



Simulating the response of a threatened amphibian to climate-induced reductions in breeding habitat

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Abstract

Context Amphibians are declining worldwide due to disease, invasive species, and habitat loss. Climate change may exacerbate habitat loss by altering the availability or suitability of aquatic breeding habitat through changes in precipitation, temperature, and the biophysical factors they influence. Measuring biological vital rates and the environmental covariates that affect them are crucial to understanding amphibian responses to a changing climate. However, doing so can be difficult due to access constraints, funding limitations, and difficulty of measuring spatially structured populations at landscape scales. Simulation-based approaches may provide reliable approximations of amphibian responses to changing environmental conditions.

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Objectives In this study, we constructed a spatially explicit individual based model to simulate the response of the Arizona treefrog (*Hyla wrightorum*), a species of conservation concern, to reductions in breeding habitat availability. The Arizona treefrog metapopulation in the Huachuca Mountains and Canelo Hills of Arizona is known to breed at fewer than 20 breeding ponds that may become unsuitable due to climate change-induced shifts in hydroperiod, increased rates of invasion by non-native predators, or filling by sedimentation.

Methods We simulated Arizona treefrog response to bioclimatically realistic scenarios that included reduced breeding habitat availability, failed recruitment, and a combination of both. Simulations included variable landscape configuration through space and time that were informed by an empirical hydroperiod dataset.

Results We found that climate-driven reductions in breeding habitat alone resulted in mean population declines of nearly 65%, even when reductions targeted the ponds least likely to fill with water. However, scenarios with concurrent breeding habitat loss and recruitment failure or very high recruitment failure resulted in 79% and 83% population declines, respectively. Reduced breeding habitat also increased spatial synchrony of occupancy through time and among simulations, pointing to a potential transition from a metapopulation to multiple isolated populations.

Conclusions In the face of anthropogenically driven climate change and continually emerging

management challenges, individual-based models provide a useful, mechanistic tool to explore how a combination of biological and environmental factors may interact to influence the future of species of conservation concern. We found evidence of a potential transition to isolated populations that may lead to limited functional connectivity and an increased risk of regional extinction for this species of conservation concern. Sensitivity analyses suggest our model was robust to uncertainty in model parameters and point to the critical role of dispersal in maintaining demographic and landscape connectivity among spatiotemporally heterogeneous habitat. A spatially explicit approach also enabled identification of specific habitat patches that may be less sensitive to climate change as well as those that may require more intensive management to conserve key populations or preserve metapopulation dynamics.

Keywords Dryland ecology · Hydroperiod · Climate change · American Southwest · Spatially explicit individual-based models · HexSim

Introduction

Ongoing global declines and extinctions of amphibians worldwide are well-documented (Stuart et al. 2004; Grant et al. 2016). Habitat loss, invasive species, and disease are among the primary threats to many amphibians (Sodhi et al. 2008; Grant et al. 2020), and climate change is exacerbating many of these stressors (e.g. disease Pounds et al. 2006; Cohen et al. 2019). For decades, the importance of metapopulation dynamics in amphibian conservation has been recognized (Marsh and Trenham 2001), with specific calls to study and understand the mechanisms that contribute to and drive metapopulation dynamics to inform more effective conservation strategies for managers who must consider both maintenance of regional connectivity and local habitat quality (Smith & Green 2005; Moss et al. 2021). Landscape fragmentation and loss of habitat due to environmental and climate change present interacting threats to biodiversity (Mantyka-Pringle et al. 2012). Both fragmentation and habitat loss can lead to a decline in metapopulation dynamics, giving way to isolated populations and reducing diversity and connectivity that may buffer species from environmental

variability or disturbance that act heterogeneously in space and time (Schindler et al. 2010). As the need for understanding drivers and consequences of metapopulation dynamics in amphibians grows (Smith & Green 2005; Scroggie et al. 2019), empirically driven modeling and simulation approaches have emerged as an important tool in incorporating key factors such as dispersal, behavior, vital rates, and spatially explicit environmental attributes to inform management of at-risk amphibians (e.g., Brooks et al. 2019; Bertassello et al. 2022).

In the arid southwestern United States, much of the historical aquatic breeding habitats used by the region's amphibians have been heavily modified to meet a range of human water requirements (Mims et al. 2020). Continued urban and agricultural development in the region have resulted in escalating water needs, with demand projected to exceed supply in many regions (Marshall et al. 2010; Elias et al. 2016). In addition, climate change is poised to further reduce habitat for many aquatic species in the region (Jaeger et al. 2014; Zylstra et al. 2019), particularly via projected declines in surface water availability (Seager et al. 2013; Miller et al. 2021).

Many amphibians worldwide now rely on artificial habitats to complete key portions of their lifecycles (Valdez et al. 2021). In the southwestern United States, ponds built to retain stormwater runoff and reservoirs built to support livestock are a dominant form of aquatic habitat throughout the region. These "stock tanks" (hereafter referred to as stock ponds) are increasingly recognized as important surrogate habitat for the region's native aquatic fauna (Rosen & Schwalbe 1998; Hale et al. 2015). For example, in the Huachuca Mountains and San Rafael Valley of southeastern Arizona, the endangered Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*) now breeds almost exclusively in stock ponds throughout its small range (Storfer et al. 2014; Hossack et al. 2021), and stock ponds are important breeding habitat for the threatened Chiricahua leopard frog (*Rana chiricahuensis*; Rosen & Schwalbe 1998). Stock ponds span a range of hydroperiods (length of time the ponds hold water) from perennial to intermittently wetted, thus representing critical, yet dynamically available, amphibian habitat.

Appropriate stock pond management will likely be critical to the persistence of many of the region's amphibians (Mims et al. 2020), including the Arizona

treefrog (*Hyla wrightorum*) in the Huachuca Mountains and Canelo Hills (HMCH) region of southeastern Arizona. Yet, management of stock ponds can be complex and involves consideration of livestock husbandry practices, game species management, protection for native aquatic species, and control of invasive species (Hale et al. 2015; Drake et al. 2017a). Furthermore, projected changes in land use, precipitation, temperature, and surface-water availability (Seager et al. 2012; Miller et al. 2021) may alter both the number of wetted ponds and their hydroperiods in the future (Drake et al. 2017b). The frequency and intensity of wildfires in the region are also anticipated to increase with climate change (Westerling et al. 2006; Dennison et al. 2014; Holden et al. 2018), and monsoon rains that follow fire season can produce intense floods and erosion in recently burned areas. Floods result in scouring and sedimentation events that may severely alter or destroy aquatic habitat and may fill artificial ponds with sediment (Hossack & Pillod 2011).

Arizona treefrogs are one of only a few pond-breeding amphibians in the HMCH region, and though their specific roles in pond communities and ecosystems have yet to be determined, they are likely key drivers of nutrient cycling and community composition and may serve as an important prey item for other aquatic and terrestrial species in the region (Hocking & Babbitt 2014). Arizona treefrog populations within the HMCH region were considered a candidate for federal protection under the Endangered Species Act (U.S. Fish and Wildlife Service 2013) but have not received protection for distinct populations (USFWS 50 CFR Part 17 2016). However, Arizona treefrog populations in the HMCH region are listed as “highest priority” among the state of Arizona’s Species of Greatest Conservation Need (Arizona Game and Fish Department 2012). The geographic range occupied by the Arizona treefrog in the HMCH region is small compared to the larger two portions of its distribution, with known breeding sites occurring within an area no larger than 85 km². Effective population size estimates range from hundreds to many thousands, and population genetic structure suggests significantly differentiated populations that likely exist within a metapopulation (Mims et al. 2016). Potential threats to local persistence of this species include disease (Bradley et al. 2002), loss and degradation of breeding habitat (Mims et al. 2020), and

predation by invasive American bullfrogs (*Lithobates catesbeianus*, Jones & Timmons 2010).

In the HMCH region, Arizona treefrogs breed primarily in intermittent aquatic habitat (i.e., dry for at least some part of the year), where inundation often does not occur every year. The number of verified breeding sites is currently less than 20 (USFWS 50 CFR Part 17 2016; Mims et al. 2016), and all are sites considered human modified environments (stock ponds and one wetland resulting from a road crossing of a stream). Due to extensive ranching practices in the region, many of the once naturally occurring wetland areas have been converted to stock ponds. Although Arizona treefrogs are occasionally observed in perennial streams or their wetlands, which likely serve as important dispersal corridors (Mims et al. 2016; Parsley et al. 2020), there are no records of treefrog breeding at those sites to-date. A reliance on lentic, intermittently wetted breeding habitat is in contrast to other amphibians in the region, such as canyon treefrogs (*Hyla arenicolor*) and red-spotted toads (*Anaxyrus punctatus*), which often breed in intermittent streams and rock pools in the region (Mims et al. 2015). Reduced precipitation, sedimentation of ponds, or increased evaporation rates due to higher temperatures may eliminate breeding habitat or reduce hydroperiods such that Arizona treefrog larvae are not afforded sufficient time to metamorphose, resulting in failed recruitment. Whether and how Arizona treefrogs respond to and survive reductions in available breeding habitat due to climate and landscape change remains unclear. Modelling approaches that allow for spatially-explicit simulations of future responses of the species to landscape change may help identify specific areas for conservation as well as provide an understanding of potential responses that integrate behavior, life history, and demographics (DeAngelis & Mooij 2005).

This study used spatially explicit, individual-based simulations to evaluate the response of the Arizona treefrog to different scenarios of climate-induced breeding habitat reduction throughout its range in the Huachuca Mountains. Individual-based models provide an opportunity to test empirically derived, hypothesized demographic responses to environmental change through simulation of individual organisms on a landscape and allowing for the incorporation of behavior, life history, and vital rates. Model simulations are also particularly useful in cases where

experimental or observational approaches in the field would present logistical and practical challenges. Climate change is projected to further decrease surface water availability in the southwestern United States (Seager et al. 2013; Miller et al. 2021), but the consequences of climate change for specific breeding sites are difficult to model, with projections not yet available at a temporal and spatial scale that capture the complexity and heterogeneity characteristic of and important to ponds and the organisms that rely upon them (Gendreau et al. 2021). For that reason, we used an empirical dataset of historical hydroperiods reflecting observed dynamics in wet and dry years, and we tested a range of possible reductions in breeding habitat to account for the uncertainty in hydrological responses (Wenger et al. 2013) while also capturing projections of generally drier conditions. First, we hypothesized that population numbers and breeding patch occupancy would decline as breeding habitat was lost directly or effectively through failed recruitment events, even in scenarios with only the loss of ponds that rarely fill with water. Second, we hypothesize a loss of metapopulation dynamics due to reduced connectivity among breeding sites, leading to spatial synchrony among simulations and a loss of variability in patch occupancy and population size through time and across replicate simulations. To test these hypotheses, we created a spatially explicit individual based population model for the Arizona treefrog in the Huachuca Mountains of southeastern Arizona. We examined Arizona treefrog responses to a range of scenarios of breeding habitat loss, and we also evaluated the performance of the simulation through sensitivity analyses manipulating key biological and environmental parameters.

Methods

To simulate the response of the Arizona treefrog to changes in breeding habitat availability, we constructed an individual-based simulation and population model using the software HexSim (Version 3.2.2; Schumaker 2015). HexSim is a spatial modeling platform that models individual organisms, their life cycles, and their interactions with each other and the environment. HexSim allows the user to define demographic parameters, annual time steps composed of event sequences, regular censuses, and temporally

variable spatial data (Schumaker & Brookes 2018). A defining feature is the use of hexagon-based grids to model spatial inputs. This allows for the representation of landscape variables as hexagons that define landscape structure and quality, enabling any number of individuals with associated life history traits to be spatiotemporally tracked through annual time series event sequences (Schumaker & Brookes 2018). HexSim has been used to address a range of ecological and management questions, including predicting futures for reintroduced species (Andersen et al. 2021), evaluating the influence of landscape fragmentation (e.g., roadways) on wildlife populations (Barbosa et al. 2019), and evaluating source-sink dynamics of populations under a range of management and land-use scenarios (Heinrichs et al. 2018). Our model was informed by empirical spatial and ecological information for Arizona treefrogs in the Huachuca Mountains of Southeastern Arizona (details to follow), allowing for spatially explicit ecological and management inferences such as identifying resilient or at-risk breeding sites that may require mitigation strategies under future climate change scenarios. Analytical code is available via a public GitHub Repository: https://github.com/MimsLabVT/HYWR_HexSim_Mimsetal

Spatially explicit individual-based model scenarios

We created a model event sequence (Fig. A1) that describes an annual cycle describes an annual cycle (Marra et al. 2015) for Arizona tree frogs for Arizona treefrogs in the study area. First, the model was initiated with adult individuals at known historical locations of Arizona treefrog occupancy. Then, the annual sequence begins with all individuals exploring the landscape and is followed by an orientation and movement toward detectable ponds. After movement and range establishment, pond wet-dry status is modeled based on historical hydroperiod data, with likelihood of wetted status informed by historical satellite imagery of ponds that capture over 20 years of hydroperiod dynamics through wet and dry years (Parsley et al. 2020). Individuals at dry ponds attempt to disperse toward wet ponds. Those individuals already located at wet ponds explore local pond habitat. Reproduction initiates following this movement event. Population census is taken before and after reproduction to examine impact of climatic scenarios

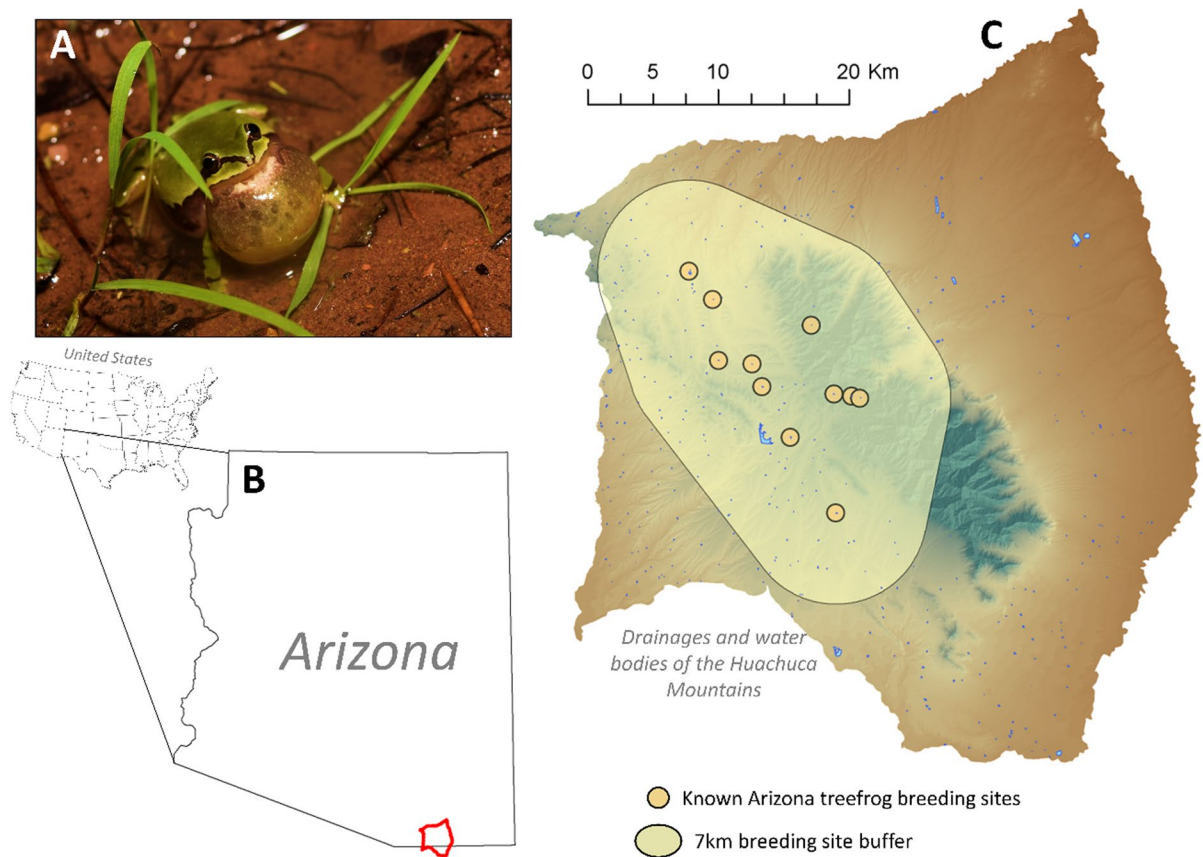


Fig. 1 **A** A vocalizing adult male Arizona treefrog in the Huachuca Mountains. **B** Location of map C in the state of Arizona, United States. **C** Map of the Huachuca Mountains, the extent of their drainages, and the ponds and lakes from the database

created for this project. Arizona treefrog breeding sites are shown by orange circles, and 7-km buffer area is denoted by yellow shaded area

(e.g., number of wetted ponds) on recruitment and population dynamics. After the reproductive event has finished, all individuals in the scenario increase in age, and post-breeding movements are initiated to simulate migration to over-wintering habitat, including nearby upland habitats. After non-breeding/over-wintering habitat ranges are established, a foraging and overwintering season induces mortalities with stage-based survival rates, and a final census is taken before the event cycle repeats.

The demographic, dispersal, and non-breeding habitat, which use parameters described below, are assembled to simulate the behavior and characteristics of the Arizona treefrog (Table A1, Fig. A1). Demographic parameters were paired with 6 breeding habitat map series to simulate population response to different breeding habitat availability scenarios

over 100 generations. All simulations were run with the Baseline map series for 30 generations burn-in to allow populations to reach the Baseline equilibrium, at which point alternative map series were implemented at generation 31 to simulate reduced breeding habitat, reduced recruitment, or both. Each scenario (run for 100 generations) was repeated for 100 iterations using maps of randomized habitat availability informed by hydroperiod (see below), allowing for stochastic variation in population dynamics to emerge in response to system perturbations. Finally, we compared population size, number of occupied ponds, and number of ponds contributing to recruitment for the last 20 generations (81–100) for all six scenarios (100 replicates each) and performed analysis of variance (ANOVA) tests followed by a post hoc test using

Table 1 (A) Breeding habitat reduction scenarios for simulations of Arizona treefrog metapopulation dynamics in the Huachuca Mountains and Canelo Hills of Arizona, USA. (B) Sensitivity analysis parameter themes

A		
Scenario	Breeding habitat reduction	Larval recruitment reduction
Baseline	67 of 91 Ponds	All Available
Dry 1	30%	All Available
Dry 2	60%	All Available
Sink 1	Baseline	30%
Sink 2	Baseline	60%
Dry + Sink	30%	60%
B		
Group	Description	Focal parameter values
A	Baseline	Baseline values; see Appendix S1
B	Survival: low	Average survival (stage-based)
C	Survival: high	Average survival (stage-based)
D	Range size area: low	Non-breeding range size and span
E	Movement: high	Movement means, SD, and upper bounds
F	N and birth rates: high	N births average and upper bounds (stage-based)
G	Group membership: high	Maximum group size at pond hexagons
H	Dispersal pathways	Landscape influence on dispersal

a Tukey's HSD. Statistical analyses were conducted in R Version 4.1.1 (2021).

Study area and spatial data

Breeding habitat

We used a spatial database of ponds and lakes within the Huachuca Mountain Range, Canelo Hills, and their drainages to build simulated landscapes for our SIBM (pond dataset described in Parsley et al. 2020, Fig. A2). All intermittent ponds (i.e., those observed to dry at least once) were considered candidate ponds for use as breeding habitats in the SIBM for Arizona treefrogs. We defined the study's spatial focal area as all intermittent ponds within a 7-km buffer of all known breeding sites for Arizona treefrogs in the Huachuca Mountains, a distance estimated to be largest between known breeding sites in the range (Mims et al. 2016). All perennial ponds (those always observed with water) and dry basins (those never observed to hold water) were excluded from the candidate set of breeding ponds for the simulation; perennial ponds in the region often contain invasive vertebrates (e.g., American bullfrogs) which can

extirpate Arizona treefrogs locally (Jennings & Hayes 1994; Bradford et al. 2005).

Through analysis of > 20 years of historical imagery, we identified 92 intermittent ponds within the study area. On average, 70% of intermittent ponds per year within the buffer area were filled during the wet season (N=65). We used this to represent our *Baseline* scenario's available breeding habitat (Table 1A, Fig. A3). To simulate breeding habitat loss due to anticipated reductions in surface water availability due to climate change, we created additional pond map series. *Dry 1* represents a 30% reduction in breeding habitat (N=45 ponds available) and *Dry 2* represents a 60% reduction in breeding habitat (N=26 ponds available). We also explored additional scenarios in which ponds were available for breeding, but larval recruitment failure occurs in a subset. *Sink 1* has the same number of ponds capable of attracting individuals as *Baseline* but with only 45 ponds allowing successful reproduction. *Sink 2* also had the same number of ponds available for breeding as *Baseline* but with only 26 allowing successful reproduction. We also tested a cumulative *Dry + Sink* scenario in which 45 ponds were capable of attracting individuals (the same as *Dry 1*) but only 26 ponds allowed successful reproduction (the same as *Sink 2*).

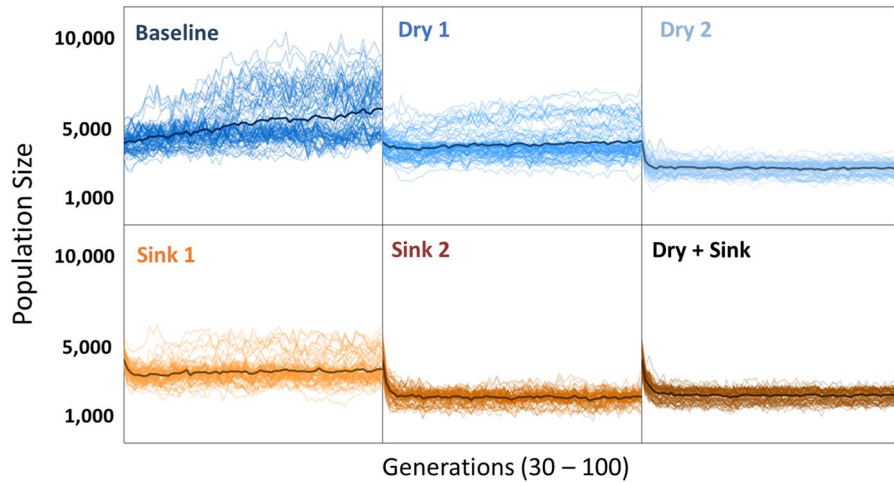


Fig. 2 Simulated population sizes of Arizona treefrogs in the Huachuca Mountains for generations 30–100. Thicker, darker lines in each panel represent the mean population size across 100 iterations of the simulation. *Baseline*: breeding habitat based on historical pond inundation (Parsley et al. 2020). *Dry 1*: breeding habitat reduction by 30%. *Dry 2*: breeding habi-

tat reduced by 60%. *Sink 1*: larval recruitment success in any given year was reduced by 30%. *Sink 2*: larval recruitment success in any given year was reduced by 60%. *Dry + Sink*: 30% reduction in available breeding habitat and a 60% reduction in ponds with successful larval recruitment

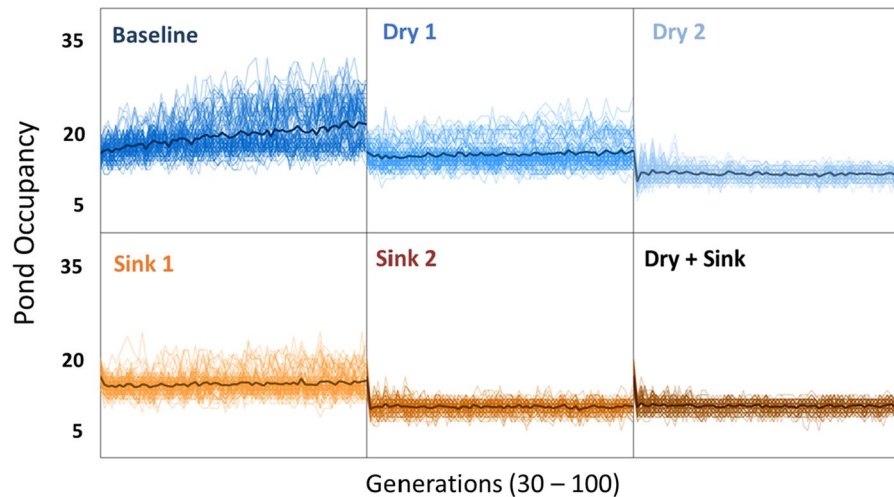


Fig. 3 Number of ponds occupied by Arizona treefrogs for generations 30–100 by scenario. Thicker, darker lines in each panel represent the mean population size across 100 model iterations. *Baseline*: breeding habitat based on historical pond inundation (Parsley et al. 2020). *Dry 1*: breeding habitat reduction by 30%. *Dry 2*: breeding habitat reduced by 60%. *Sink 1*:

larval recruitment success in any given year was reduced by 30%. *Sink 2*: larval recruitment success in any given year was reduced by 60%. *Dry + Sink*: 30% reduction in available breeding habitat and a 60% reduction in ponds with successful larval recruitment

Summer monsoonal precipitation events in the form of sporadic, isolated, and intense thunderstorms are responsible for filling intermittent ponds in the region. Therefore, not all ponds fill every summer. To

simulate this temporal and spatial heterogeneity, we constructed 10 variable pond landscapes informed by historical imagery. These 10 variable pond landscapes were randomly shuffled in 10 sets to feed into

100 replicate runs for each scenario, producing spatial variation in available breeding habitat. The pond database also incorporates “wet” season and “dry” season indices based on the annual percent of ponds containing water to act as breeding habitat. The “wet season” index provides a value for each individual pond was calculated as the % of images from the months of July through November (the primary breeding and larval development season for the Arizona treefrog), across all observed years for which a pond was observed to have water. The “dry season” index (water present from April to June) was also calculated for each pond. The annual percent of ponds wetted during the wet season was used to determine how many ponds should be available. Ponds were then selected using a random draw weighted by the wet season index. Ponds were removed from a series by inverse ranking of their wet season index such that ponds with shorter hydroperiod length and stability were removed. This simulates observed dry year dynamics, and in the absence of site-specific climate change projections, these empirical data provide some insight into habitat availability in future years with reduced precipitation and surface water availability (Seager et al. 2013). These removal rules targeted ponds most likely sensitive to reduced hydroperiods induced by projected shifts in precipitation and temperatures (Karl et al. 2009) and that have been observed as the most likely to dry or remain dry during the ongoing megadrought in the region (Williams et al. 2020). In the case of ties, ponds with lower dry season index values were removed first.

Non-breeding habitat

To simulate non-breeding habitat requirements, we also characterized percent canopy cover (from 0 to 100), which may be important for Arizona treefrogs for shelter (e.g., desiccation avoidance, overwintering, or predation avoidance) and may also provide important food resources for treefrogs (Chapel 1939; Degenhardt 2005). Habitat patches were considered eligible for the overwintering or “non-breeding” range of the Arizona treefrog if canopy cover was 15% or greater, and total canopy in an individual’s non-breeding range summed to at least 30 (2 hexagons with at least 15% canopy cover). We quantified slope using a digital elevation model and scaled from 1 to 100, and hexagons with an average slope $<45^\circ$

were considered suitable for overwintering. Finally, we estimated that movement likely occurs along low slope corridors (Murphy et al. 2010; Mims et al. 2015) and/or along streams (Mims et al. 2016). To simulate these hypothesized corridors, we created a dispersal surface in which low slope (flat land) and riparian areas were given a high “attraction” score to promote the movement of individuals through those areas rather than steep, dry regions. Slope was characterized in the same manner described above, and riparian habitat was constructed using a 100-m buffer around streams as defined in the National Hydrography Dataset (NHD Plus, USGS). The composite raster summed the inverse of slope scaled from 1 to 100 (such that flat land = 100, the highest value) and the riparian habitat data (riparian corridor = 100, non-corridor = 1).

To import all spatial data into HexSim, we used the HexMap Builder to convert bitmap rasters (all 1 m cell size) into a landscape of hexagonal cells, each 30-m in width. Hexagon values were determined using a 120-point sampling scheme where 120 points within each hexagon were “sampled” from each input raster. This enabled proportional value assignment for hexagons that spanned more than one grid cell from the input raster. For the slope, canopy, and dispersal surfaces, the final hexagon value was determined by averaging across all 120 sampling points. To construct HexMaps for breeding ponds, groups of hexagons belonging to a breeding habitat were scored with a sequentially unique identifier (i.e. 1, 2, 3, etc....) corresponding to individual ponds and 0 if no pond was detected.

Demographic parameters

Our primary goal was to examine the effect of changes in breeding pond availability on population persistence and metapopulation dynamics over time. Thus, we attempted to set demographic parameters that allowed for stable populations over time such that differences between scenarios could be attributed to changes in breeding pond availability, the primary factor of interest. We performed sensitivity analyses to determine whether simulations responded in a predictable, proportional way to changes in key demographic parameters and vital rates such as fecundity, mortality, and model carrying capacity. We include short description of parameters by category and

detail all demographic parameters in Table A1 and Fig. A1. We used literature-derived values for all demographic parameters; if parameter values were not available for the Arizona treefrog, we consulted values for congeners or ecologically similar species. We modelled annual population dynamics using discrete generations wherein individuals cycled through a series breeding, growth, dispersal, and survival events (Fig. A1). Each simulation was initiated with 100 adult frogs distributed across known breeding locations. Censuses were taken at different time steps throughout the annual cycle to track movement, reproductive success, and mortality.

Population attributes for breeding events

Individuals were assigned three simple traits: sex (female or male), age (Age Class 0 = larvae, 1 = 1 year old, 2 = 2 years old, 3 = 3+ years old; accumulated once per time step), and group status (group member or transient). One hundred individuals of Age Class 2 and 3 were initiated at Arizona treefrog breeding sites known in 2015 (Fig. 1). Range data were used to control group membership. Groups are collections of individuals within populations that may breed or occupy the same habitat area. We defined the range for inclusion within groups as being at a breeding pond. Only group members, such as individuals in breeding habitat and not in the matrix, were allowed to breed during the reproduction events, and thus breeding habitat requirements were tied to specific locations (i.e., available ponds) on the landscape. Range area and span were set to encompass the largest pond (54,300 m²) in the dataset, and breeding was only allowed in ponds with water present (i.e., wet ponds). Based on observed low abundances of Arizona treefrogs in the Huachuca Mountains (Gergus 1999), group membership was limited to 200 individuals for baseline simulations. We also examined the model with a sensitivity analysis to allow for a maximum group size at pond hexagons of 400 individuals per 30 m hexagon cell (Table 1B).

Reproduction

We modelled reproduction with a female-only model. Average body size for females was derived from snout-to-vent lengths (SVL) for adults sampled in the Huachuca Mountains (M.C. Mims, unpublished

data on file with Arizona Game and Fish Department) and was used to calculate fecundity following relationships between fecundity and body size for Hylidae (Table A1; Wells 2007). Reproductive contributions are likely lower for younger females; thus, we allowed reproduction for 2-year-olds but with half the fecundity of age class 3 (3-year-olds and older) females. Fecundity was also adjusted for larval mortality. Average Arizona treefrog larval mortality was estimated from values reported for tadpoles of a sympatric congener (the canyon treefrog, *H. arenicolor*) in temporary ponds (Sredl & Collins 1992). We explored model sensitivity to maximum fecundity by running a scenario with a 50% increase in the maximum number of births per female allowed.

Population attributes, non-breeding events

Range sizes are poorly known for individuals of many amphibian species, including the Arizona treefrog. Therefore, we set range size according to published values for a surrogate species (*Pseudacris triseriata*, Table A1). Finally, maximum group size was set to no more than 5 group members per hexagon to overwinter. To examine model sensitivity to the size of our range, we reduced the maximum allowed range area to approximately 15% of original range area to examine constraints to range and movement (Table 1B, Table A1).

Mortality

Mortality was implemented following group membership assignment. Because non-breeding range parameters allow high densities of individuals and set relatively low requirements for hexagon range eligibility, we set mortality for any remaining transients (e.g., those not assigned to a group) to 100%. This implemented a conservative density-dependence function in the model that prevented exponential growth while still allowing for high population numbers. Mortality is likely higher for recently metamorphosed individuals. Accordingly, Age Class 1 group member mortality was set to 70%. Finally, mortality for Age Class 2 and 3 group members was set to 50%. Although mortality rates for the Arizona treefrog are limited, adult anurans have been found to average roughly 60% in mark-recapture studies (Wells 2007); thus, we consider our mortality rates of 50% for adult group

members to be conservative. We explored model sensitivity to mortality rates using both high and low mortality wherein Age Class 1 individuals had a 76% or 64% mortality rate respectively, while Age Class 2 and 3 individuals had 60% or 40% mortality rates (Table 1B, Table A1).

Dispersal parameters

Movement to breeding ponds

A spatial affinity parameter was used to “attract” individuals to the closest pond, and the dispersal surface either (1) provided more favorable routes along streams and flat ground in the baseline model (Mims et al. 2016; Parsley et al. 2020), or (2) was uniform, as evaluated in a sensitivity analysis. Individual movements were set to a maximum of 35 hexagons (maximum 1050 m straight-line distance, Fig. A4). Autocorrelation of dispersal paths was set to 90%, allowing relatively straight paths with only occasional lateral movement (Joly 2019). Dispersal distances > 700 m have been recorded for another sympatric dryland anuran (*Anaxyrus punctatus*, Tevis 1966), and high mobility of dryland-adapted anurans is thought to contribute to high genetic connectivity of some desert anurans (Chan & Zamudio 2009; Mims et al. 2015); thus, this maximum distance was set to allow for even the most extreme movement events. Even so, we tested model sensitivity to this upper limit and conducted a separate analysis of all scenarios based on a doubling of maximum straight-line distance to 2100 m (Table 1B). Upon reaching the breeding pond, a dispersal event terminates; thus, in most instances dispersal events were much shorter than the maximums reported. Movement was logged for each individual for both movement to and away from breeding ponds and designated to allow for differentiation in movement types.

Movement away from breeding ponds

Non-breeding movements in anurans are likely more random than directional movement to breeding ponds (Coster et al. 2014). Distances traveled also likely follow the more traditional leptokurtic distribution as individuals forage and seek appropriate cover rather than move directly toward a breeding site. To simulate movement to non-breeding or “overwintering”

locations, dispersal paths for individuals were drawn from a log normal distribution with a mean of 10 hexagons (300 m) and a standard deviation of 2 hexagons (60 m). Paths were not allowed to exceed 35 hexagons (1050 m) in the baseline analysis, while a sensitivity analysis allowed the maximum path to reach 70 hexagons (2100 m). Values were selected to incorporate the maximum observed movement distances for other sympatric anurans (Tevis 1966) and to allow for uncertainty in assumptions. Autocorrelation of movements were informed from spatial data over a trend period of 5 hexagons, and no stopping criteria were used. Individuals were then permitted to explore the occupied hexagon and 6 neighboring hexagons before initiating an optional second movement event. If suitable habitat was not found after two dispersal and exploration events, individuals remained transients and were assigned mortality rates of 100%.

Results

We found that Arizona treefrog population sizes declined in response to all breeding habitat reduction scenarios (Figs. 2, 3; Table 2), even when reductions targeted the ponds least likely to fill with water. Mean treefrog population size was 5,071 (SD=1,176) for time steps 81–100 for *Baseline*, and the percent difference between *Baseline* and *Dry* scenarios ranged from – 29.1 to – 64.4% *Dry 1* and *Dry 2*, respectively (Table 2). Population sizes were statistically different from *Baseline* in all other scenarios ($F=350.4$, $df_1=5$, $df_2=594$, $p < 0.001$). We also found that the variation of population size among replicates decreased in *Dry* scenarios, indicative of greater synchrony and consistent with a loss of metapopulation dynamics that would otherwise produce heterogeneity among simulations as observed with *Baseline* results. Represented by the percent differences in the magnitudes of the standard deviations among scenarios, variation reduction ranged from – 44.3 to – 120.8% of standard deviation compared to variation among *Baseline* simulations (Table 2).

Mean population numbers declined in both *Sink 1* and *Sink 2* scenarios, which allowed attraction to breeding ponds that were then simulated to have failed recruitment (no reproduction), with a – 41.8% and – 83.6% reduction in *Sink 1* and *Sink 2* respectively. Variability among replicates and

Table 2 Mean output values for Arizona treefrog simulations. Results are averaged for the last 20 generations of each of six breeding habitat availability scenarios for the population size, pond occupancy, and ponds with successful larval recruitment (Table 1). *Mean % Difference* and *SD % Difference* represents the mean and magnitude of differences in standard deviation between *Baseline* and other scenarios simulated

	Scenario	Mean	Mean % difference	SD	SD % difference
<i>Population</i>	Baseline	5071.1		1176.1	
	Dry 1	3784.5	- 29.1	749.7	- 44.3
	Dry 2	2600.2	- 64.4	290.4	- 120.8
	Sink 1	3319.3	- 41.8	580.7	- 67.8
	Sink 2	2080.6	- 83.6	280.2	- 123.0
	Dry + Sink	2191.8	- 79.3	275.6	- 124.1
<i>Occupancy</i>	Baseline	23.5		4.8	
	Dry 1	17.9	- 27.1	3.0	- 47.8
	Dry 2	13.1	- 56.6	1.3	- 114.2
	Sink 1	16.7	- 33.7	2.6	- 60.5
	Sink 2	11.3	- 70.1	1.3	- 114.9
	Dry + Sink	11.5	- 68.2	1.2	- 118.0
<i>Recruitment</i>	Baseline	20.5		4.8	
	Dry 1	14.9	- 31.6	3.0	- 47.8
	Dry 2	10.1	- 67.7	1.3	- 114.2
	Sink 1	13.7	- 39.7	2.6	- 60.5
	Sink 2	8.3	- 84.7	1.3	- 114.9
	Dry + Sink	8.5	- 82.3	1.2	- 118.0

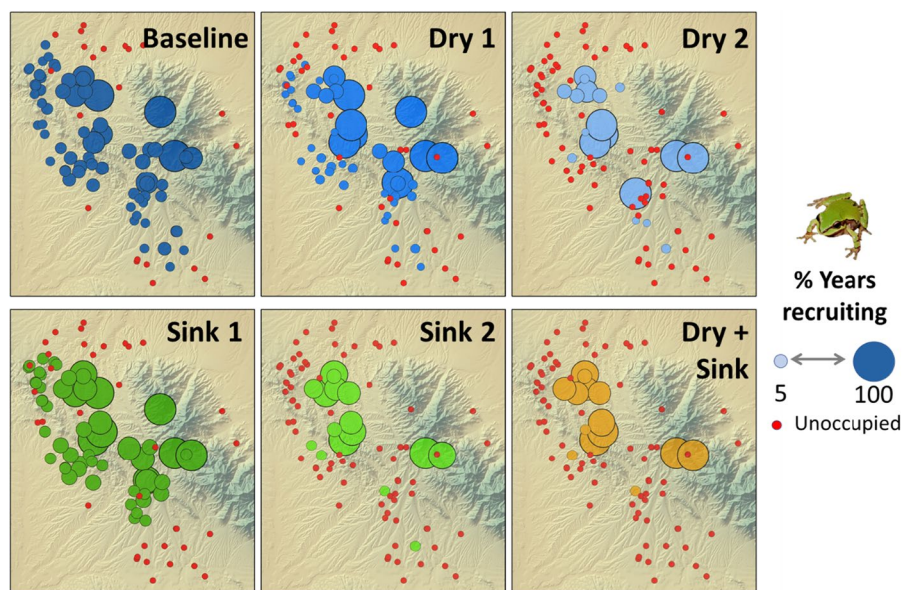
across time was also greater in *Sink 1* relative to *Sink 2* (Fig. 2, Table 2). Yet, both *Sink 1* and *Sink 2* produced a reduction in magnitude of variability (- 67.8% and - 123.0% respectively) compared to *Baseline*. The additive effects of both habitat reduction and sink dynamics found in the *Dry + Sink*, which simulated a 30% reduction in available wetted ponds and a 60% failure of larval recruitment as compared to *Baseline*, produced similar reductions in population size as *Sink 2*.

Simulated occupancy dynamics also showed significant support for hypotheses of population decline and loss of metapopulation dynamics ($F = 341.5$, $df_1 = 5$, $df_2 = 594$, $p = < 0.001$; Table A3, Fig. 3). The mean number of ponds occupied in *Baseline* was 23.5 (± 4.8 SD) with a mean difference of - 56.6% for *Dry* scenarios and -68.2% for *Sink* scenarios, greater than the percent of breeding habitat loss introduced in each scenario. Although *Dry 1* and *Sink 1* had reduced variation in the number of ponds occupied among replicates (- 47.8% and - 60.5% respectively), the reduction in the magnitude of variation in model iterations was larger (approximately - 114%) for both *Dry 2* and *Sink 2* (Table 2). *Dry + Sink* produced the largest reduction in variation among all scenarios. The reduction in variation was captured

spatiotemporally as well (Fig. 4), supporting the hypothesis of reduced metapopulation dynamics due to individuals and recruitment restricted to specific ponds or clusters of ponds.

The number of years each pond was occupied varied among ponds in *Baseline*, from zero years for some ponds to nearly the entire time period for other ponds that were more centralized or in proximity to ponds that filled every or nearly every year (Fig. 4). As breeding habitat was reduced across model iterations in the *Dry 1* and *Dry 2* scenarios, ponds exhibiting occasional occupancy in *Baseline* simulations were not occupied, particularly on the range edges. In *Dry 2*, most continually occupied ponds were isolated in a few core clusters of occupied patch networks, and *Sink* scenarios generally reflected similar patterns. In those cases, individuals were isolated at a few breeding ponds that infrequently dried during the time series, with treefrog individuals rarely recolonizing extant wetted ponds beyond a few core clustered ponds potentially due to dispersal limits (Fig. 4). Thus, pond occupancy was increasingly limited to a core sub-network of reliably wetted ponds with limited (re)colonization beyond core ponds. These patterns produced a relatively synchronous occupancy compared to the colonization and extinction patterns observed in *Baseline* (Fig. 4).

Fig. 4 Proportion of recruiting years for each pond over the 100-year simulation among scenarios. *Baseline*: breeding habitat based on historical pond inundation (Parsley et al. 2020). *Dry 1*: breeding habitat reduction by 30%. *Dry 2*: breeding habitat reduced by 60%. *Sink 1*: larval recruitment success in any given year was reduced by 30%. *Sink 2*: larval recruitment success in any given year was reduced by 60%. *Dry + Sink*: 30% reduction in available breeding habitat and a 60% reduction in ponds with successful larval recruitment



Results of sensitivity analyses indicated that simulations responded proportionally to augmented parameters, suggesting that our simulation model was robust. For example, in Sensitivity Groups B and C (Table 1B), decreases and increases in mean population size corresponded to the lower and higher survival rates used to parameterize the model (Table A4). In Group E, extended dispersal distances resulted in higher occupancy rates and mean population sizes compared to any other sensitivity group (Tables A4–A6). Within Group E, the *Sink 2* and *Dry + Sink* scenarios produced the most dramatic mean population, occupancy, and recruitment loss of any sensitivity group. The mean standard deviation of Group E's population was also less than half of Group C's (the next highest population size), suggesting that the spatial arrangement of available breeding plays a particularly important role in mitigating climate induced habitat fragmentation.

Discussion

We found strong support for hypothesized reductions in population size and loss of metapopulations dynamics of the Arizona treefrog in response to simulated climate-induced reductions in breeding habitat availability. Ultimately, reductions in the availability of even the least likely ponds to fill with water,

whether induced via larval recruitment failure or climate change-induced hydroperiod reductions, led to reductions in total population size and more dramatically to loss in variation of population size and pond occupancy among replicate simulations. This was due to individuals becoming isolated at a subset of reliable ponds (i.e., those that fill most if not every year), resulting in shift from a metapopulation to a few isolated clusters of breeding sites. Arizona treefrog populations decreased in response to reduced pond availability on the landscape across all explored model scenarios of recruitment failure, loss of habitat patches, or both combined—even with proportionally greater loss of ponds that are typically dry. We also found that reduced habitat availability (e.g., ponds that did not fill with water) resulted in populations quickly becoming isolated at intermittent ponds that reliably filled each year. As a result, we observed smaller total population sizes with very little variation among years and across simulation replicates. Alternatively, reproductive sinks (i.e., ponds that filled with water but dried before metamorphosis and recruitment) maintained greater connectivity over time even with limited recruitment, acting as stepping-stones and potentially playing an important role in maintaining the Arizona treefrog metapopulation dynamics within the HMCH region (Mims et al. 2016).

A series of sentinel ponds emerged as potentially resilient, high-quality habitat that were occupied for many years of the study across all scenarios. The three clusters of ponds identified may serve as important, reliable habitat for the metapopulation and may warrant focused management efforts, such as invasive species removal, habitat improvement, and efforts to maintain favorable hydroperiods (e.g., through the addition of pond liners or wells to pump water into ponds). When populations are limited to fewer, more closely linked patches, there is an increased risk of local extirpation posed by spatially synchronous disturbances, such as invasive species colonization or disease outbreak. Under baseline conditions, habitat availability is spatiotemporally heterogeneous, supports dispersal at a regional scale, and enables metapopulation dynamics. Even when ponds are not occupied, they may act as stepping-stones for dispersal among more reliable breeding habitat and may be occupied sporadically through time (Hanski 1998; Drake et al. 2017a; Bertassello et al. 2022). In light of projected declines in surface water availability due to climate change, management strategies that improve connectivity among core clusters of ponds, such as the protection of dispersal corridors or addition of ponds with longer hydroperiods, may improve connectivity and retain gene flow and dispersal to avoid the clusters becoming completely isolated from one another (Mims et al. 2016; Parsley et al. 2020). Our results also revealed that some genetically distinct populations, such as those in the higher elevation ponds of northern portion of the Huachuca Mountains (Mims et al. 2016), are at risk of disappearing under drying scenarios. In addition to supporting connectivity among more stable core clusters of ponds, management strategies could also focus on habitat mitigation that help retain portions of the metapopulation that preserve overall genetic diversity in the region.

Variability over time and among simulation replicates mimics natural population fluctuations. Although population and occupancy variability reduced across all scenarios relative to the baseline, extremely low variability was observed in three of six scenarios, all of which also had significant population size reductions. Though we did not simulate additional disturbances or loss of habitat to other threats (e.g., sedimentation over time or following erosion after a fire), such losses are known to occur and can

happen spontaneously. In such instances, especially with declines in connectivity and a shift toward more isolated populations, recolonization by individuals from other ponds would become unlikely. Such scenarios have already been observed in other species, such as the threatened Chiricahua leopard frog in Miller Canyon of the Huachuca Mountains. An artificial pond, home to one of the only populations in the Huachuca Mountains, was destroyed by floods and sedimentation following the 2011 Monument Fire (S. Stone, U.S. Army, Fort Huachuca, AZ, *pers. comm.*). Mudslides and other shifts in debris are common after forest fires; larger, crowning forest fires that can increase large-scale movement of debris are also becoming more common across the American West with climate change (Holden et al. 2018). Such events can undermine habitat improvement planning and extirpate local populations. Spatially explicit simulations and their results may help inform mitigation strategies by identifying critical habitats for population persistence (e.g., core clusters of ponds) or by identifying sub-populations at risk of extinction without interventions such as hydroperiod management and habitat protection.

Other threats may also interact with climate change, compounding challenges associated with a shift from metapopulations to isolated populations. For example, populations may be vulnerable to predation or competition from other anurans similarly restricted to a few reliable ponds, such as the invasive American bullfrog, a predator of the Arizona treefrog (Jones & Timmons 2010). Pond breeding anurans will likely also face increased exposure to disease (Bradley et al. 2002; Blaustein et al. 2010). Additionally, many artificial waters in dryland regions of the American Southwest may provide relatively low quality habitat compared to their natural counterparts on the landscape due to differences in construction and ecological functioning (Griffis-Kyle et al. 2014). Although Arizona treefrogs breed almost exclusively in stock ponds, ponds vary in their quality. Habitat quality can be reduced, for example, by the presence of cattle at stock ponds (Schmutzer et al. 2008), which is common in the study area. Studies have found negative relationships of anuran population size and cattle use of wetland habitat (Burton et al. 2009), potentially related to reduction in emergent vegetation. Finally, isolation in small pockets of breeding habitat can result in reductions of the genetic health

of populations due to inbreeding and the accumulation of deleterious alleles, as observed in other native amphibians in the region that are currently restricted to permanent and isolated breeding ponds (Storfer et al. 2014).

Our results show that Arizona treefrogs may experience substantial declines in population size and connectivity in response to breeding habitat reductions associated with changes in hydroperiod—even with the loss of only 30% of the most intermittent ponds. However, there is a high degree of uncertainty surrounding their ability to cope with a decline in available breeding habitat. Although our simulation provides insight into this problem, it may not capture all individual and interacting factors influencing population size and connectivity. A loss of 30% of the most intermittent ponds on the landscape (*Dry 1*) resulted in substantial declines in population size, but the loss of 60% of ponds (*Dry 2*) caused proportionally larger declines. This may indicate some threshold effect and suggests that ponds that fill rarely provide important stepping-stones of connectivity between ponds that fill most years. *Sink 2* resulted in the smallest populations for treefrogs across all sensitivity group analyses. This may be driven by a tendency for individuals to become attracted to ponds that fill only occasionally rather than limiting their dispersal and remaining in the vicinity of a pond that fills reliably each year. This suggests that in landscapes with highly dynamic patch quality, dispersal ability may not be related linearly to probability of persistence (Tonkin et al. 2018). This is troubling, as our scenarios are conservative in several ways. In some years, landscapes may support far fewer wetted ponds than modeled in our simulations, because inconsistent and isolated monsoon rains may not refill ponds each year. Thus, long-term drought (Williams et al. 2020) or large fires may have severe consequences for population dynamics, even with increased precipitation variation among years and with occasional wet years interspersed (Pendergrass et al. 2017). Additionally, the timing of pond inundation can be highly variable (Gendreau et al. 2021) and may dictate whether wetted ponds act to benefit populations or represent reproductive sinks. Late season or light rains may trigger breeding events, yet there may be insufficient time for tadpoles to metamorphose leaving them to desiccate in quickly disappearing pools of water. Even species with larval developmental plasticity incur fitness costs when

responding to reduced hydroperiods (Brannelly et al. 2019; Gervasi & Foufopoulos 2007). This could in turn leave adults less capable of breeding in subsequent years when better conditions prevail (Becker et al. 2018). Additionally, though our model does not include specific costs associated with reproduction or dispersal, both are known to increase mortality and may influence population level outcomes of environmental change (Muths et al. 2018).

Canopy cover and riparian corridors may be important for dispersal by acting as stepping-stones between natal and breeding habitats, and canopy cover is heterogeneous throughout the landscape, particularly near lower elevation breeding ponds. Previous work on this subpopulation suggests some evidence for the contribution of canopy cover as influencing functional connectivity (Mims et al. 2016), but canopy cover is often present alongside riparian corridors and streams. These hydrologic features appear to contribute to functional connectivity for Arizona treefrogs as well (Parsley et al. 2020). Although we did not see dramatic shifts in mean demographic responses in Sensitivity Group H (uniform dispersal service), mean maximum dispersal was decreased. Available evidence suggests canopy cover can reduce desiccation rates for amphibians and prolong transience and increase dispersal distance and success via the reduction of mortality risk (Cayuela et al. 2020). Although little knowledge about the exact non-breeding habitat requirements of the Arizona treefrog is available, this result demonstrates the importance of considering functional connectivity in simulating amphibian responses to changing habitat availability (Fordham et al. 2014).

A spatially explicit, individual-based population modeling approach allows for coupling of demographic processes with functional connectivity between populations, and both can have profound influence on the projections of population viability and persistence (Fordham et al. 2014). As we become aware of the increasing number of understudied species and populations at risk in the face of anthropogenically driven disturbance, SIBMs provide a framework to test pertinent ecological and management questions in the face of limited time and data (e.g., Heinrichs et al. 2018; Mims et al. 2020; Thompson et al. 2021). Future applications for the SIBM built for our focal species and region could include evaluating hypotheses of landscape connectivity

among ponds due to changes in the landscape over time, such as canopy cover change, increased aridity, and reductions in aquatic habitat for corridors as well as breeding. Additionally, simulations could help evaluate responses of aquatic species in the region to changes in inundation timing and predictability of ponds in the region (Gendreau et al. 2021) and interactions with other known threats to aquatic organisms in the region, such as invasive species and disease (Mims et al. 2020). Specific management actions could also be tested, such as the addition of ponds in strategic locations, modification of hydroperiods of ponds that support genetically unique populations, or removal of invasive species from core habitats. More generally, investigations could consider the important role of non-breeding habitat in population persistence and connectivity (Howell et al. 2018), as well as how non-breeding habitat will be affected by climate change, and provide a more cost-effective way to test landscape-level management schemes. Such inquiries into non-breeding habitat and its impact on connectivity may help uncover the potential for a role in enhancing or reducing the interannual variation of populations and their spatial synchrony. Further, the effects of local stressors (e.g., predators or disease) may interact with hydroperiod to decrease breeding habitat suitability (Blaustein et al. 2010).

In conclusion, we found that projected reductions of available breeding habitat resulted in substantially reduced population numbers for the Arizona treefrog in a subset of its range. Loss of 60% of breeding ponds resulted in > 50% population declines for the Arizona treefrog. Perhaps more significantly, reduced breeding habitat also increased synchrony and decreased variability through time, which may indicate a loss of function of metapopulation dynamics. The transition to isolated populations produces an increased risk of regional extinction for this species of conservation concern. Sensitivity analyses suggest our model was robust to uncertainty in model parameters and illustrated the role of dispersal in maintaining demographic and landscape connectivity among spatiotemporally heterogeneous habitat (Drake et al. 2021). In the face of climate change-induced habitat loss, identifying populations that rely on disappearing windows of transient connectivity (Zeigler & Fagan 2014) may help conservation practitioners identify key habitat and management actions for sustaining threatened and sensitive species into the future.

Author contributions M.C.M. led study design, analyses, and manuscript authorship. J.C.D. assisted in analyses. J.J.L. assisted in study and analytical design. J.D.O. co-led study and analytical design. All authors helped write, edit, and review the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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