

ARTICLE

Freshwater Ecology

Stochastic metapopulation dynamics of a threatened amphibian to improve water delivery

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Abstract

Water extraction and climate change are altering the availability of surface water globally, thereby contributing to amphibian population declines. The managed delivery of water to benefit environmental values (environmental watering) is a promising conservation technique that can support amphibian recruitment and maintain viable populations. Environmental water can be delivered in various spatial patterns and with different frequencies, but comparing the effectiveness of competing strategies is complicated by variable and interactive environmental processes. We built a spatially explicit, stochastic, hydroecological metapopulation model to compare the effects of five environmental-watering scenarios on the probability of persistence of threatened southern bell frogs (*Litoria raniformis*) in a major river reach in southern Australia. We compared a no-intervention control to two managed watering frequencies (moderate and frequent) delivered in two spatial designs (managed wetlands grouped or spread across the reach). More frequent water provision to intervention sites improved the reach-wide (metapopulation) probability of persistence, and spreading intervention sites across the reach improved persistence more than grouping intervention sites together. When re-examined under severe drought conditions, *L. raniformis* had a 0.04 probability of persistence without intervention, which improved to 0.56 with high watering frequency. Model-guided environmental water provision can improve reach-wide persistence of amphibian metapopulations by guiding spatial and temporal delivery patterns to reduce the risk of extinction.

KEYWORDS

amphibian, environmental water provision, frog, hydroperiod, *Litoria raniformis*, river regulation, stochastic population model

INTRODUCTION

While the current human-caused degradation of the biosphere is affecting all taxa (Bradshaw et al., 2021),

amphibians are leading the extinction charge (Stuart et al., 2004; Wake & Vredenburg, 2008). Currently, 41% of assessed amphibian species are threatened with extinction (IUCN, 2022), but this is likely an underestimate

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given a lack of up-to-date, data-driven assessments for many species. The modification of habitats (including changes to hydrological regimes) is a main driver of amphibian declines and can result in loss of essential floodplain and wetland habitats in which many species breed. During the 20th Century alone, an estimated 64%–71% of wetland area was lost globally (Davidson, 2014), and the extent and condition of extant wetlands continue to decline (Convention on Wetlands, 2021). Climate change is driving additional changes to ground- and surface-water dynamics that will interfere with ecologically important flow regimes and increase wetland drying (Havril et al., 2018; Maleki et al., 2019). In river systems that supply water to the domestic and agricultural sectors, increasing demand creates additional stressors that further degrade the ecological function of riverine ecosystems (Greve et al., 2018) and cause local extinctions (Mathwin et al., 2023a).

Manipulating water to restore hydrological components and hydroecological processes can mitigate some of the impacts of water extraction and climate change on amphibians (Mathwin et al., 2020; Shoo et al., 2011). Managed water delivery (hereafter referred to as “environmental watering”) to constructed or natural habitats can inundate dry areas and create breeding opportunities that would not have occurred otherwise (Darcovich & O’Meara, 2008; Seigel et al., 2006). Incorporating spatial processes in management planning can potentially improve conservation outcomes (Enneson & Litzgus, 2009; Howell et al., 2020) and guide the spatial deployment of interventions (Sofaer et al., 2016). Managed water delivery to multiple breeding habitats (or subpopulations) within a metapopulation has the potential to increase population viability (Moor et al., 2022), but planning is complex and must consider the optimal number of intervention sites, the spatial arrangement of sites, and the frequency of environmental watering, all while attempting to maximize outcomes from limited resources.

Despite recognition that spatial variability in population dynamics dictates long-term trends in abundance and persistence, population viability analyses that incorporate spatial processes are still rare (Campbell et al., 2018; Zeigler et al., 2013). Collapsing spatially variable dynamics can potentially bias estimates of extinction risk by ignoring asymmetrical dispersal patterns such as source–sink dynamics (Pulliam, 1988). Systems with variable hydrology provide additional challenges when planning conservation interventions for water-dependent taxa (Bino et al., 2015). Flow regimes have strong implications for aquatic life histories (Palmer & Ruhi, 2019) and hydroecological models improve predictive capabilities by incorporating variable flow regimes into their design (Bertassello et al., 2022).

We developed a spatially explicit, stochastic, hydroecological metapopulation model to evaluate five conceptual conservation programs (each providing environmental water to amphibian breeding locations) in a 70-km-long regulated river reach in southern Australia. Our virtual water-delivery programs used different spatial patterns and frequency of environmental watering to ascertain their relative likelihood of increasing the long-term (60-year) persistence of the southern bell frog (*Litoria raniformis*) across the reach. We measured the success of each program as the average probability of survival/wetland after 60 years and compared them under both simulated hydrology and severe drought conditions. We hypothesized that programs with more frequent environmental water delivery would result in higher mean probability of persistence, and that spreading intervention sites more broadly across the reach would also spread population rescue and reinforcement, resulting in higher mean probability of persistence. We also hypothesized that during drought conditions, the probability of persistence within the reach depends on persistence at intervention sites.

MATERIALS AND METHODS

Study reach

The Murray–Darling Basin contains Australia’s longest river system and is heavily regulated for domestic and agricultural use. Our focus was 70 km of the Murray River channel between two main-channel weirs (“locks”) that dissect the river: Lock 3 (34°11’16.95” S, 140°21’29.65” E) and Lock 2 (34°4’39.31” S, 139°55’52.81” E). This reach connects laterally to 23 wetlands with historical records of *L. raniformis* (Figure 1). The reach averages 53 rain days each year with an average annual rainfall of 240 mm. This is insufficient to fill wetlands to the completion of *L. raniformis* larval stages and successful recruitment relies on elevated river levels (or the provision of environmental water via pumps or other structures) to fill these wetlands.

Historical data in the reach (collated from government surveys, citizen science programs, and university research) were too sparse to inform site-specific population dynamics. Instead, we estimated the filled surface area of the 23 wetlands using satellite imagery (Austin & Gallant, 2010) in consultation with local land managers (S. Robinson, personal communication). We then classified the 23 wetlands as: *medium*, a surface area similar to two domestic swimming pools (approximately 64 m²; $n = 3$); *large*, a surface area similar to an Olympic swimming pool (approximately 1250 m²; $n = 4$); and *very*

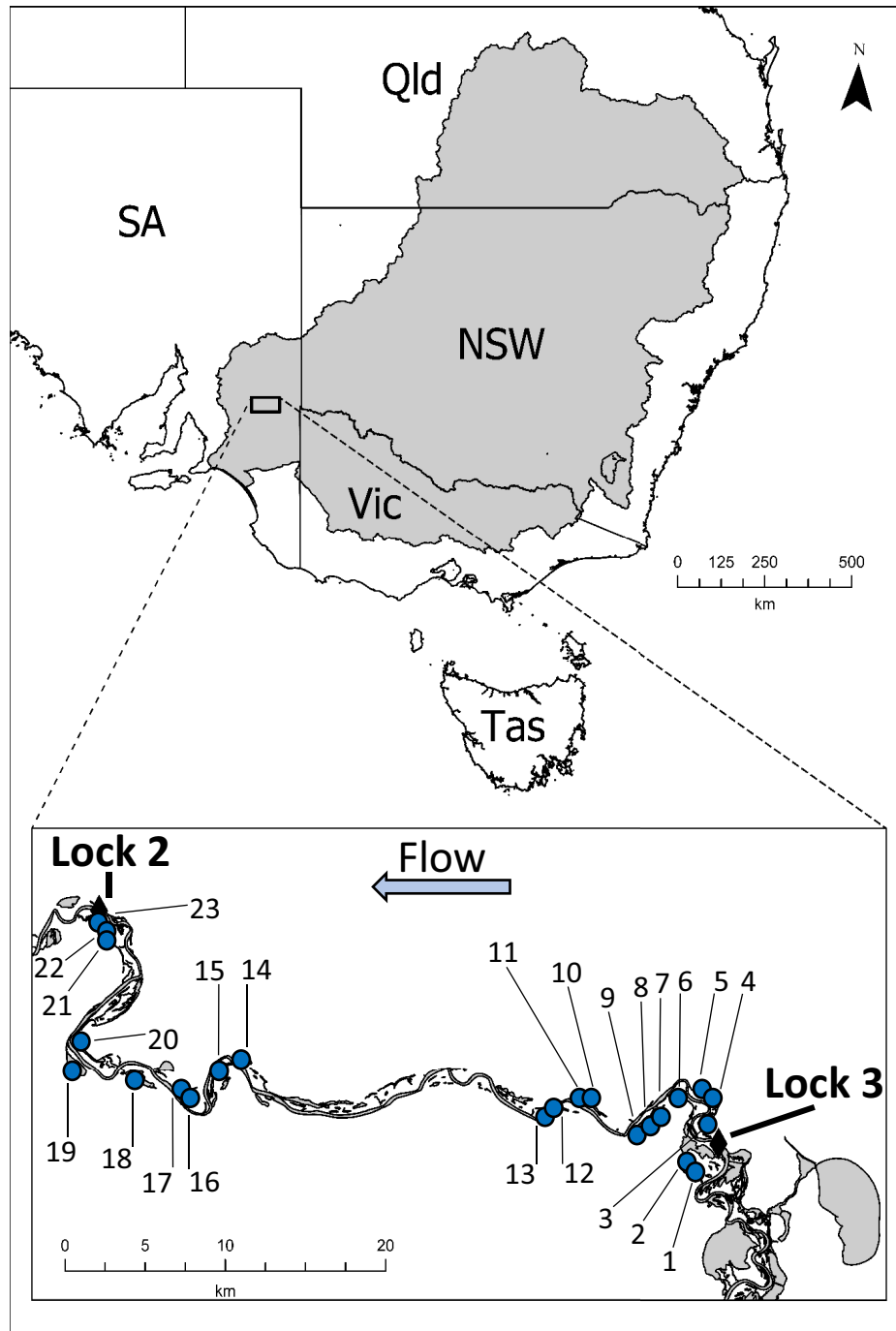


FIGURE 1 The reach between Locks 3 and 2 in the Murray–Darling Basin contains 23 historical *Litoria raniformis* habitats. Wetlands are numbered from upstream (right) to downstream and a division is present between wetlands 13 and 14 of approximately 20 km. NSW, New South Wales; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria.

large, a surface area several hundred meters in diameter (approximately 31,000 m²; $n = 17$). We used pooled monitoring data from several reaches to create mean population estimates for each wetland size category.

For each of the 23 wetlands, we estimated the river height required for the wetland to begin filling (hereafter “sill height”) and the interannual drying threshold (i.e., the climatic wetness that prevents a wetland from

drying between annual breeding events). We estimated sill heights from digital elevation models (selecting the lowest elevation flow path from the river to the wetland) which we calibrated by comparing historical gauged river height data to hydrological satellite imagery using Water Observations from Space (WofS; Geoscience Australia, 2015). To estimate the interannual drying threshold, we first identified the years that each site filled enough to

remain full over the subsequent summer–autumn period (WofS; Geoscience Australia, 2015). We then calculated the sum of gauged daily river heights during winter and spring that filled these sites and selected the smallest value for each site.

Life history of southern bell frogs

The southern bell frog (*L. raniformis*) is a wetland specialist that was once common through south-eastern Australia (Pyke, 2002). Declines in range and abundance were first noted in the 1970s, and the species is currently listed as *Endangered* under the IUCN Red List of Threatened Species (Hero et al., 2004). Declines are being driven by multiple interactive processes, including the regulation of natural flow regimes that reduces breeding opportunities and fragment populations (Mathwin et al., 2023a), the fungal pathogen *Batrachochytrium dendrobatidis* (Turner et al., 2021), and stochastic drought events (Heard et al., 2012b). The provision of environmental water to create breeding opportunities has stabilized the species to some degree, and a recent review has recommended downgrading their threat category to *Vulnerable* (Gillespie et al., 2020).

There are empirical estimates for most *L. raniformis* vital rates (reproduction, developmental rate, survival, and recruitment). These frogs breed in temporary wetlands during spring or early summer. Eggs hatch two to four days after laying (Anstis, 2018), with the likelihood of hatch (a proxy for egg survival rate) between 0.933 and 1. We used the larval duration of 70–80 days calculated at a constant water temperature of 23°C (Cree, 1984), which is a close approximation of average daily temperature for this reach during larval periods. We used estimates of larval survival for *Crinia signifera* (15%–26% and 7%–56%) (Williamson & Bull, 1999) that were derived from field research in a similar climate making them the most suitable estimates available. Both sexes reach maturity in their first year (Heard et al., 2012b) and females breed annually (Anstis, 2018), laying between 1885 and 4563 eggs each season (mean = 3237, SD = 891) (Germano & White, 2008; Humphries, 1979). We used annual adult survival probability from the closely related *Litoria aurea* (mean = 0.2172, SD = 0.087) (Pickett et al., 2016). These species are similar in size, appearance, and behavior, although *L. aurea* occurs along a more northerly latitude than *L. raniformis*.

Using lines of arrested growth in the shaft of the medial phalanx to determine age (skeletonochronology), *L. raniformis* can survive into their fifth year (G. Heard and A. Turner, personal communication; Mann et al., 2010). In an R programming environment

(R version 4.2.2: “Innocent and Trusting,” R Core Team, 2022), we constructed a population model using an age-classified (Leslie) matrix (Leslie, 1945) (Appendix S1: Figure S1) to model the female population with forced senescence following breeding in the sixth year. We stochastically resampled all parameters in the model from their observed distribution for each calculation. We calibrated population growth at each wetland using three compensatory density-feedback relationships (Berven, 2009; Harper & Semlitsch, 2007; Holling, 1959). For more detailed demographic calculations, see Appendix S1: Figure S2 and Mathwin et al. (2023a). We modeled over a forecast horizon of 60 years that we selected to represent no fewer than 25 generations.

Modeling hydrology

We used historical river height measurements immediately downstream of Lock 3 (A4260517) (Figure 1) to generate flow scenarios. We first collated the mean daily river height data (meters with respect to Australian height datum, mAHD) from 1926 until 2009, which we supplemented with data from A4260528 (6.5 km downstream of Lock 3) during periods of high flow (i.e., when A4260517 became inoperable).

From this, we compiled river-height time series for 83 winters and springs. For each season, we classified the mean daily river heights into 10-cm increments and used the daily transitions between height increments to calculate modified Markov chains for each season. This created the daily probability of increase, decrease, and no change for each of the 10-cm river-height increments, for each winter and spring. Similarly, we calculated an extent of change observed for each increase or decrease at each height increment, for each winter and spring.

To simulate hydrological scenarios, we randomized a starting river height from the observed, right-skewed distribution of river heights on the first day of winter, and then incremented it through 92 consecutive days of winter and 91 days of spring using the modified Markov chains. We repeated this process for each simulated year ($n = 60$). To order each year within the iteration (to incorporate intra-annual and supra-seasonal climate trends), we used the mean seasonal river heights observed during winter and spring for the 83 historical years to generate a second modified Markov chain as described above. We then generated a time series of 60 mean seasonal river heights and reordered the 60 simulated years of flow to match the relative sum of the simulated seasonal river heights (for more detail, see Appendix S2). We repeated this process 10,000 times.

Based on the hydrological behavior of wetlands in the reach, we used the rule that if the mean daily river height was ≥ 10 cm above the wetland's sill height for ≥ 10 days during winter and spring, then it had filled sufficiently to support frog recruitment that year (K. Mason, personal communication). It was not necessary that these 10 days be consecutive to fulfill this criterion.

We used the 10th highest daily river height observed during each simulated year to determine which wetlands filled (and supported breeding), and we used the sum of river heights during winter and spring to determine whether each wetland dried between successive wetting events (determined by the wetland's drying threshold). When a wetland retained water between two successive breeding events, the subsequent breeding event incurred a penalty to tadpole numbers (divided by 600) to incorporate the observed effects of accumulating aquatic predators (e.g., fish, insects, crustaceans) (Hoffmann, 2018).

Modeling dispersal

We measured the shortest-possible dispersal distance between each pairwise combination of wetlands using two caveats: (1) we allowed only a single overland movement of ≤ 700 m; otherwise, dispersal follows wetted channels; and (2) where dispersal crossed the main river channel, this occurred only once and was perpendicular to the bank. To incorporate the effects of channel flow on landscape resistance (facilitating downstream or inhibiting upstream dispersal), we modified these distances by a factor of 1.25 (upstream and along the bank), 1.5 (upstream and crossing the river), 0.5 (downstream and along the bank), or 0.75 (downstream and crossing the river). We used expert opinion to assign these values that we calibrated to generate the expected response.

To calculate wetland dispersal probability, we used a compensatory density-feedback function of the form:

$$E = 1 - F = D \left(\frac{n_t}{K} \right)^2 \quad (1)$$

where E is the probability of emigration (F = probability of site fidelity), n_t is the total number of adults present at the wetland, and K is the adult carrying capacity. We set D to 0.16, the mean rate of experimentally observed frog-dispersal rates, and constrained E between 0.02 and 0.3, which is the range of experimentally observed dispersal rates for frogs (Cayuela et al., 2020). We divided emigrants among adult age classes using the proportion of that age class and assigned additional members to the youngest available age class. We calculated dispersal distances (step size) using a Lévy-walk model

(Shlesinger et al., 1993; Appendix S1: Figure S3). Rather than the random walk typical of the Lévy model, we assigned the destination as the wetland closest to the calculated step size. When multiple wetlands shared the same distance, we randomly selected from among those wetlands. When step size was sufficient to allow emigration from the study reach, we calculated a proportional probability of departure. We assumed balanced emigration and immigration, and so each emigrant from the reach was replaced by a new individual with a randomly assigned age class that entered the reach from the nearest upstream or downstream site following the above movement rules. We assigned a 0.5 probability of surviving dispersal (in addition to annual survival probability).

Modeled scenarios

For each iteration, we assigned the 23 wetlands a starting population of adult females that was 50% of the average adult population for that wetland size (*L. raniformis* has a 50:50 sex ratio), divided across five age classes. We assigned the 0–1 age class using an *a priori* number of spawning masses determined by wetland size ($n = 30, 85, \text{ or } 150$) and stochastically resampled the number of eggs in each spawning mass (halved to model females only). This created a homogenous initial age structure that we managed by running the model for 25 years to generate stochastic expressions of stable-age distributions. We then exposed the 10,000 starting metapopulations to 23 years of historical drought conditions from 1990 to 2012. This period of severe drought reduced the size and distribution of *L. raniformis* populations across their range and continues to shape species dynamics in this reach. We then exposed the post-drought populations to 15 years of simulated hydrology and the resultant terminal population structures formed our 10,000 starting metapopulations.

We simulated two sets of 10,000 replicate hydrological scenarios. The first treatment used historical river conditions to simulate 60 consecutive years (described above). The second treatment reused this hydrology but replaced the 30th–53rd years with 23 years of historical drought conditions (from 1990 to 2012). We did this to examine the effects of environmental watering through a severe drought. We used the 10,000 starting metapopulations to populate each of the two hydrological scenarios that were repeated for each of the five intervention programs: (1) control (no intervention), (2) environmental-watering sites were spread across the 23 available wetlands (wetlands 4, 8, 13, and 21) and received water independent of river height and at high frequency that ensured no more than one dry year occurred every three years,

(3) environmental watering was spatially spread across the reach and delivered at moderate frequency to ensure that no more than three dry years occurred in every five years, (4) environmental-watering sites were grouped more tightly within the 23 available wetlands (wetlands 11, 13, 14, and 16 received water) and were watered at high frequency, and (5) environmental-watering sites were grouped together and watering occurred at moderate frequency (Figure 2). The two spatial intervention programs were case-controlled for the size and sill height of intervention wetlands to ensure that the frequency and water volumes deployed were comparable between programs (Figure 3). We estimated the probability of

persistence at each of the 23 wetlands in the reach for each program.

Global sensitivity analysis

To quantify the relative influence of model parameters on the reach-wide probability of survival, we constructed a global sensitivity analysis (Prowse et al., 2016). We applied Latin-hypercube resampling to generate 5000 parameter sets from a 16-dimension parameter space using the lhs library in R (Carnell, 2022). We expanded each parameter of interest beyond the range used in the

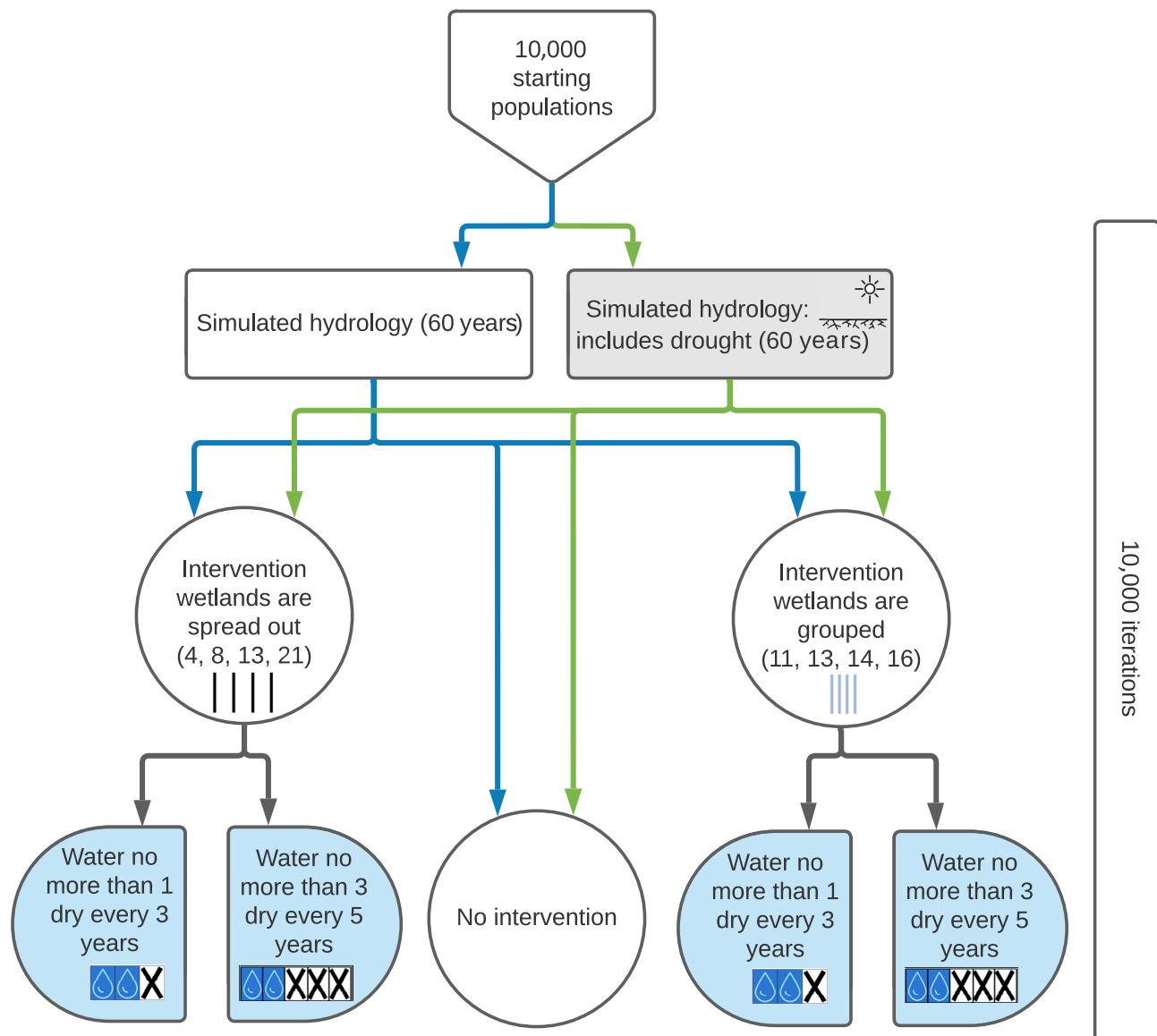


FIGURE 2 The modeling approach combines two hydrological scenarios (simulated with/without severe drought) with two spatial intervention strategies: *spreading* or *grouping* intervention sites, and two intervention frequencies: *high* (to ensure \leq one dry year every three years) or *moderate* (to ensure \leq three dry years every five years). We also modeled both hydrological scenarios with a control scenario (where no intervention took place).

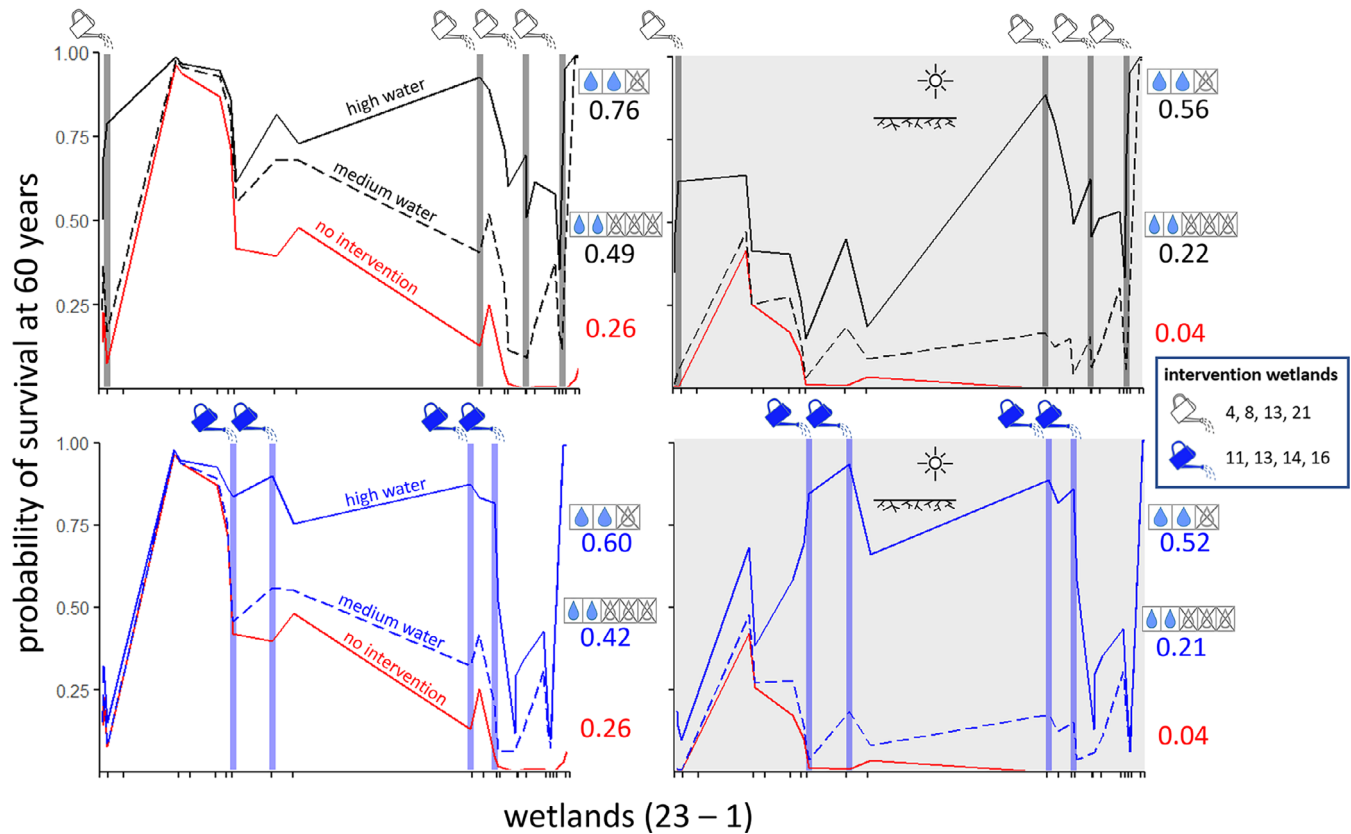


FIGURE 3 Probability of survival at each of the 23 wetlands in the reach under five different environmental-watering programs. The x-axis represents the lineal distance along the river channel at which the 23 wetlands (tick marks) occur. Black lines represent the spatially spread watering programs, blue lines represent the grouped programs, and red lines are the control (no intervention). Solid lines are the high watering programs that ensure \leq one dry year every three years, and the long-dash lines are the medium watering programs that ensure no more than three dry years in every five years. Plots with a gray background display the same scenarios but include a severe drought from the 30th to the 53rd modeled years.

model to create the following broad but plausible parameter ranges (Prowse et al., 2016): (1) clutch size (1500–6000), (2) duration of egg phase (0.5–5 days), (3) hatch probability (0.5–0.98), (4) duration of tadpole phase (50–90 days), (5) mean tadpole survival (0.03–0.6), (6) mean annual adult survival (0.03–0.35), (7) tadpole carrying capacity (the population of this life stage where density feedback on survival probability is initiated) at a *medium* wetland (150–750 females), (8) adult carrying capacity at a *medium* wetland (100–700 females), (9) tadpole carrying capacity at a *large* wetland (400–1500 females), (10) adult carrying capacity at a *large* wetland (300–1250 females), (11) tadpole carrying capacity at a *very large* wetland (500–3000 females), (12) adult carrying capacity at a *very large* wetland (500–2000 females), (13) probability of surviving dispersal (0.1–0.6), (14) base probability of dispersing (0.1–0.6), (15) maximum possible dispersal distance used in the Lévy-walk calculations (10–50 km), and tadpole reduction factor at sites that remain wet (100–600). Each parameter set ran for 50 iterations using the first 50 sets of simulated hydrology

(60 years). We then applied a boosted regression tree emulator implemented using the *dismo* library in R (Hijmans et al., 2021) to quantify the influence of each parameter on the sum of surviving wetlands, setting the error distribution family as Poisson, the bag fraction to 0.75, learning rate to 0.001, tolerance to 0.0001, and tree complexity to 2, with 200,000 maximum trees.

RESULTS

The mean generation time of *L. raniformis* in the model was 2.1 years, and each 60-year iteration spanned approximately 28.5 generations. The greatest improvement in reach-wide probability of persistence occurred when intervention sites were spread (intervention at wetlands 4, 8, 13, and 21) and watering intervention frequency was high (\leq one dry year in every three years) (Figure 3). This combination resulted in an average probability of persistence per wetland = 0.76 compared to the control scenario (no intervention) that gave a persistence

probability = 0.26. The high-frequency water programs produced higher persistence than the moderate-frequency water programs in both spatial scenarios. Moderate watering resulted in an average probability of persistence per wetland <0.5 in both spatial scenarios. Spreading the four intervention sites increased the probability of persistence (high frequency: 0.76; moderate frequency: 0.49) relative to grouping sites more closely (high frequency: 0.6; moderate frequency: 0.42).

When the reach was exposed to severe historical drought conditions, the average probability of persistence per wetland without intervention was 0.04, and the highest probability of persistence at any individual wetland was <0.5. Under drought conditions, spatially spread programs produced comparable persistence probabilities to spatially grouped programs (high frequency: 0.56 vs. 0.52; moderate frequency: 0.22 vs. 0.21).

All intervention programs improved the minimum adult population size compared to the control scenario (Figure 4). The spatial distribution of intervention sites had a negligible impact on minimum adult population size. High-frequency watering increased the minimum adult population size minimum by approximately the same amount in both simulated and drought scenarios. Moderate watering frequency produced comparable improvements to high watering frequency in the simulated hydrology scenario, but these improvements were reduced in the drought scenarios.

The only program that produced a mean increase in site occupancy (where recolonizations exceed local extinctions) was when intervention sites were spread and watering frequency was high (Figure 5). Spreading intervention sites and moderate watering frequency resulted in stable mean site occupancy. High watering frequency improved site occupancy following the cessation of severe drought for both spread and grouped spatial scenarios. Moderate watering produced negative trends in site occupancy under both hydrological scenarios and colonization rates did not increase in the seven years following cessation of drought conditions.

The boosted regression tree showed that the most influential parameters in the model were mean adult survival (relative influence = 40.21%) and mean tadpole survival (relative influence = 36.9%). All other parameters had a relative influence score of <5% (Figure 6). These parameter ranges explained 91.74% ($\pm 0.35\%$) of the observed variance in the sum of surviving wetlands.

DISCUSSION

The targeted provision of environmental water has successfully supported amphibians in habitats impacted by

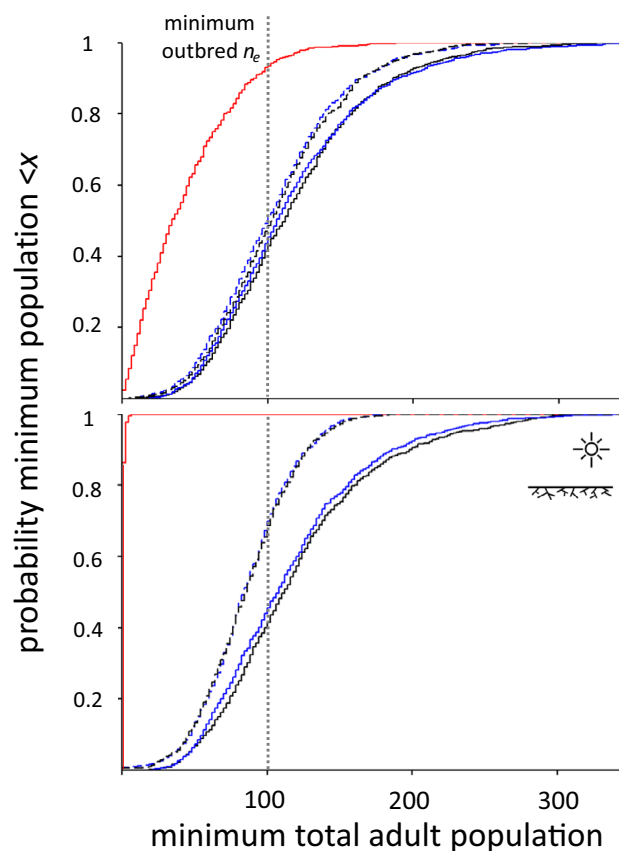


FIGURE 4 The cumulative probability density of minimum population size showed minimal variation with the spatial distribution of intervention sites (black lines represent the spatially spread programs, and blue lines represent the spatially grouped programs). It was influenced more strongly by watering frequency (solid lines represent high watering programs and dashed lines represent moderate watering programs). The red line is the control scenario and the plot with a gray background presents the hydrological scenarios that include a severe drought from the 30th to the 53rd years.

high rates of water extraction and flow modification (Mathwin et al., 2020). Environmental water delivery can trigger amphibian breeding and can maintain inundation until metamorphosis is complete, thus supporting recruitment where catastrophic breeding failure would have otherwise occurred. Targeted delivery can be achieved through irrigation infrastructure including pumps (McCaffery & Phillips, 2015) or flow-regulating structures (Darcovich & O'Meara, 2008), meaning that wetland habitats can be created and maintained even under dry conditions.

The temporal and spatial patterns of environmental water delivery are important considerations for achieving ecological targets. Our high-frequency watering programs had a higher relative likelihood of improving persistence probability than the moderate-frequency programs

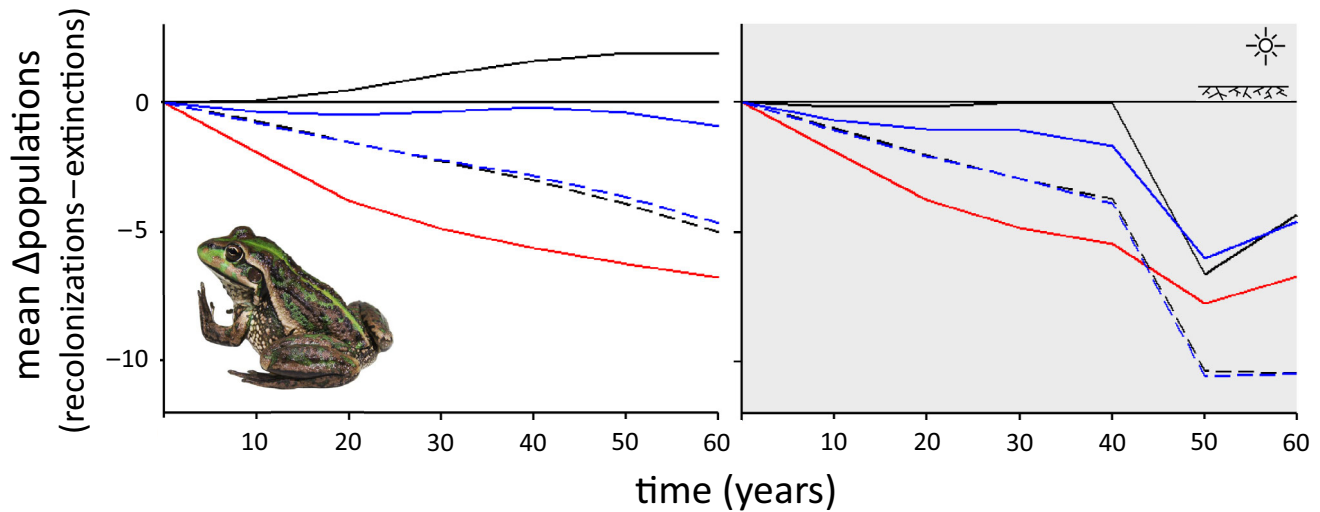


FIGURE 5 Average change in the number of occupied sites over the 60 modeled years (the balance of local extinction and recolonization). Black lines represent the spatially spread programs, and blue lines represent the spatially grouped programs, high watering frequency programs are represented by solid lines, and moderate watering frequency programs are presented as dashed lines. The red lines represent the control scenario and the plot with the gray background are the hydrological scenarios that include a severe drought from the 30th to the 53rd years.

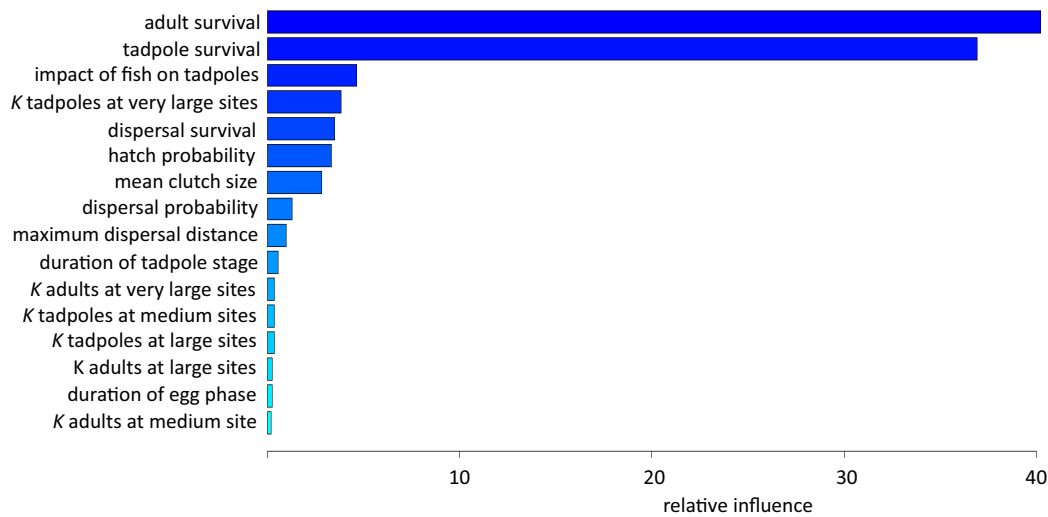


FIGURE 6 The relative influence scores of the 16 parameters selected for global sensitivity analysis derived from Latin-hypercube resampling and cross validated using a boosted regression tree procedure.

(Figure 3). This arises because increasing the frequency of breeding events increases the rate of population growth, thereby reducing the probability of extinction (Loison et al., 2001). More frequent breeding also creates a more complex age structure in long-lived species, and probably increases the local population size and number of emigrants. Increased watering frequency also increases the proportion of inundated sites, thereby increasing the

likelihood that emigrants will arrive at a site that supports breeding (rather than arriving at a dry site and surviving until inundation and breeding opportunities return).

More frequent breeding improves recruitment, but predicting outcomes is complicated when sites remain wet between successive breeding events. Protracted wetting supports the survival and accumulation of aquatic

predators (fish and invertebrates) that can inhibit amphibian recruitment (Julian et al., 2006; Pilliod & Peterson, 2001). In this reach, wetlands that retain water from the previous breeding season produce 2–3 orders of magnitude fewer tadpoles than wetlands that dried between seasons (Hoffmann, 2018). To incorporate this aspect, we set a reduction factor of 600 (that we calibrated to produce the reported population response) and applied this to *L. raniformis* tadpole abundance at sites that remained wet between breeding events. We acknowledge that predator-accumulation relationships are more complex than we have expressed here, that *L. raniformis* is adapted to breed in floodplain wetland systems that support native predators, and that complete drying could remove hydric refugia that might be essential for the persistence of amphibians during nonbreeding years. Regardless, the strong negative feedback we implemented was insufficient to outweigh the benefits of additional breeding opportunities.

The spatial configuration of intervention sites also influenced the success of environmental-watering outcomes. Both spread and grouped programs improved the persistence probability at intervention sites, and also throughout the reach (Figure 3). The largest improvements occurred when sites were spread across the reach, producing a positive ratio of recolonization to local extinctions and a higher frequency of subpopulation rescue (Figure 5). The dispersal parameters (dispersal probability and distance) we used were derived from a global review of frog-dispersal studies and are somewhat generalizable (Appendix S1: Figure S3; Cayuela et al., 2020). We expect dispersal to vary strongly in modified environments due to higher landscape resistance. This is demonstrated in some farmlands used for cropping (Goldberg & Waits, 2010; Ray et al., 2002), and can be especially strong in urban environments (Van Buskirk, 2012). For example, a busy two-lane road in Denmark added mortality of 0.34–0.61 during dispersal for six species of amphibians, which increased to 0.89–0.98 when crossing a multilane motorway (Hels & Buchwald, 2001).

In urban environments, *L. raniformis* has high patch turnover (Hamer et al., 2016; Heard et al., 2012a) and dispersal distances are shorter than those we applied in our model—a maximum of 1–2 km (Heard, 2010) and most <200 m (Heard et al., 2012a). However, in regional landscapes, tracked animals can move up to 212 m in a single night (Wassens et al., 2008) and have been found several hundred meters from the nearest water during pitfall trapping (Herbert, 2000) and 5 km from the nearest water during terrestrial surveys (D. Parker, personal communication). A recolonization was recorded at a wetland that was 500 m from the nearest waterbody following pumped delivery of environmental water (Department for

Environment and Heritage, 2004), and recolonization has occurred 5 km from the nearest source population during flood conditions (Wassens et al., 2020). Floods facilitate broad-scale dispersal by creating contiguous pathways that are often viable for several months (Bino et al., 2018). Wetted corridors as the basis of interpatch dispersal are realistic in this example due to the aridity of the landscape matrix (Goldberg & Waits, 2010; Mims et al., 2015).

Model assumptions

Uncritical use of metapopulation structure to estimate persistence probability for amphibians is potentially problematic given the assumptions of patch connectivity (Marsh & Trenham, 2001; Smith & Green, 2005). However, *L. raniformis* in this system meets the four characteristics of a metapopulation (Hanski et al., 1995): (1) habitat patches (wetlands) support local breeding populations, (2) no single population is large enough to ensure long-term survival, (3) patches are not too isolated to prevent recolonization, and (4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely (Figure 3). There are no mark–recapture or genetic studies that explicitly address site fidelity in this catchment. We contend that movement between breeding wetlands and seasonal foraging areas might be common in the study area but that dispersal between wetlands is comparatively infrequent and suggests that classical metapopulation theory is applicable (Heard et al., 2012a).

We sampled dispersal metrics stochastically as a function of local population size. Our model did not incorporate context-dependent dispersal that might increase dispersal probability with wetness (Lobos & Jaksic, 2005) or pond drying (Fellers & Kleeman, 2007), nor did we incorporate asymmetrical dispersal probabilities to/from source/sink populations. We were also unable to account for biotic and abiotic differences in patch quality that could influence local carrying capacity—for example, variability in wetland vegetation that could affect recruitment (Wassens et al., 2010), or antecedent wetting patterns that influence trophic dynamics (e.g., availability of prey items). Regardless, our results are largely insensitive to variation in the biology and ecology of *L. raniformis* (Figure 6) and are driven predominantly by the availability of breeding habitats and the annual probability of survival. Additional research to quantify the above relationships could inform more ecologically realistic models, but more accurate parameter estimates are unlikely to alter our general conclusions. To improve opportunities for predictive modeling, we encourage

prioritized research into the ecological drivers of survival probability in *L. raniformis*.

Conserving amphibians in flow-regulated river systems

River regulation drives the homogenization of fluvial dynamics and alters the function of riverine ecosystems (Poff et al., 2007), including a reduction in the frequency and extent of flooding events and in the active area of floodplains (Nilsson & Berggren, 2000). For species that rely on floodplain inundation to breed, such habitat modifications can threaten the long-term persistence of the species (Mathwin et al., 2023a). In situations where regulation, extraction, or climate change substantially reduce habitat suitability, effective management of amphibian populations could require the creation of inundation and breeding events beyond the status quo. Environmental water provision is a promising conservation technique when baseline hydrology does not meet the requirements of the target species. We found that environmental-watering programs that increased the frequency of local breeding events also improved the probability of persistence beyond intervention sites. We also found that the spatial organization of intervention sites altered the relative likelihood of successful conservation. Spatially explicit hydroecological models incorporating stochastic expressions of the main parameters are therefore useful tools to compare the relative value of competing conservation programs. By comparing watering scenarios, we could select which conservation program had the highest relative likelihood of achieving the greatest improvement in the probability of persistence of southern bell frogs. Effective techniques for comparison are essential to develop conservation programs that maximize returns on the investment of limited resources. Although we modeled a lacustrine amphibian, this approach is potentially useful wherever environmental water delivery targets a single species. It can also be more broadly applied to any species where vital rates and spatial dynamics are measured and where conservation interventions are anticipated to alter recruitment.

AUTHOR CONTRIBUTIONS

Rupert Mathwin and Matthew S. Gibbs completed the hydrological modeling. Rupert Mathwin and Corey J. A. Bradshaw designed and constructed the population models. All authors contributed to the manuscript and provided editorial advice.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.


DATA AVAILABILITY STATEMENT

The source code and data (Mathwin et al., 2023b) are available from Zenodo: <https://doi.org/10.5281/zenodo.8374892>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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