with the distance between waterbodies. Therefore, spatial effects were handled at the landscape scale by using random effects for landscapes and waterbodies.

4.3 Counts and species richness of calling males: Big Dry, Big Wet and post-Big Wet

All models for species richness and species-specific counts of calling males fitted the data well (all $0.44 < \text{PPfit} < 0.79$, Table 1). Landscape type (remnant forest vs agricultural) did not much affect the response variables (Table S2). Fringing vegetation cover was positively related to richness and numbers of calling males of four species (Table S3). Tree basal area was positively associated with most responses, while survey-period drying of waterbodies was negatively related to four response variables (Table S3). There were no important statistical relationships, based on the posterior probability criteria listed above, between breeding evidence and measured waterbody attributes (Table S3).

Table 1 Details of proportional differences: mean [2.5%, 97.5%] for analyses of richness and counts of calling males and evidence of breeding. $\text{Pr}(>1)$ is the probability that the proportion exceeded 1 ($e^0 = 1$); bold designates an important increase, $\text{Pr}(>1) > 0.90$, and italics show an important decrease $\text{Pr}(>1) < 0.1$. PPfit is a measure of model fit; $0.05 < \text{PPfit} < 0.95$ implies the model plausibly could generate the data (closer to 0.5 is better)

	Phase (Big Wet/Big Dry) Proportional difference $\text{Pr}(>1)$	Phase (post-Big Wet/ Big Wet) Proportional difference $\text{Pr}(>1)$	Phase (post-Big Wet/ Big Dry) Proportional difference $\text{Pr}(>1)$	PPfit
Richness	1.15 [0.85, 1.58] (0.80)	<i>0.65</i> [0.47, 0.87] (0)	0.75 [0.58, 0.95] (0.01)	0.71
All calling males	2.10 [1.20, 3.71] (1.0)	<i>0.29</i> [0.15, 0.56] (0)	<i>0.62</i> [0.37, 1.02] (0.03)	0.79
<i>Crinia parainsignifera</i>	1.71 [0.85, 3.55] (0.93)	<i>0.33</i> [0.16, 0.68] (<0.01)	<i>0.57</i> [0.33, 0.98] (0.02)	0.63
<i>Crinia signifera</i>	2.10 [1.20, 3.71] (1)	<i>0.29</i> [0.15, 0.56] (0)	<i>0.62</i> [0.27, 1.02] (0.13)	0.56
<i>Limnodynastes tasmaniensis</i>	<i>0.47</i> [0.20, 1.41] (0.08)	1.44 [0.54, 3.20] (0.82)	0.68 [0.33, 1.62] (0.21)	0.57
<i>Limnodynastes dumerilii</i>	4.56 [1.46, 14.67] (>0.99)	<i>0.16</i> [0.05, 0.49] (<0.01)	0.74 [0.26, 2.21] (0.74)	0.44
<i>Litoria ewingi</i>	3.18 [0.63, 11.34] (0.92)	<i>0.25</i> [0.06, 1.13] (0.03)	0.81 [0.16, 2.51] (0.43)	0.61
<i>Litoria peroni</i>	0.87 [0.18, 3.89] (0.43)	0.90 [0.27, 3.25] (0.44)	0.78 [0.16, 4.01] (0.43)	0.51
Evidence of breeding	3.35 [1.72, 6.93] (1)	<i>0.24</i> [0.11, 0.52] (0)	0.82 [0.35, 1.93] (0.33)	0.48

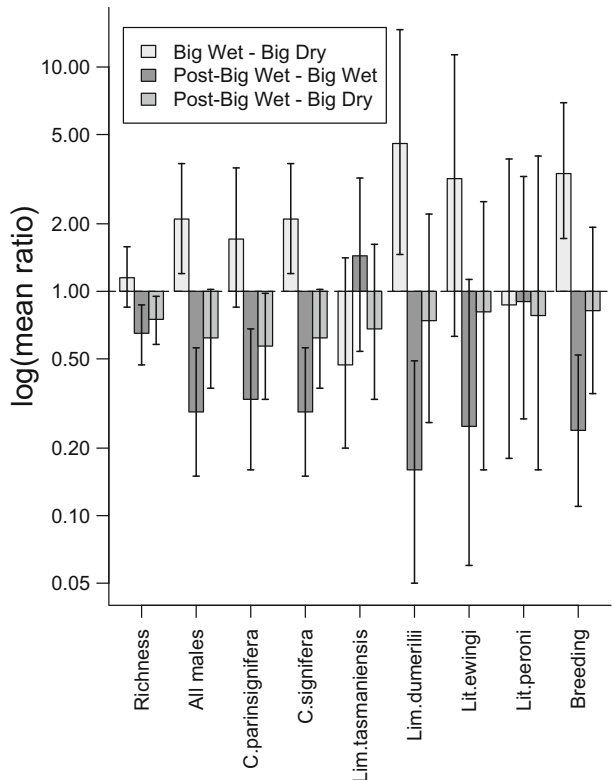
There appeared to be important increases in numbers of calling males for four species and total numbers of all species during the Big Wet compared with the Big Dry, but counts of *L. tasmaniensis* declined substantially (Table 1, Fig. 2). Comparisons of the post-Big Wet period with the Big Wet showed that all of those increases were reversed, and richness declined further despite not increasing during the Big Wet (Table 1, Fig. 2). All ratios were <1 in comparing counts for the post-Big Wet with the Big Dry, with richness, total counts of all species and numbers of *C. parinsignifera* being substantially <1 (Table 1, Fig. 2).

4.4 Evidence of breeding

The probability of detecting eggs or tadpoles at a waterbody in any single visit was substantially higher in the Big Wet years compared with the Big Dry, increasing 3.35-fold (Table 1, Fig. 2). The detection probability declined dramatically in the post-Big Wet compared to the Big Wet 0.24 (0.24, Table 1, Fig. 2). The probability of finding breeding evidence was similar to the post-Big Wet and the Big Dry.

The number of waterbodies with evidence of breeding in any of the six Big Dry surveys (2006–07) was 17 (21%); for only one waterbody was there detection of eggs or tadpoles on more than one visit. There were 36 waterbodies with evidence of breeding in the Big Wet (45%), and 17 of those had multiple surveys with detections of breeding evidence. In the post-Big Wet phase, there were 17 (21%) waterbodies with breeding detected once in the six rounds, and in four of these, there was evidence in at least two survey periods.

Fig. 2 Proportionate change for nine response variables comparing the Big Wet with the Big Dry (light grey), the post-Big Wet with the Big Wet (dark grey) and the post-Big Wet with the Big Dry (mid grey). Response variables are as follows: mean species richness; mean total number of calling males; mean numbers of calling males of *Crinia parinsignifera*, *C. signifera*, *Limnodynastes tasmaniensis*, *Lim. dumerilii*, *Litoria ewingi* and *Lit. peroni* and waterbodies with evidence of breeding (eggs or tadpoles). Error bars are 95% credible intervals



Sixteen of the 17 waterbodies with evidence of breeding in the Big Dry had evidence during the Big Wet, but in only five of those 17 was there evidence of breeding in the post-Big Wet phase. Therefore, there was little suggestion of a systematic pattern to the waterbodies in which breeding occurred throughout the decade.

4.5 Reporting rates among phases

Mean reporting rates are shown in Fig. 3a. Statistical comparisons are as follows, where ‘=’ means no statistically important difference and ‘>’ means ‘is greater than statistically’ (i.e. $\Pr(\text{difference} > 0) > 0.90$). The numerals correspond to the five phases: (1) 1990–1996, (2) 1997–2003, (3) the Big Dry (2006–2007), (4) the Big Wet (2011–2012) and (5) post-Big Wet (2014–2015). Comparisons of mean reporting rates among phases were as follows: *C. parinsignifera*: 1 = 2 > 4 > 3 = 5; *C. signifera*: 1 > 2 > 4 > 3 = 5; *L. tasmaniensis*: 1 > 2 > 3 = 4 = 5; *L. dumerilii*: 1 = 2 > 4 > 3 = 5; *Litoria ewingi*: 1 = 2 > 3 = 4 = 5; and *L. peroni*: 1 = 2 > 3 = 4 = 5. The degree of recovery among all species in the Big Wet was relatively small compared with the historical values, and all gains were lost in the post-Big Dry period (Fig. 3a). The post-Big Dry reporting rates for all species were small fractions of the 1990–1996 and, for most species, were small relative to the 1997–2003 rates (Fig. 3a). Another seven species listed in Atlas surveys were not recorded or recorded very rarely by hearing calls from long distances from our study waterbodies.

5 Discussion

The context for this work is that the Big Dry and projected droughts of similar character in future (Timbal 2015) are abnormally long and intense relative to past events. Recent simulations of retrospective sequences of rainfall suggest that dry periods, defined as -0.5 SD anomalies lasting ≥ 3 years in 11-year filtered rainfall reconstructions, occurred relatively often in the past 200 years (18 events between 1800 and 2000 in south-eastern Australia) (Gergis and Henley 2016). However, none of those dry periods resembled the duration and depth of the Big Dry [Fig. 5 of (Gergis and Henley 2016)]. Relatively wet periods also were common (27 events between 1800 and 2000), although these more closely resembled the Big Wet in being rarely > 2 years in duration. Other millennial length reconstructions of past climates (Palmer et al. 2015; Tozer et al. 2016) suggested frequent alternation of dry and wet periods, which also are evident in the instrumental record of the twentieth century, but the evidence for events like the Big Dry is difficult to discern. Therefore, the extreme precipitation amplitudes seen since the late 1990s appears to be abnormal relative to reconstructed evidence.

5.1 Summary of anuran responses

We considered 15 response variables for the anurans of the study region, including seven measures of abundance of calling males (all males and males of each species), six spatial distribution measures (reporting rates), richness and evidence of breeding (Table 1; Fig. 2). There were statistically important increases associated with the intense rainfall events of late 2010–mid-2012 for six responses (Table 1; Fig. 2). The increase in numbers of waterbodies with evidence of breeding, and the greater number of waterbodies in which there were repeated observations of breeding within seasons, provided some expectation that the Big Wet may have induced recovery.

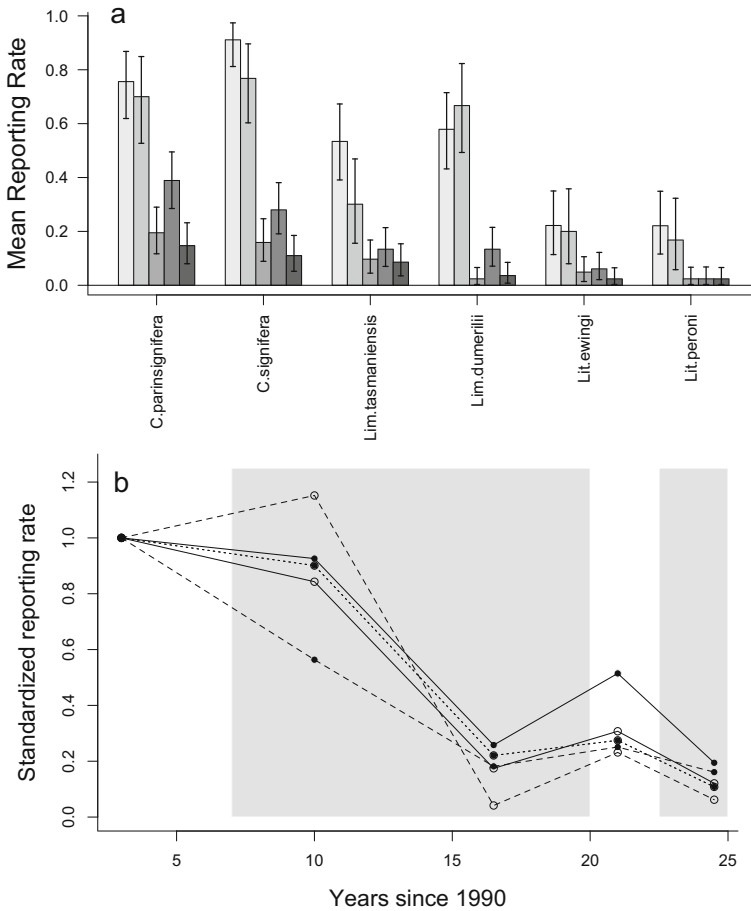


Fig. 3 **a** Reporting rates for six species of anuran amphibians using wildlife atlas data (1990–2003) and our survey data (2006–2015). Species are *Crinia parinsignifera*, *C. signifera*, *Limnodynastes tasmaniensis*, *Lim. dumerilii*, *Litoria ewingi* and *Lit. peroni*. Error bars are 95% credible intervals. **b** Representation of standardized reporting rates for the six frog species in the mode of Fig. 1, with grey bars indicating periods of imposed pressure (drought). Key: solid lines are genus *Crinia* (solid circles = *C. parinsignifera*, open circles = *C. signifera*), dashed lines are *Limnodynastes* (solid circles = *Lim. tasmaniensis*, open circles = *Lim. dumerilii*) and dotted lines are *Litoria* (solid circles = *Lit. ewingi*, open circles = *Lit. peroni*)

All response variables declined during the post-Big Wet and that the gains in the Big Wet generally were lost. For reporting rates, occurrences of the six species in the post-Big Wet were statistically indistinguishable from those in the Big Dry (Fig. 3), but all measures of abundance, richness and evidence of breeding had proportionality factors relative to the Big Dry <1 (Table 1). While only three of the latter measures were statistically important by our criteria, the mean proportionality factors generally fell well short of unity. The 3.35-fold increase in evidence of breeding following the Big Wet was more than offset by the 0.24 proportionate decline in the post-Big Wet period (Table 1).

We previously cautioned our evidence reflects patterns for calling males rather than the demographically more significant signs of recruitment (Selwood et al. 2015), particularly

production of metamorphlings (Mac Nally et al. 2014). The increases in numbers of waterbodies with evidence of breeding during the Big Wet (Mac Nally et al. 2014) did not appear to translate into significant increases in recruits over a longer time through the post-Big Dry. Males of all species would have had sufficient time to have matured between the Big Wet and post-Big Wet survey periods (Hoser and Game 1989). High adult mortality rates may be offset by high recruitment rates in some situations (Scheele et al. 2015), but we saw little evidence of the latter despite declining densities of calling adult males.

5.2 Resistance and resilience

There are four contrasting modes for resistance and resilience in relation to the repeated imposition/relaxation of a pressure, such as deep drought (Nimmo et al. 2015). The ‘full recovery’ mode, where resilience equals resistance in each successive phase, does not hold for the current system, at least based on the temporal sequence of reporting rates, which we represent in a form similar to Fig. 2 of Nimmo et al. (2015) for comparison (Fig. 3b). While the reporting rates in the first years of the Big Dry (1997–2003) generally were similar to the years preceding the Big Dry (1990–1996), the declines were pronounced by the later Big Dry, with previously widespread and abundant taxa (*C. signifera* and *C. parinsignifera*) also declining precipitously (Fig. 3b).

The Big Wet ‘bounce’ fell well short of the early Big Dry period for all species, and the declines in the post-Big Wet phase to rates seen in the Big Dry or lower showed that the Big Wet recoveries were both limited in magnitude and ephemeral. The data from 1990 to 2003 were obtained from a wildlife atlas (DNRE 2003) whereas the reporting-rate information for 2006–2015 was from our survey programmes. The use of two different methods might induce some exaggeration of the declines in spatial occurrence. Surveys conducted with no recorded species may not have been entered into the atlas database, which would bias reporting rates. However, there were *C. signifera* at every lentic waterbody (>200) surveyed in the late 1970s (Mac Nally 1985), so that at least that species was much more widespread than in the 2006–2015 period.

Results were not consistent with any of the other three modes depicted in Fig. 2 of Nimmo et al. (2015)—declining resistance only, declining resilience only or declining resistance and resilience. The trajectories indicated a very severe decline (very little resistance) once the Big Dry went beyond 6 years (i.e. after 2003) and relatively little resilience–recovery – across the board (Figs. 2 and 3) during the Big Wet. The severity and extended duration of the Big Dry (13 years) seems to have pushed the anuran fauna to a depressed state that relatively short intervals of even very favourable weather did not reverse. In the resistance–resilience parlance, there was very little resistance to the Big Dry once the drought extended beyond 6 years (i.e. very steep declines) and there was little resistance in the subsequent pressure phase (post-Big Wet). Resistance did not, or rather could not, decline much because there was little scope for the frogs to decline further given the small resilience seen in response to the Big Wet.

5.3 Management of such declines

The management of freshwater biota, especially fish, waterbirds (e.g. egrets, cormorants, ibis) and invertebrates, now often involves the provision of ‘environmental water’ to waterways from water reserves allocated for this purpose (Poff and Zimmerman 2010). Subsidiary benefits from such flows are the inundation of floodplains to sustain floodplain vegetation (Merritt et al. 2010) and the replenishment of floodplain wetlands (Powell et al. 2008).

The waterbodies we studied are located in the extreme south of the vast inland plains to the west and north of the Great Dividing Range that runs along Australia's eastern seaboard (Fig. S3). Like most plain waterbodies, these generally are rainfall-fed (Wassens et al. 2013). In extended drought, refilling is rare or insufficient to fill lentic waterbodies. From the standpoint of amphibian breeding, the absence of rain does not provide the necessary cues to stimulate breeding activity for many species (Cynthia et al. 2005). The extent of the plain drought in eastern Australia from 2013 is shown in Fig. S3 so that we expect that the levels of breeding activity and success upon which we report will be similar over a potentially vast area.

The provision of environmental flows over enormous plain areas (hundreds of thousands km²) clearly is infeasible and probably would be ineffective if rainfall-induced breeding cues do not concurrently occur (Walls et al. 2013a). Individual waterbodies can be managed to provide better habitat for some anuran species. Fringing vegetation and tree cover around waterbodies were associated with more species, and greater densities of calling males of several species (Table S3), so at small scales, some improvements can be made. We note that none of the waterbody features was associated with higher probabilities of evidence for breeding (Table S3). However, the difficulty of filling large numbers of waterbodies over extensive flat areas coupled with the absence of breeding cues arising from a lack of rainfall makes conservation management particularly difficult for plains-based, water-dependent taxa.

Since the 1990s, the anuran fauna of the region has been 'homogenized' (Dodd et al. 2007) and now largely consists of six species that were the previously most widespread and abundant of the 13 species reported in this region (DNRE 2003). While none of the six species is likely to be threatened with extinction given that all have large geographic ranges with substantial topographic variation (Hero et al. 2005), overall geographic representation of most of the species is likely to be effectively much smaller in future decades. There will almost certainly be consequential ecological effects because frogs are important prey for many species of waterbirds (Taylor and Schultz 2008) and snakes (Shine 1977) and the massive decline in frog numbers over vast inland areas probably will make the persistence of many snake species, which are so much less mobile than waterbirds, more problematic.

5.4 How general are these results?

The expectation of a pattern of long, intense dry periods with intervening short periods of intense rainfall for the region now is becoming increasingly more certain from climate models (Timbal 2015). An intense El Niño established in 2015 (Schiermeier 2015) and much of eastern Australia moved into an even more severe drying phase (Fig. S3). Our study region lies in the heart of the worst drought-affected region of the extreme south-east (Fig. S3), but even more severe drying occurred between 2013 and 2015 in inland regions of Queensland in north-eastern Australia (Fig. S3). The inland plain anuran faunas generally consist of species of our study region or closely related congeners, most of which breed in lentic waterbodies (Anstis 2013). Ours is one of the most detailed and spatially extensive survey programmes of such anuran faunas, and we expect that our results will be representative of a vast area of eastern Australia. In southern New South Wales, to the north of our study region, from 2002 to 2009, frog faunas in lentic waterbodies came to consist only of more generalized species, as we found, but with even fewer species breeding over winter (Wassens et al. 2013). There is evidence of adaptations to differing degrees of environmental harshness in the congener of two of our species, *Crinia pseudinsignifera* (Reniers et al. 2015), so it is possible that the selective pressures associated with increased climatic amplitudes may induce adaptive responses in

some circumstances. However, the widespread lack of evidence of breeding upon which we report suggests that the amount of ‘material’ with which evolution has to work might be small in the future and such adaptive responses might be too little and too slow.

The prognosis globally is for a general increase in drought occurrence and duration, with vast areas of western and southern Africa, Amazonia, southern Russia, Europe and much of the USA likely to be affected adversely (Burke et al. 2006). Although the dynamics of drought are expected to differ greatly among regions (Burke et al. 2006), one expects that the patterns of substantial declines in anuran faunas due to overall drying for many parts of the world will play out in coming decades. There is increasing evidence of drought-linked declines in amphibians (Daszak et al. 2005; McMenamin et al. 2008; Walls et al. 2013b), although these studies do not report on sequences of deep drought and intense rainfall upon which we report. The additional pressure exerted by climate change on many species of frogs subjected to disease and other factors (Kiesecker et al. 2001) signals a bleak future for anuran amphibians (Hero et al. 2005; Mendelson et al. 2006), although climate changes may advantage some amphibian species in certain circumstances (Werner et al. 2009; McCaffery and Maxell 2010).

Acknowledgements The work was supported by the Australian Research Council (LP120200217, DP120100797). J. R. Thomson, J. L. D. Yen, S. Nerenberg, R. H. Clarke, P.S. Lake and A.C. Taylor provided valuable assistance.

Compliance with ethical standards Ethics approvals BSCI/2006/04 and CEAE 14–11 were obtained from Monash University and The University of Canberra, respectively.

References

- Anstis M (2013) Tadpoles and frogs of Australia. CSIRO, Melbourne
- Burke EJ, Brown SJ, Christidis N (2006) Modeling the recent evolution of global drought and projections for the twenty-first century with the Hadley centre climate model. *J Hydrometeorol* 7:1113–1125
- Chiew FHS, Young WJ, Cai W, Teng J (2011) Current drought and future hydroclimate projections in southeast Australia and implications for water resources management. *Stoch Env Res Risk A* 25:601–612
- Coumou D, Rahmstorf S (2012) A decade of weather extremes. *Nat Clim Chang* 2:491–496
- Cynthia PA, Uetanabaro M, Haddad CFB (2005) Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia* 26:211–221
- Daszak P, Scott DE, Kilpatrick AM, Faggioni C, Gibbons JW, Porter D (2005) Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. *Ecology* 86:3232–3237
- DNRE (2003) Atlas of Victorian Wildlife: Victorian Fauna and Flora databases. Department of Natural Resources and Environment, Victoria
- Dodd CK Jr, Barichivich WJ, Johnson SA, Staiger JS (2007) Changes in a Northwestern Florida Gulf coast herpetofaunal community over a 28-y period. *Am Midl Nat* 158:29
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK (2005) Global consequences of land use. *Science* 309:570–574
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat Sci* 457–472
- Gelman A, Meng X-L, Stern H (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Stat Sin* 6:733–787
- Gergis J, Henley BJ (2016) Southern Hemisphere rainfall variability over the past 200 years. *Clim Dyn* 1–19
- Harrison GW (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. *Am Nat* 113:659–669
- Hazell D, Cunningham R, Lindenmayer D, Mackey B, Osborne W (2001) Use of farm dams as frog habitat in an Australian agricultural landscape: factors affecting species richness and distribution. *Biol Conserv* 102:155–169
- Hero JM, Williams SE, Magnusson WE (2005) Ecological traits of declining amphibians in upland areas of eastern Australia. *J Zool* 267:221–232
- Hoser RT, Game C (1989) Australian reptiles & frogs. Pierson & Company Pty Limited

- Kass RE, Raftery AE (1995) Bayes factors. *J Am Stat Assoc* 90:773–795
- Kiesecker JM, Blaustein AR, Belden LK (2001) Complex causes of amphibian population declines. *Nature* 410: 681–684
- Leblanc M, Tweed S, Van Dijk A, Timbal B (2012) A review of historic and future hydrological changes in the Murray-Darling basin. *Glob Planet Chang* 80:226–246
- Lemckert F, Penman T (2012) Climate change and Australia's frogs: how much do we need to worry. *Wildlife & Climate Change: Towards Robust Conservation Strategies for Australian Fauna*:92–97.
- Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Stat Comput* 10:325–337
- Lunn DJ, Best N, Whittaker JC (2009) Generic reversible jump MCMC using graphical models. *Stat Comput* 19: 395–408
- Mac Nally RC (1984) Chorus dynamics of two sympatric species of *Ranidella* (Anura): within-year and between-year variation and their determination. *Z Tierpsychol* 65:134–151
- Mac Nally RC (1985) Habitat and microhabitat distributions in relation to ecological overlap in two species of *Ranidella* (Anura). *Aust J Zool* 33:329–338
- Mac Nally R, Bennett AF, Thomson JR, Radford JQ, Unmack G, Horrocks G, Vesik P (2009a) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Divers Distrib* 15:720–730
- Mac Nally R, Horrocks G, Lada H, Lake PS, Thomson JR, Taylor AC (2009b) Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: effects of climate change in an aridifying region. *Glob Ecol Biogeogr* 18:575–585
- Mac Nally R, Nerenberg S, Thomson JR, Lada H, Clarke RH (2014) Do frogs bounce, and if so, by how much? Responses to the 'Big Wet' following the 'Big Dry' in south-eastern Australia. *Glob Ecol Biogeogr* 23:223–234
- Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Glob Chang Biol* 18:1239–1252
- McCaffery RM, Maxell BA (2010) Decreased winter severity increases viability of a montane frog population. *Proc Natl Acad Sci* 107:8644–8649
- McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London
- McMenamin SK, Hadly EA, Wright CK (2008) Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc Natl Acad Sci U S A* 105:16988–16993
- Mendelson JRI, Lips KR, Gagliardo RW, Rabb GB, Collins JP, Diffendorfer JE, Daszak P, Roberto Ibáñez D, Zippel KC, Lawson DP, Wright KM, Stuart SN, Gascon C, Da Silva HR, Burrowes PA, Joglar RL, La Marca E, Lötters S, Du Preez LH, Weldon C, Hyatt A, Rodriguez-Mahecha JV, Hunt S, Robertson H, Lock B, Raxworthy CJ, Frost DR, Lacy RC, Alford RA, Campbell JA, Parra-Olea G, Bolaños F, Domingo JJC, Halliday T, Murphy JB, Wake MH, Coloma LA, Kuzmin SL, Price MS, Howell KM, Lau M, Pethiyagoda R, Boone M, Lannoo MJ, Blaustein AR, Dobson A, Griffiths RA, Crump ML, Wake DB, Brodie ED Jr (2006) Confronting amphibian declines and extinctions. *Science* 313:48
- Merritt DM, Scott ML, LeRoy P, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshw Biol* 55: 206–225
- Nimmo DG, Mac Nally R, Cunningham SC, Haslem A, Bennett AF (2015) Vive la résistance: reviving resistance for 21st century conservation. *Trends Ecol Evol* 30:516–523
- Oksanen J, Kindt R, Legendre P, O'Hara R (2006) Vegan: community ecology package. 1.8-2 edn. R project for statistical computing. URL: <http://cran.r-project.org/>.
- Palmer JG, Cook ER, Turney CSM, Allen K, Fenwick P, Cook BI, O'Donnell A, Lough J, Grierson P, Baker P (2015) Drought variability in the eastern Australia and New Zealand summer drought atlas (ANZDA, CE 1500–2012) modulated by the Interdecadal Pacific Oscillation. *Environmental Research Letters* 10
- Poff NL, Zimmerman JKH (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshw Biol* 55:194–205
- Powell SJ, Letcher RA, Croke BFW (2008) Modelling floodplain inundation for environmental flows: Gwydir wetlands, Australia. *Ecol Model* 211:350–362
- Reniers J, Brendonck L, Roberts JD, Verlinden W, Vanschoenwinkel B (2015) Environmental harshness shapes life-history variation in an Australian temporary pool breeding frog: a skeletochronological approach. *Oecologia* 178:931–941
- Scheele BC, Hunter DA, Skerratt LF, Brannelly LA, Driscoll DA (2015) Low impact of chytridiomycosis on frog recruitment enables persistence in refuges despite high adult mortality. *Biol Conserv* 182:36–43
- Schiermeier Q (2015) Hunting the Godzilla El Niño. *Nature* 526:490–491
- Selwood K, McGeoch MA, Mac Nally R (2015) The effects of climate change and land-use change on demographic rates and population viability. *Biol Rev* 90:837–853
- Shine R (1977) Habitats, diets, and sympatry in snakes: a study from Australia. *Can J Zool* 55:1118–1128

- Taylor IR, Schultz MC (2008) Breeding season diets of egrets in Southeast Australia: implications for future population viability. *Waterbirds* 31:593–601
- Thomson JR, Kimmerer WJ, Brown LR, Newman KB, Mac Nally R, Bennett WA, Feyrer F, Fleishman E (2010) Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecol Appl* 20:1431–1448
- Timbal B (2015) Murray basin cluster report. Climate change in Australia projections for Australia's natural resource management regions: cluster reports, eds. Ekström, M. et al., CSIRO and Bureau of Meteorology, Australia
- Tozer CR, Vance TR, Roberts JL, Kiem AS, Curran MAJ, Moy AD (2016) An ice core derived 1013-year catchment-scale annual rainfall reconstruction in subtropical eastern Australia. *Hydrol Earth Syst Sci* 20: 1703–1717
- Verdon-Kidd DC, Kiem AS (2009) Nature and causes of protracted droughts in southeast Australia: comparison between the Federation, WWII, and Big Dry droughts. *Geophys Res Lett* 36
- Walls SC, Barichivich WJ, Brown ME (2013a) Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–418
- Walls SC, Barichivich WJ, Brown ME, Scott DE, Hossack BR (2013b) Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. *Wetlands* 33:345–354
- Wassens S, Walcott A, Wilson A, Freire R (2013) Frog breeding in rain-fed wetlands after a period of severe drought: implications for predicting the impacts of climate change. *Hydrobiologia* 708:69–80
- Werner EE, Relyea RA, Yurewicz KL, Skelly DK, Davis CJ (2009) Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. *Ecol Monogr* 79:503–521