**Informing recovery in a human-transformed landscape: drought-mediated coexistence
alters population trends of an imperiled salamander and invasive predators**

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Abstract

Understanding the additive or interactive threats of habitat transformation and invasive species is critical for conservation, especially where climate change is expected to increase the severity or frequency of drought. In the arid southwestern USA, this combination of stressors has caused widespread declines of native aquatic and semi-aquatic species. Achieving resilience to drought and other effects of climate change may depend upon continued management, so understanding the combined effects of stressors is important. We used Bayesian hierarchical models fitted with 10-yr of pond-based monitoring surveys for the federally-endangered Sonoran Tiger Salamander (*Ambystoma mavortium stebbinsi*) and invasive predators (fishes and American Bullfrogs, *Lithobates catesbeianus*) that threaten native species. We estimated trends in occupancy of salamanders and invasive predators while accounting for hydrological dynamics of ponds, then used a two-species interaction model to directly estimate how invasive predators affected salamander occupancy. We also tested a conceptual model that predicted that drought, by limiting the distribution of invasive predators, could ultimately benefit native species. Even though occupancy of invasive predators was stationary and their presence in a pond reduced the probability of salamander presence by 23%, occupancy of Sonoran Tiger Salamanders increased, annually, by 2.2%. Occupancy of salamanders and invasive predators both declined dramatically following the 5th consecutive year of drought. Salamander occupancy recovered quickly after return to non-drought conditions, while occupancy of invasive predators remained suppressed. Models that incorporated three time-lagged periods (1 to 4 yrs) of local moisture conditions confirmed that salamanders and invasive predators responded differently to drought, reflecting how life-history strategies shape responses to disturbances. The positive 10-yr trend in salamander occupancy and their rapid recovery after drought provided partial support for the

hypothesis of drought-mediated coexistence with invasive predators. These results also suggest management opportunities for conservation of the Sonoran Tiger Salamander and other imperiled organisms in human-transformed landscapes.

Keywords: amphibian; bullfrog; climate resilience; drought; fragmentation; invasive species

1. Introduction

Additive or interactive threats can increase extinction risk, especially for populations that have declined substantially or for species with small distributions (Didham et al., 2007; Fagan et al., 2002; Laurance and Williamson, 2001). In highly-altered landscapes, effects of habitat loss or transformation are often compounded by invasive species that directly (e.g., predation) or indirectly (e.g., competition or disease) reduce survival and other fitness components of native species (Didham et al., 2007; Johnson et al., 2008; Lozon and MacIsaac, 1997). Imperiled species in altered landscapes are also at greater risk from extrinsic forces, such as stochastic variation in climate (Maschinski et al., 2006; Opdam and Wascher, 2004).

Forecasted increases in drought for many areas, and increased variation in precipitation as a whole, portend a bleak future for many aquatic species (Cook et al., 2015; IPCC, 2013). Accelerated drying of water bodies during drought increases the risk of losing entire cohorts, and crowding of individuals into smaller volumes of water can increase predation and disease transmission (Greer et al., 2008; Holling, 1959). One strategy to reduce negative effects of climate change is to manage for climate resilience, such as through maintenance of habitat heterogeneity and population connectivity or by protecting particularly important habitats that

are resistant to change (Pittock et al., 2008; Wilby et al., 2010). For example, land managers can construct or modify basins or manage flows so water bodies hold water long enough to benefit target species (Chandler et al., 2015; DeMarais and Minckley, 1993; Hamer et al., 2016).

In landscapes with few natural water bodies, managing for climate resilience presents a dilemma, because increased permanence of water can aid invasion by non-native species (González-Bernal et al., 2012; Hobbs and Huenneke, 1992). Disturbances such as severe drought can also have unpredictable effects on community structure. In some cases, drought can facilitate coexistence between native and invasive species (Hobbs and Huenneke, 1992), but in other cases, drought can facilitate invasion or magnify species interactions (Bêche et al., 2009; Rehage et al., 2014). Therefore, understanding how the combination of increased drought and climate variation, habitat management, and invasive species affect imperiled species is critical for conservation.

In the southwestern USA, the compounded threats of land transformation, limited water, and spread of non-native, invasive predators have caused high rates of decline for many native, aquatic species (Fagan et al., 2002; Olden and Poff, 2005), including amphibians such as the federally-endangered Sonoran Tiger Salamander (*Ambystoma mavortium stebbinsi*) (USFWS, 2002). This subspecies occurs only in one valley along the USA–Mexico border. As is common in arid landscapes worldwide (e.g., González-Bernal et al., 2012; Davies et al., 2013), most naturally-occurring aquatic habitats were destroyed or highly altered and replaced with impoundments for livestock (Maret et al., 2006; Meffe, 1984). In these situations, persistence of some native species might depend upon continued human interventions. To design and manage for water body features that will provide resilience to climate change in the face of numerous

pressures, managers need detailed information on status and trends of native species, what threatens them, and how habitat features can ameliorate those threats.

To determine the status of the Sonoran Tiger Salamander and changes in its stressors, we used hierarchical models to estimate annual occupancy of salamanders and invasive, non-native (hereafter, invasive) fishes and American Bullfrogs (*Lithobates catesbeianus*) using 10-yr (2004–2013) of surveys of water impoundments (hereafter, ponds). We had four objectives. First, we estimated changes over time (trend) in proportion of ponds occupied by the Sonoran Tiger Salamander with models that incorporated hydrological dynamics of ponds. Second, we assessed changes in threats to salamanders by estimating trends in annual occupancy of invasive predators. Third, we used a two-species interaction occupancy model (MacKenzie et al., 2004; Richmond et al., 2010) that incorporated variation in habitat features to explicitly estimate how presence of invasive predators affected the probability of presence of salamanders. Last, we used different time lags (1 to 4 yrs) of the Standardized Precipitation Evaporation Index (Vicente-Serrano et al., 2010) to evaluate a conceptual model developed for this system that predicted drought could mediate coexistence of native and invasive species (Maret et al., 2006). Our objectives and analyses provide important information for the management and recovery of an endangered salamander and inform how interactions among land-use change, invasive species, and climate change can affect resilience of rare species.

2. Materials and methods

2.1 Study system

The Sonoran Tiger Salamander is limited to the upper drainages of the Santa Cruz and San Pedro rivers in the San Rafael Valley and surrounding foothills in Arizona, USA, and northern Sonora,

Mexico (Jones et al., 1988; USFWS, 2002). This valley is a mix of private and public lands characterized by grasslands, evergreen woodlands, and narrow riparian forests. The salamander was federally listed as endangered without critical habitat in 1997, with primary threats including small geographic range, predation from invasive fishes and American bullfrogs, frequent die-offs from disease, and introgression with Barred Tiger Salamanders (*A. mavortium mavortium*) that were introduced as part of the bait trade (Jones et al., 1988; USFWS, 2002). Small population sizes and limited gene flow have caused inbreeding that may further reduce population viability (Jones et al., 1988; Storfer et al., 2004). Hybrid animals cannot be identified reliably in the field and the current extent of introgression is unknown, but for management purposes, all tiger salamanders in the San Rafael Valley are treated as Sonoran Tiger Salamanders (Hossack et al., 2016).

Sonoran Tiger Salamanders are large (>330 mm total length) and can metamorphose and colonize land, where they presumably spend most of their time underground (Petranka 1998). Alternatively, in ponds that retain water for >1 year, salamanders can mature as gilled, aquatic paedomorphs (branchiate adults). Breeding occurs primarily from February through early April and larvae require 14–16 weeks to metamorphose (Collins et al., 1988). In the absence of fish, larval and paedomorphic tiger salamanders are often the dominant predators (Holomuzki et al., 1994). Historically, Sonoran Tiger Salamanders would have occurred primarily in ciénegas (spring-fed wetlands) and possibly riverine marshes and backwaters. Since most of these habitats were destroyed or heavily altered during the late 19th and early 20th centuries (Hendrickson and Minckley, 1984), most available water bodies are now impoundments that have been constructed or modified to provide water for livestock.

2.2 Data collection

Monitoring was conducted from 2004 to 2013 by sampling ponds for presence of salamanders and other aquatic species. Each year, 42–70 ponds were selected randomly from the population of ~300 accessible sites that had potential to hold water during the breeding season (Table 1, Fig. 1). In total, 156 ponds were sampled during December–July (mean = 19 March, range = 01 Dec – 01 July) for 1 to 8 years (mean = 3.5, SD = 1.9). Across all years, the distance to the nearest sampled pond averaged 1.02 km (SD = 0.63, range: 0.07–3.8 km) and the average distance to all other surveyed ponds was 12.4 km. We know little about the dispersal tendencies of Sonoran Tiger Salamanders, but between years, <8% of marked California Tiger Salamanders (*A. californiense*) dispersed to other ponds >500 m away in an oak woodland that was probably more hospitable to amphibian movement than our study system (Trenham et al., 2001). Since we make no assumptions about between-year movement, and because we sampled during months that average < 2 cm of precipitation (<http://www.wrcc.dri.edu/summary/climsmaz.html>), we suspect that changes in the occupancy status of ponds during the sampling season were infrequent.

Most surveys consisted of three pulls of a 10.6-m bag seine across the full length or width of a pond. If ponds were too shallow to seine, surveyors took 40 sweeps with a dip-net or searched the area visually. To provide information on detection probability, an average of 11.5 ponds (range = 4–27) was sampled a second time on different dates within years (Table 1). Repeated surveys were conducted an average of 47 days apart. During each survey, biologists recorded the presence, dimensions, and depth of water (Table 2); number of each developmental class of salamanders observed; and invasive species. We detected 5 species of non-native fishes (*Ameiurus natalis*, *Gambusia affinis*, *Lepomis cyanellus*, *L. macrochirus*, *Micropterus*

salmoides) that have been stocked in the valley. Invasive crayfish (*Orconectes virilis*, *Procambarus clarkii*) also prey upon amphibians but they were not detected in any ponds. Information on pond vegetation was also recorded, but it was rare (mean = 6.3%) in most ponds and was not included in the analyses.

2.3 Salamander occupancy

Using the detection/non-detection data described above, we modeled trend in pond occupancy by salamanders from 2004 to 2013 using Bayesian hierarchical models with a detection component (P) and an occupancy component (Ψ). Because few ponds were sampled in consecutive years, we estimated occupancy separately each year rather than use dynamic models that estimated rates of colonization and extinction. We considered a pond occupied if any life stage of salamander was present. For all models for salamanders and invasive predators, detection was limited to animals that were in the water column or on the pond bottom and were available to be captured by a seine or net or detected visually.

To accommodate the large fraction of dry ponds surveyed each year (Table 1), we estimated detection probability separately for ponds that were inundated versus dry when surveyed. For inundated ponds, we made an *a priori* decision based on experience and conversations with other amphibian experts to include the quadratic effect of sampling date (standardized to mean = 0, SD = 1). We also evaluated the effect of pond area (standardized to mean = 0, SD = 1), pond depth (standardized to mean = 0, SD = 1), and sampling method (seined or not) on probability of detecting salamanders, given that the species was present. All of these covariates except depth (the 95% credible interval easily included 0) helped explain variation in detection and were retained in the model (Table 4).

After running several initial detection models, we fixed detection of salamanders in dry ponds to 0.60, a value similar to the estimated detection (0.57) in ponds with water that were sampled with methods other than seining (see Results). We fixed detection for dry ponds to avoid biasing estimates of occupancy caused by rare discoveries of salamanders at those sites. Specifically, when we initially modeled detection for wet and dry ponds as equal, rare encounters of salamanders in dry ponds caused models to underestimate detection across all sites, subsequently inflating occupancy estimates (with poor precision) across the study area. Fixing detection to $P = 0.60$ for dry ponds was a conservative approach because salamanders in dry ponds are not obscured by water, and therefore should be relatively easy to detect if they were on the surface (i.e., their detection probability is close to 1.0).

We ensured that our choice of detection probability for dry ponds did not bias results by evaluating a range of detection values; all $P > 0.5$ produced similar estimates (Table 3). Thus, occupancy and trend estimates for salamanders were not highly reliant upon our choice of the detection value for dry ponds. Although few dry ponds seemed occupied by salamanders based on naïve data, our approach to fix detection, rather than fix occupancy to zero, at least allowed the possibility for dry ponds to be occupied sometime during the season that data were collected (e.g., before the pond dried).

After determining the best model structure for estimating detection probability, we estimated the average rate of change across the study period by including an inter-annual trend parameter (MacKenzie et al., 2006). We did not include any other covariates for salamander occupancy, so the resulting trend estimates represent overall occupancy across the entire sampled landscape. The trend estimates were not adjusted for local variation in habitat and assume annual selection of ponds was unbiased.

A large section of private land was added to the monitoring program in 2009. Because this modification of the sampling design could have affected results, we evaluated the effect of this change by comparing salamander occupancy in the 125 sampled ponds in the original sampling frame to that of 31 ponds sampled on the added private land. Estimated occupancy of salamanders during 2009–2013 was similar on the added private land (0.408, 95% credible interval [CI] = 0.186–0.649) and elsewhere in the valley (0.355 [0.161–0.568]), so we did not distinguish between land ownership in the models.

2.4 Invasive species occupancy

We used a similar approach to estimate annual changes in occupancy of invasive predators from 2004 to 2013 as we did for estimating occupancy of salamanders. We considered a pond occupied by invasive predators if any life stage of fish or American Bullfrog was present. We pooled all life stages of fishes (detected in five ponds) and bullfrogs (detected in 50 ponds) because there were too few fish observations to estimate their effects separately. These observations also included one record of a native fish (Longfin Dace, *Agosia chrysogaster*), which we included with the invasive predators because it could prey upon salamander eggs or small larvae.

To estimate annual occupancy of invasive predators, we modeled detection probability separately for ponds that were inundated when surveyed versus those that were dry, and then produced a single estimate for occupancy. We used the same detection covariates as for salamanders, but only sampling method (seined or not) had a meaningful effect on detection probability of invasive predators (Table 4). Because surveys were sometimes ended upon detection of salamanders (e.g., only one seine pull instead of three), we evaluated the effect of

sampling effort (number of seine pulls or dip-net sweeps) on detection of invasive predators. Its effect was inconclusive; thus, we kept the simpler model structure (seined vs. not) that captured most of the variation in detection. For dry ponds, we fixed detection of invasive predators to 0.89, the estimated probability of detection in ponds that were seined. We fixed detection in dry ponds to be equal to that of seined ponds because we assumed that detection of aquatic species would be high in sites without water. After determining the best detection structure, we estimated rate of change in occupancy by invasive predators across the study period by including a trend parameter for the occupancy component of the model. We did not include habitat covariates in the occupancy portion of the model because our goal was to assess the trend across the landscape, regardless of local habitat conditions.

As done for the salamander data, we evaluated the effect of modifying the sampling frame in 2009. During 2009–2013, mean occupancy of invasive species was higher on the added private land (0.299 [0.113–0.526]) than elsewhere in the valley (0.157 [0.053–0.309]). But the 95% CI around the estimated trends in occupancy on private land (-8.55%–1.81%) and elsewhere (-1.66%–1.19%) overlapped broadly, so we did not distinguish between land ownership in the models.

2.5. Predator-prey occupancy

To estimate how habitat covariates affected occupancy by Sonoran Tiger Salamanders and invasive species, as well as how invasive species affected occupancy by salamanders, we used a two-species occupancy model with a dominant-subordinate structure (MacKenzie et al., 2004; Richmond et al., 2010), using invasive species as the dominant species. This model estimates three occupancy parameters, adjusted for detection uncertainty: (1) occupancy of invasive

predators, independent of salamander status; (2) occupancy of salamanders in the absence of invasive predators; and (3) occupancy of salamanders given presence of invasive predators. The advantage of this model structure is that we estimated the presence of invasive predators for each pond, so uncertainty from imperfect detection is explicitly incorporated into the effect of invasive predators on salamander occupancy. We modeled the effect of invasive predators on salamanders with an offset (i.e., a separate intercept for the two salamander occupancy parameters described above). We used the same model structure for detection in the two-species model as for the one-species models described above, with separate detection for wet and dry ponds.

We evaluated linear and quadratic effects of pond depth and pond area on occupancy of Sonoran Tiger Salamanders, invasive predators, and the parameter that describes their co-occurrence. However, pond depth and area were positively correlated (Pearson's $r = 0.65$) and including both covariates in the same models caused problems for interpretation. Because area was less informative, we used depth instead. In contrast to the two models described for estimating overall trends for salamanders and invasive predators, for this model we estimated occupancy separately for wet and dry ponds to accurately assess the influence of invasive predators on salamanders when water was present.

All models were coded in JAGS and implemented in R (version 3.2.2), using package `rjags` (Plummer, 2013; all models and code are provided in Appendix A and B). We used flat priors for all model parameters: uniform distributions $U(0,1)$ for probability parameters and normal distributions $N(0,1000)$ for regression coefficients. For each model, we ran three chains in parallel and used 100,000 MCMC posterior samples for inference, after a burn-in period of 5,000 samples. Convergence of MCMC chains was assessed from plots of sample paths and the

Brooks–Gelman–Rubin diagnostic (Brooks and Gelman, 1998), using $R\text{-hat} = 1.01$ as an *a priori* threshold of proper convergence. In the Bayesian framework, missing covariate values are treated as "unknowns" and are inferred from all information available in the data (including values and correlations of independent and response variables) under the constraints established by the model.

To facilitate interpretation, we report most estimates on the original scale of the corresponding parameter (e.g., a detection value of 1.331 on the logit scale was back-transformed to a probability interpreted as “detection averaged 0.791”). Regression coefficients ($\hat{\theta}$) correspond to mean posterior distributions of parameters and are on the logit-scale. We express uncertainty for parameter estimates as posterior standard 95% credible intervals (95% CI) unless otherwise stated.

2.6 Drought-mediated coexistence

Based on theory and empirical data that show reductions in disturbance frequency (e.g., drying) can promote invasion (Doubledee et al., 2003; Hobbs and Huenneke, 1992; Meffe, 1984), Maret and others (2006) developed predictions about how drought-related drying of ponds could affect the occurrence of the Sonoran Tiger Salamander and invasive predators in our study system. They predicted that in *the short-term*, drought-related drying of ponds would eliminate fishes and most bullfrog and salamander larvae. Juvenile and adult bullfrogs can survive pond drying and would presumably move in search of dormancy sites, such as springs or other moist retreats, or they may emigrate to a nearby pond, if available (Thrall, 1971). However, we expect that increased severity of seasonal drought conditions are likely to reduce survival during dispersal or reduce dispersal distance. In contrast, because some salamanders can

metamorphose and persist underground until more favorable moisture conditions return, they could colonize ponds that were free of fish and bullfrog larvae the next time they filled. Thus, over the *longer-term*, occasional drying of ponds that re-set the predator community was predicted to benefit native species (Maret et al., 2006).

To evaluate the hypothesized relationships among drought, salamanders, and invasive predators, we used different time lags of drought as a predictor variable for occupancy. We represented drought with 12 mo., 13–24 mo., and 25–48 mo. values of the Standardized Precipitation Evapotranspiration Index (SPEI; <http://sac.csic.es/spei/database.html>) for a 0.5° cell centered on our study area. The SPEI is similar to the commonly-used Standardized Precipitation Index, except it incorporates the large effect of temperature on soil-moisture conditions (Vicente-Serrano et al., 2010). We indexed drought to March for each year because that was when salamander eggs were detected most frequently. Annual values of SPEI ranged from -1.29 to 1.20 (mean = -0.31); negative values indicate seasonal drought conditions that occurred during 6 of the 10 yrs (Appendix D).

To evaluate the effect of drought separately for salamanders and invasive predators, we used a model that incorporated all three time-lagged measures of drought in single species models, with the same detection covariates as described above. The three measures of drought were weakly correlated (range of Pearson's r : -0.07–0.19) and thus provided distinct information. As for the two-species interaction model, we estimated occupancy separately for dry and wet ponds. If changes in occupancy during the 10 yrs of monitoring followed predictions, we would expect more severe measures of drought during the previous 12 mo. to be associated with reduced occupancy of salamanders and invasive predators, whereas longer-term measures of drought (25–48 mo.) would be positively associated with occupancy of salamanders but negatively

associated with occupancy of invasive predators (Maret et al., 2006). Our predictions were conditioned on opposing short-term (12 mo.) and long-term (25–48 mo.) effects, but we did not have *a priori* predictions for the direction of effect of drought during the intermediate term (13–24 mo.).

3. Results

3.1 *Salamander occupancy*

Detection of the Sonoran Tiger Salamander increased with pond area (area $\hat{\theta} = 2.493$ [95% CI = 1.474– 3.639]) and from December through July (Fig. 2A and 2B). For inundated ponds, mean annual occupancy was 59.2% (Appendix C). Detection averaged 0.791 (0.687–0.880) when ponds were seined and 0.572 (0.321–0.807) when ponds were sampled with dip-nets or searched visually. From 2004 to 2013, only 9.2% of dry ponds were estimated to have been occupied at some time during that season (Appendix C). Estimated occupancy of salamanders increased by an average of 2.2% (0.4%–3.8%) per year. The corresponding average rate of relative increase in occupancy was 1.053, i.e., an increase of ~5.3 per year. The 95% CI for these estimates excluded zero; therefore, our analyses indicate that occupancy of the Sonoran Tiger Salamander increased from 2004 to 2013.

3.2 *Invasive species occupancy*

For inundated ponds, mean annual occupancy of invasive predators was 34.9% (Appendix D). Average detection of invasive predators was 0.870 (0.784–0.938) when ponds were seined and 0.442 (0.173–0.777) when ponds were not seined. Occupancy of invasive predators ranged from 0.191 (0.082–0.346) to 0.563 (0.320–0.834) in inundated ponds and from 0.014 (0.002–

0.042) to 0.077 (0.012–0.221) in dry ponds (Fig. 3A and 3B, Appendix D). Across all sampled ponds, occupancy of invasive predators decreased by an average of 1.29% (-9.11%–6.44%) annually. Because the 95% CI around the trend estimate contains zero, our results indicate little change in occupancy by invasive predators.

3.3. *Predator-prey occupancy*

Across years, estimated occupancy of salamanders in the absence of invasive predators ranged from 0.331 (0.106 – 0.636) to 0.863 (0.632 – 0.989) in inundated ponds and from 0.016 (0.001 – 0.072) to 0.208 (0.012 – 0.712) in dry ponds (Fig. 4A and 4B, Appendix C). Estimated occupancy of salamanders in ponds where invasive predators were present ranged from 0.274 (0.047 – 0.667) to 0.784 (0.453 – 0.985) in inundated ponds and from 0.014 (0.000 – 0.078) to 0.151 (0.006 – 0.640) in dry ponds (Appendix C). Across all years, in inundated ponds, invasive predators reduced salamander occupancy by a mean of 23.01% (8.72% – 43.73%; Fig. 4A and B).

Occupancy of salamanders and invasive predators both increased with pond depth. However, the benefit of deeper ponds for salamanders was evident primarily in the absence of invasive predators (depth $\hat{\theta} = 1.707$ [0.699 – 3.007]; Fig. 5). When invasive predators were present, the estimated effect of pond depth on occupancy by salamanders was still positive, but it was imprecise and indistinguishable from 0 (invasive predators $\hat{\theta} = 0.459$ [-0.548 – 1.502]).

3.4 *Drought-mediated coexistence*

Consistent with our predictions, the model that incorporated three weakly correlated time periods of drought conditions showed that drought during the previous 12 mo. reduced

salamander occupancy (-0.339 [-0.593 – -0.087]), had no effect between 13 and 24 months prior to sampling (0.142 [-0.106 – 0.391]), and drought during the 25–48 mo. prior to sampling was associated with greater occupancy (0.428 [0.102 – 0.757]). However, the effect of drought on invasive predators did not follow predictions. Drought did not affect occupancy of invasive predators during the 12 mo. (0.090 [-0.170 – 0.354]), 13–24 mo. (-0.069 [-0.330 – 0.195]), or 25–48 mo. (0.131 [-0.204 – 0.465]) periods preceding sampling.

4. Discussion

Understanding the additive or interactive threats of habitat loss or transformation, drought, and invasive predators on imperiled species is critical for conservation, especially where drought conditions are expected to become more frequent and severe. Long-term (2004–2013) monitoring of ponds along the Arizona–Mexico border that were constructed primarily for livestock revealed that pond occupancy of the endangered Sonoran Tiger Salamander increased, annually, by 2.2%. These increases occurred despite multiple stressors that threaten salamander populations. Our results also support the hypothesis that native species that evolved in highly dynamic ecosystems such as the arid Southwest are more resistant to drought than species from areas with more stable moisture conditions.

Monitoring plans for rare or endangered species often exclude monitoring of the threats that originally contributed to declines (Lawler et al., 2002; Troyer and Gerber, 2015). This lack of information about threats can greatly impede managing for resilience in the presence of invasive species, reduce the efficacy of management actions, and limit potential management actions. In our case, however, concurrent monitoring of an endangered endemic and invasive predators that contributed to the decline of salamanders provided a rare opportunity to explicitly estimate how

their dynamics co-varied. Across all pond conditions and years, presence of invasive predators reduced salamander occupancy by 23%.

The lack of trend in occupancy for invasive predators was influenced heavily by a large decrease in 2009, the 5th consecutive year of drought conditions. From 2004 to 2008, there was a positive trend in occupancy of invasive predators. After 2009, their occupancy remained below levels observed during 2004–2008 even though drought conditions eased. Salamander occupancy declined briefly in 2009 by a similar magnitude as for invasive predators. This decline could reflect the cumulative effects of reduced recruitment during dry conditions as well as the loss of potential breeding habitat. For example, in northwestern Florida, pond-level extinction of the mole salamander (*A. talpoideum*) was associated with drying of ponds during a severe drought (Walls et al., 2013). Variation in availability of surface water strongly influences recruitment, survival, and growth of amphibian populations across a wide range of habitats (Church et al., 2007; Hamer et al., 2016; Hossack et al., 2013; Zylstra et al., 2015).

In contrast to the pattern observed for invasive species, salamander occupancy increased quickly after drought conditions eased and remained high for the rest of the study. These contrasting responses by native and non-native species may reflect how life-history strategies can shape responses to serial disturbances such as extended drought or hydrological disturbances (Meffe, 1984; Trexler et al., 2005). Metamorphosed salamanders can persist in the terrestrial environment and are likely more resilient to variation in recruitment than non-native species that are more dependent upon permanent water and consistent recruitment to aid invasion and persistence (Church et al., 2007; Doubledee et al., 2003; Morris et al., 2008).

Occupancy of salamanders and invasive predators both increased with pond depth, which reflects their shared requirements for water for at least one life stage. But the benefit of deep

ponds for salamanders was evident primarily when invasive predators were absent. As a result, the increase in salamander occupancy from 2004 to 2013 was greater in ponds that lacked invasive predators than in ponds with invasive predators. This relationship with depth presents both management opportunities and challenges. Historically, Sonoran Tiger Salamanders would have occurred primarily in long-hydroperiod habitats such as spring-fed wetlands, but most of those habitats have been destroyed or host invasive predators that exclude salamanders (USFWS, 2002). Converting these habitats from seasonal to permanent hydroperiods could also increase disease risk and threats of genetic introgression (Fitzpatrick and Shaffer, 2007; Greer and Collins, 2008; North et al., 2015), further increasing management challenges.

Drought is often considered only as a limiting factor for wetland-dependent species (Hossack et al., 2013; Walls et al., 2013), rather than a potential benefit. In many ecosystems, however, occasional drought-related drying of wetlands is critical for limiting predator communities, ultimately facilitating landscape-scale coexistence between predators and prey and increasing local biodiversity (Hobbs and Huenneke, 1992; Trexler et al., 2005). Our results provided partial support for a model that predicted drought could mediate predator-prey coexistence for this system (Maret et al., 2006). Results for Sonoran Tiger Salamanders matched predictions: drought during the previous 12 mo. was associated with reduced occupancy, whereas drought during the previous 25–48 mo. was associated with increased occupancy. In contrast, the effect of drought on invasive predators did not follow predictions. Although the large drop in occupancy of invasive predators in 2009 coincided with extended drought, overall, occupancy of invasive predators was not associated with drought during any of the three time periods we evaluated.

There was significant variation in the effect of invasive predators on salamander occupancy across years, which could have been driven by several factors, including stochasticity, spatial variation in sampling, and lack of detailed information on drying rate of ponds and on abundance of different life stages of bullfrogs. The model developed by Maret and others only considered a bullfrog population to be present if larvae were detected, because detection of a small number of juveniles or adults could indicate transient presence and weak predator effects. While our results partially support the hypothesis of drought-mediated coexistence, we need more complete information on life-stages of different invasive predators and drying rate of ponds to better understand how drought affects species interactions and vital rates of native and invasive species. Also, if native and non-native species respond to drought on different time scales, then we may not expect the simple models we evaluated to adequately describe community dynamics.

Temporal variation in the effect of invasive predators on salamanders also likely resulted from pooling fish and bullfrogs into a common group for analysis. Fish are typically stronger predators than bullfrogs, but we did not have enough information to estimate their effects separately or to determine if the presence of both predators resulted in additive, antagonistic, or synergistic effects (e.g., Simberloff & Von Holle, 1999; Adams et al., 2003). If Sonoran Tiger Salamanders and other native aquatic species can coexist long-term with bullfrogs, there would likely be more management options because it is easier to eradicate and prevent fish from recolonizing isolated ponds than species that disperse terrestrially (Atobe et al., 2014; Knapp et al., 2007). The lack of data on temporal and spatial variation in drying of ponds, and thus our assumption of uniform drought conditions across the valley, also limits inferences about mechanisms and our ability to estimate the effect of drought on both native and invasive species.

This information is critical for managing for climate resilience when invasive predators limit occurrence and population growth rates of native species.

Like many imperiled aquatic species in the southwestern USA, the loss of natural habitats free of invasive predators means that preventing further declines of the Sonoran Tiger Salamander may require sustained management. The ability to rank particular habitats according to their potential contribution to metapopulation recovery and growth would help inform management options. For example, typical for studies of occupancy across a network of water bodies (e.g., Walls et al., 2013; Chandler et al., 2015; Hossack et al., 2015), we implicitly assumed the ecological and management value of all subpopulations was equal, but we know this assumption is false. We suspect that long-hydroperiod ponds that support paedomorphs (i.e., salamanders that breed in the aquatic form) are the most stable subpopulations, but these habitats are also the most likely to support invasive predators. In contrast, ponds that dry frequently might have a small number of larvae when surveyed and thus are considered occupied, yet they might contribute little to the metapopulation. Incorporating information on abundance of imperiled species and their threats would provide much richer information on which to base population viability assessments and other risk projections that can be used to rank management options and design habitats for future climate resilience.

Acknowledgments

We thank the many biologists and data managers for their contributions to the data used in these analyses. L. Allison, D. Cox, J. Francis, C. Lutz, C. Nelson, and T. Snow contributed extensively to project design or field surveys. Use of trade, firm, or product names are descriptive and does not imply endorsement by the U.S. Government. We also thank S. Walls, J. Houlahan, and two

anonymous reviewers for comments that improved the manuscript. The authors have no conflicts of interest to declare. Financial support was provided by the USGS Quick Response Program (QRP) and the USGS Amphibian Research and Monitoring Initiative (ARMI). This manuscript is ARMI contribution no. 570.

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Table 1

Surveys of ponds per year, detections of Sonoran Tiger Salamanders and invasive predators, and number of dry ponds in the San Rafael Valley, Arizona (USA), from 2004 to 2013.

Year	Surveyed once	Surveyed twice	Salamanders detected	Invasive predators detected	Dry
2004	15	27	13	8	17
2005	18	24	14	12	17
2006	46	10	8	10	22
2007	36	6	15	10	8
2008	39	5	17	13	18
2009	62	8	15	9	24
2010	49	4	24	8	8
2011	58	10	24	10	9
2012	62	8	23	15	21
2013	50	13	24	12	17

Table 2

Survey and habitat attributes of ponds surveyed from 2004 to 2013. The All sites columns include ponds that were dry.

	All sites (n = 655 surveys)		Inundated sites (n = 482 surveys)	
	mean (SD)	range	mean (SD)	range
Day of survey ^A	170 (45.6)	62– 275	164 (41.1)	62– 275
Pond depth (m)	0.80 (0.74)	0.00– 3.00	1.13 (0.64)	0.01– 3.00
Pond area (m ²)	763 (1228)	0– 14310	1060 (1334)	7– 14310

^ADay within water year (starting on 01 October), where day 170 is March 19.

Table 3

Effect of different fixed probabilities of detection of Sonoran Tiger Salamanders in dry ponds

P(dry) on the estimated trend in pond occupancy from 2004 to 2013.

P(dry)	Trend Estimate	95% Credibility Interval
0.25	2.7%	0.5%–4.9%
0.50	2.5%	0.5%–4.5%
0.60	2.2%	0.4%–3.8%
0.75	2.1%	0.3%–3.8%
0.99	1.7%	0.2%–3.2%

Table 4

Estimated effects (logit scale) of covariates on the probability of detecting Sonoran Tiger Salamanders and invasive predators. The Source model column indicates whether estimates are from the one-species trend model for salamanders or the two-species interaction model.

Covariate	Source model	Sonoran Tiger Salamanders	Invasive predators
Seine ^A	Trend	1.047 (-0.100– 2.184)	2.203 (0.592– 3.698)
	Interaction	0.448 (-0.619– 1.486)	1.656 (0.249– 3.052)
Area ^B	Trend	2.493 (1.474– 3.639)	—
	Interaction	2.019 (1.205– 2.993)	—
Day ^C	Trend	0.933 (0.499– 1.393)	—
	Interaction	0.722 (0.308– 1.152)	—
Day ^C × Day ^C	Trend	-0.075 (-0.360– 0.235)	—
	Interaction	0.093 (-0.178– 0.412)	—

^A Effect of seining a pond.

^B Effect of surface area of the water in the pond.

^C Day of the water year, where March 19 is day 17.

Fig. 1. Ponds included in the analyses of occupancy by Sonoran Tiger Salamanders and non-native, invasive predators in the San Rafael Valley, Arizona, during 2004 to 2013. Black shapes are ponds where salamanders were detected and white shapes are ponds where salamanders were never detected. Circles represent ponds that were part of the original sampling frame and triangles represent ponds on private land that were added to the monitoring program starting in 2009. The horizontal line is the USA-Mexico border.

Fig. 2. The effect of pond area (A) and sample date (B) on probability of detecting Sonoran Tiger Salamanders (from the trend model). The black line represents the mean estimated effect and the gray lines represent the limits of the 95% credible intervals.

Fig. 3. Estimated ($\pm 95\%$ credible intervals) annual occupancy of salamanders and invasive predators in inundated ponds (A) and dry ponds (B). For dry ponds, the estimate is the probability that a pond was occupied at some time during the sampling season. Estimates are from the two-species predator-prey model.

Fig. 4. Estimated ($\pm 95\%$ credible intervals) annual occupancy of salamanders according to the presence or absence of invasive predators in inundated ponds (A) and dry ponds (B). For dry ponds, the estimate is the probability that a pond was occupied at some time during the sampling season.

Fig. 5. Estimated ($\pm 95\%$ credible intervals) effect of pond depth on the annual occupancy of salamanders according to the estimated presence or absence of invasive predators.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.