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Resilience of native amphibian communities following catastrophic drought: Evidence from a decade of regional-scale monitoring

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ABSTRACT

The increasing frequency and severity of drought may exacerbate ongoing global amphibian declines. However, interactions between drought and coincident stressors, coupled with high interannual variability in amphibian abundances, can mask the extent and underlying mechanisms of drought impacts. We synthesized a decade (2009–2019) of regional-scale amphibian monitoring data (2273 surveys, 233 ponds, and seven species) from across California's Bay Area and used dynamic occupancy modeling to estimate trends and drivers of species occupancy. An extreme drought during the study period resulted in substantial habitat loss, with 51% of ponds drying in the worst year of drought, compared to <20% in pre-drought years. Nearly every species exhibited reduced breeding activity during the drought, with the occupancy of some species (American bullfrogs and California newts) declining by >25%. Invasive fishes and bullfrogs were also associated with reduced amphibian occupancy, and these taxa were locally extirpated from numerous sites during drought, without subsequent recovery– suggesting that drought may present an opportunity to remove invaders. Despite a historic, multi-year drought, native amphibians rebounded quickly to pre-drought occupancy levels, demonstrating evidence of resilience. Permanent waterbodies supported higher persistence of native species during drought years than did temporary waterbodies, and we therefore highlight the value of hydroperiod diversity in promoting amphibian stability.

1. Introduction

A widely-recognized result of global climate change is the increased frequency of drought, which has worsened in severity and extent over the past century (Dai, 2013). Drought can trigger widespread mortality (Hillman and Hillman, 1977), shifts in community composition (Batllori et al., 2020), and biotic homogenization (Aguirre-Gutiérrez et al., 2020), with cascading effects on ecosystem function that can last well beyond the cessation of drought (Schwalm et al., 2017). However, some systems are robust to periodic drought, and natural drought regimes can enhance diversity within communities adapted to them (Pérez-Camacho et al., 2012; Prugh et al., 2018). Understanding the factors that confer resistance and resilience to drought is critical to assessing risk to different communities and identifying methods for preserving adaptive capacity (Mahardja et al., 2020).

Amphibians are highly susceptible to drought, especially those species utilizing ephemeral freshwater habitats such as ponds and vernal pools for breeding (Walls et al., 2013). Because temporary ponds often rely on precipitation to fill, they are more sensitive to drought conditions than permanent waterbodies, and during drought they may exhibit reduced hydroperiod or may not fill at all (Brooks, 2009). This results in reductions of breeding habitat that can lead to catastrophic reproductive failure (Pechmann et al., 1991). Further, drought conditions may interact with other stressors in the environment, in some cases reducing an amphibian population's capacity to resist or recover from drought. For example, infectious diseases like chytridiomycosis can alter demographic structure such that populations are less able to compensate for drought-induced recruitment failure (Scheele et al., 2016).

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Moreover, invasive species relying on permanent waterbodies, such as American bullfrogs and predatory fish, can exacerbate the sensitivity of native taxa to drought by decreasing the suitability of key refugia (Ryan et al., 2014). Given widespread declines in amphibian species globally (Stuart et al., 2004), promoting amphibian stability during climatic extremes is a high priority (Shoo et al., 2011), and effective management requires a deeper ecological understanding of the multitude of mechanisms through which drought affects sensitive taxa.

Although drought-induced amphibian declines are well-documented (e.g. Daszak et al., 2005; McMenamin et al., 2008; Zylstra et al., 2019), there is wide variation in species' responses (Davis et al., 2017; Muths et al., 2017; Miller et al., 2018). Numerous species are adapted to successfully reproduce in seasonally-drying wetlands or exhibit phenological and developmental plasticity that buffer against variation in hydroperiod (Wellborn et al., 1996; Jakob et al., 2003). Other species exhibit resistance by switching from breeding in ephemeral to permanent waterbodies during dry years (Lannoo and Stiles, 2020). Species with long-lived adult forms may display resilience, quickly recovering from a skipped breeding season (Mccaffery et al., 2012; Price et al., 2012). Further, local extirpations of drought-intolerant natural enemies (e.g., fishes and bullfrogs) can increase the likelihood of post-drought occupancy by native species (Werner et al., 2009; Hossack et al., 2017). Therefore, even as drought represents a large environmental disturbance, differences in life history strategy, interactions with other stressors, and demographic variability (Pechmann et al., 1991) can lead to complex responses.

Longitudinal monitoring datasets that span both drought and the subsequent recovery period are essential for understanding the consequences of drought and for ultimately mitigating its effects. Because individual monitoring programs are often limited in spatial, temporal, or biological extent, synthesizing multiple monitoring datasets can provide a more holistic view of how environmental change alters communities on larger spatial and temporal scales (Magurran et al., 2010; Maas-Hebner et al., 2015). Analyzing these combined datasets requires accounting for variation in survey techniques across time and space (Maas-Hebner et al., 2015). Dynamic occupancy modeling is one such approach; these methods account for imperfect detection, or cases in which a species is present but not observed (MacKenzie et al., 2017), which is essential when joining information across sampling protocols that differ systematically in detection bias. Dynamic occupancy models also evaluate changes in occupancy status across time, enabling testing of the relationships among local extinction, colonization, and hypothesized predictors (Royle and Kéry, 2007; MacKenzie et al., 2017). By providing more mechanistic insight into the processes shaping occupancy, dynamic occupancy models are a powerful tool for disentangling the effects of multiple stressors and estimating unbiased trends in occupancy.

Herein, we synthesized and analyzed a long-term amphibian occupancy dataset, allowing us to quantify regional trends for an entire community of lentic (i.e., pond) breeding amphibians. Specifically, we combined data from multiple monitoring programs across the past decade (2009–2019) within the California Bay Area, a region of both high biodiversity and heightened drought risk (Connor et al., 2002; Diffenbaugh et al., 2015). Using dynamic occupancy models, we estimated temporal patterns in occupancy for juvenile forms of both native and invasive amphibians and quantified the effects of drought while controlling for land use and the presence of invasive species. These data are particularly useful because they span the duration of the 2012–2015 drought (the most severe drought event in California's recorded history prior to 2020; Griffin and Anchukaitis, 2014, Swain et al., 2014), and 4 years of post-drought recovery. By comparing how multiple species responded to the same extreme climate event, we generate insight into how species that differ in life history strategy and conservation status vary in their resistance and resilience. This information can be used to guide decisions for the management of freshwater systems experiencing the effects of a changing climate.

2. Materials and methods

2.1. Study area

This study was conducted over a 5010 km^2 area located within the East and South Bay of California (Santa Clara, Alameda, and Contra Costa Counties). Study sites (n = 233) consisted of small (<2 ha) modified or constructed stock ponds situated within grassland, chaparral, and oak woodlands and surrounded by a matrix of developed urban areas (Fig. 1). Ponds were located primarily on publicly managed lands supporting multiple uses, including recreation, fisheries, watershed management, grazing, and preservation (Appendix A, Table A.1).

2.2. Survey data

We compiled survey data for six native amphibian species, the California red-legged frog (*Rana draytonii*), California tiger salamander (*Ambystoma californiense*), western toad (*Anaxyrus boreas*), Pacific chorus frog (*Pseudacris regilla*), California newt (*Taricha torosa*), rough-skinned newt (*Taricha granulosa*), and one invasive species, American bullfrog (*Lithobates catesbeianus*). These species vary in the timing of their reproduction and larval development, with American bullfrogs having the longest development time and western toads the shortest (Table A2). Two species, California tiger salamanders and California red-legged frogs, are federally protected following severe population declines (Table A2).

We combined survey data collected between 2009 and 2019 from three separate monitoring programs that were independently conducting pond surveys to evaluate the presence of larval and metamorphic amphibians (Appendix A). We filtered this dataset to include only surveys conducted during the peak period of amphibian larval development (late April – August). Generally, ponds were visited twice per year during this developmental window, and a combination of methods (seines, dip net sweeps, and visual encounter surveys) were employed at each survey visit (Appendix A). For species detection data, we used the overall detection (1) or non-detection (0) of a species across

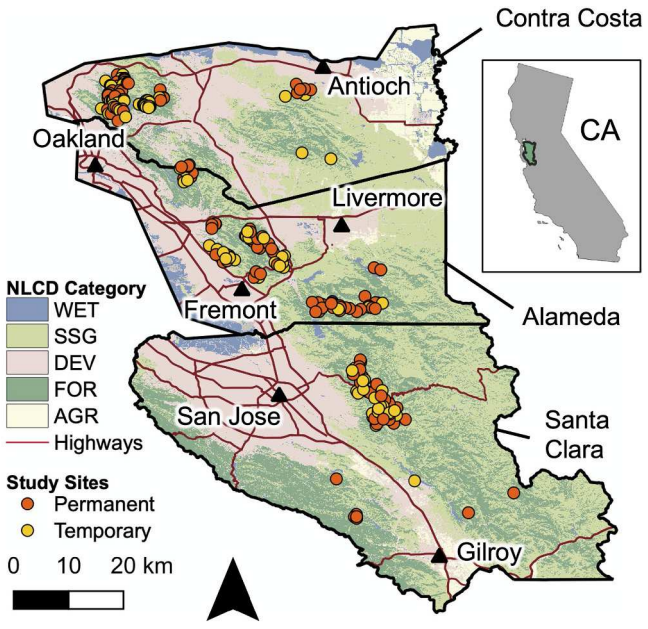

Fig. 1. Locations of 223 ponds surveyed for amphibians in the California Bay Area. Ponds were located within a matrix of open water/wetlands (WET), shrub/scrub/grasslands (SSG), developed (DEV), forest (FOR), and agricultural (AGR) landcover types. Both permanent (n = 138) and temporary (n = 97) ponds were represented. Landcover category was obtained from the National Land Cover Database (NLCD; Homer et al., 2015).

all methods deployed at a given visit, using data on juvenile life-stages only. Only a subset of ponds was surveyed in each year; thus, detection histories included null values for years where a pond was not visited. After pooling data, we further filtered the dataset to include only ponds surveyed in at least 2 years and ponds within the range of each species (Appendix A).

We analyzed data on juvenile life-stages rather than adults because larvae are constrained to the waterbody until metamorphosis, which increases the likelihood of detection and satisfies the assumption of geographic closure in occupancy models (MacKenzie et al., 2017). Analyses reported herein represent trends in the occupancy of juvenile amphibians (e.g. trends in breeding activity), rather than trends in adult occupancy or population abundance.

2.3. Covariate data

We tested the influence of several covariates with the potential to influence amphibian occupancy dynamics (colonization and persistence probabilities), including invasive species, pond hydroperiod, annual weather metrics, and surrounding land use (Table 1). Invasive species (fishes and bullfrog) presence was determined using the same survey methods as native amphibians (Appendix A). We grouped all fish species into one category and all life-stages of bullfrogs into one category. Owing to high detection rates, the presence of fishes and bullfrogs in a given year were modeled as directly observed covariates rather than latent variables (Appendix A). The presence of either taxon during the current year (t) was used as a covariate for colonization, whereas presence during the previous year ($t-1$) was used as a covariate for persistence (Table 1, Appendix A). For sites not surveyed in a given year, we imputed the presence of fish or bullfrogs using the most recent observation (Appendix A).

Table 1
Covariates used in dynamic occupancy models as potential predictors of colonization, persistence, and detection. All continuous variables were centered and scaled. For full model equations, see Appendix A, Eqs. A1–A4.

Covariate name	Description
Colonization and persistence	
Fish[a]	Any species of fish present (1) or not (0)
Bullfrog[b]	Any lifestage of bullfrog present (1) or not (0)
Spring PDSI	Mean Palmer Drought Severity Index, March–June of year t
Fall PDSI	Mean Palmer Drought Severity Index, August–December of year $t-1$
Spring precip	Mean monthly precipitation total (mm), March–June of year t
Winter precip	Mean monthly precipitation total, October (year $t-1$)–February (year t)
Temporary	Pond permanence: whether a pond was classified as temporary (1) or permanent (0)
Spring PDSI × Temporary	Interaction between Spring PDSI and temporary (effect of spring PDSI in temporary ponds)
DEV	Proportion of land within 1 km buffer of pond classified as developed
SSG	Proportion of land within 1 km buffer of pond classified as shrub, scrub, or grassland
Detection	
Seine	Whether seines were used (1) or not (0) at a given survey event
Dipnet	Whether dipnets were used (1) or not (0) at a given survey event
VES	Whether visual encounter surveys were used (1) or not (0) at a given survey event
Julian day	Julian day of a survey event
Year	Year of a survey event
Observer	Group conducting the survey (dummy-coded such that CU is the reference level)

[a] Fish in year prior ($t-1$) was included in persistence model, while fish in current year (t) was included in colonization model.

[b] Bullfrog in year prior ($t-1$) was included in persistence model, while bullfrog in current year (t) was included in colonization model.

We compiled annual variables related to precipitation and drought severity, based on our knowledge of amphibian breeding phenology in the California Bay Area (see Appendix A for detailed description). First, we obtained regional estimates of drought severity using the Palmer Drought Severity Index (PDSI; Palmer, 1965), which ranges from −10 (extremely dry) to 10 (extremely wet). We aggregated monthly PDSI estimates into annual metrics that described either spring PDSI (March–June) in year t or fall PDSI (August–December) in year t-1 (Appendix A). Spring PDSI could impact egg laying and hatching, larval development, and pond inundation, whereas fall PDSI in the year prior could impact the survival and dispersal of metamorphic and adult individuals. We also included an interaction term between spring PDSI and pond permanence to test whether the impact of spring drought was more severe in temporary ponds than in permanent ponds (Table 1). For more fine-scale metrics of weather, we used PRISM (Appendix A; PRISM Climate Group, 2019) to obtain downscaled estimates of mean monthly precipitation at each site during the first and second half of the Bay Area rainy season: winter (October–February) and spring (March–June). Precipitation influences pond inundation and is an important cue for dispersal and egg laying (spring, winter) as well as successful egg hatching (spring).

Site-level (time invariant) data included pond permanence and surrounding landcover. Ponds that held water year-round were classified as permanent, while those that occasionally dried were classified as temporary (for more details see Appendix A). For landcover type, we considered the proportion of shrub, scrub, or grassland landcover (SSG) and the proportion of developed land (DEV) within a 1-km buffer of a pond (Appendix A).

Finally, we included survey-level variables as predictors of detection probability (Table 1). The methods used (seines, dipnets, or visual encounter surveys) were incorporated as separate binary predictor variables, as each survey event could include any combination of these methods. The group conducting the survey was modeled as a dummy-coded categorical variable, as a given survey event was conducted exclusively by one survey group. We also modeled the effects of survey date and year to account for detection rates changing over time (Appendix A).

2.4. Occupancy models

We fit dynamic occupancy models for all species using a Bayesian state-space approach (Royle and Kéry, 2007). Models assumed that occupancy status was constant within a year but varied across years via extinction and colonization (Appendix A). We estimated the probability of occupancy for each species in site i in year t ($\psi_{i,t}$) along with the following parameters:

1. Detection probability ($p_{i,\,k,\,t}$): probability that a species was detected at site i at survey k in year t, given the site was occupied by that species.
2. Colonization probability ($\gamma_{i,\,t}$): probability that a site i that was unoccupied in year t became occupied in year $t+1$.
3. Persistence probability ($\phi_{i,\,t}$): probability that a site i which was occupied in year t remained occupied the following year $t+1$; equivalent to 1 - extinction probability (ε).

Detection, colonization, and persistence probabilities were modeled as functions of covariates previously described (Table 1) using linear models with a logit-link (see Eqs. A.1–A.4 in Appendix A). We fit a separate model for each species containing all covariates for detection, colonization, and persistence (Appendix A). To avoid overfitting and ensure model convergence, we used vaguely informative priors on the logit-scale as suggested by Northrup and Gerber (2018). For full details of model parameterization and fitting, see Appendix A.

3. Results

3.1. Survey data

Our final dataset contained 2273 surveys of 233 unique ponds managed by eight different public and private agencies (Table A.1). Due to local range limits (Fig. A.1; Appendix A), a subset of these data was used in analyses of California tiger salamanders (110 ponds; 1013 surveys), western toads (126 ponds; 1262 surveys), rough-skinned newts (79 ponds; 1158 surveys), and California newts (167 ponds; 1902 surveys). Ponds were monitored across 5.7 years on average, and in years where a pond was monitored, it was generally visited on two separate occasions (mean surveys per year = 1.7; details in Appendix A).

3.2. Drought

Between 2012 and 2015, California experienced extreme drought, which peaked in 2014 (Fig. 2a). Following the low winter precipitation of 2014 (Fig. 2b), pond hydroperiods decreased sharply, with 81% of temporary ponds and 27% of permanent ponds drying in 2014 (Fig. 2a). In 2014, 15% of surveyed sites were dry at the first survey event, suggesting they may not have filled at all. Shorter hydroperiods reduced the occurrence of invasive fish (Fig. 2c), which declined from 20% occupancy before drought (2009–2012) to 8% following drought (2016–2019).

3.3. Amphibian occupancy trends

Mean annual occupancy of juvenile amphibians (averaged across all sites during a year) was strongly affected by drought, with the lowest probability of occupancy occurring between 2013 and 2015 for all species besides California red-legged frogs (Fig. 3). Bullfrogs showed the largest proportional reductions in occupancy, with the proportion of sites occupied falling from 0.22 prior to drought in 2012 (95% confidence interval [0.17, 0.28]) to 0.11 during drought in 2015 (95% CI [0.09, 0.13]) – a loss of 50%. Pacific chorus frogs and California newts also showed large decreases in occupancy, dropping from 0.92 in 2012 (95% CI [0.87, 0.95]) to 0.74 in 2014 (95% CI [0.67, 0.81]) for chorus frogs, and from 0.75 in 2013 (95% CI [0.71, 0.80]) to 0.53 in 2014 (95% CI [0.46, 0.60]) for California newts.

Most species showed evidence of recovery in occupancy after the drought ended in 2015, such that occupancy equaled or exceeded pre-drought occupancy within 2 years (although a second drought in 2018 [Fig. 2] caused a second, short-lived decline in several species [Fig. 3]). The exception to this resilience was bullfrogs, for which mean occupancy had not returned to 2012 levels by 2019 (Fig. 3). The California red-legged frog was the only other species to show a significant decadal trend, with mean occupancy in 2019 (0.49, 95% CI [0.42, 0.56) significantly higher than in 2009 (0.31, 95% CI [0.23, 0.42]). For all other species, long-term occupancy was stable, and the 95% CI at the end of the study (2019) overlapped the 95% CI at the beginning (2009).

3.4. Extinction-colonization dynamics

Dynamic occupancy models estimated the effect of covariates on the log-odds of persistence, colonization, or detection probability (Appendix A). Herein we report coefficient estimates as a mean (β) and standard deviation (SD) of the posterior credibility interval. All coefficient estimates are available in Table A.4 (detection), Fig. A.2 (persistence), and Fig. A.3 (colonization).

Drought severity and pond permanence were strongly associated with species persistence, with species varying in which variables were most informative (Fig. A.2). Bullfrogs and rough-skinned newts were more likely to persist in permanent relative to temporary ponds, with 15.1 and 7.6 times greater odds, respectively (bullfrogs: $\beta_{temporary} = -2.72$, SD = 0.65; rough-skinned newts: $\beta_{temporary} = -2.03$, SD = 0.64).

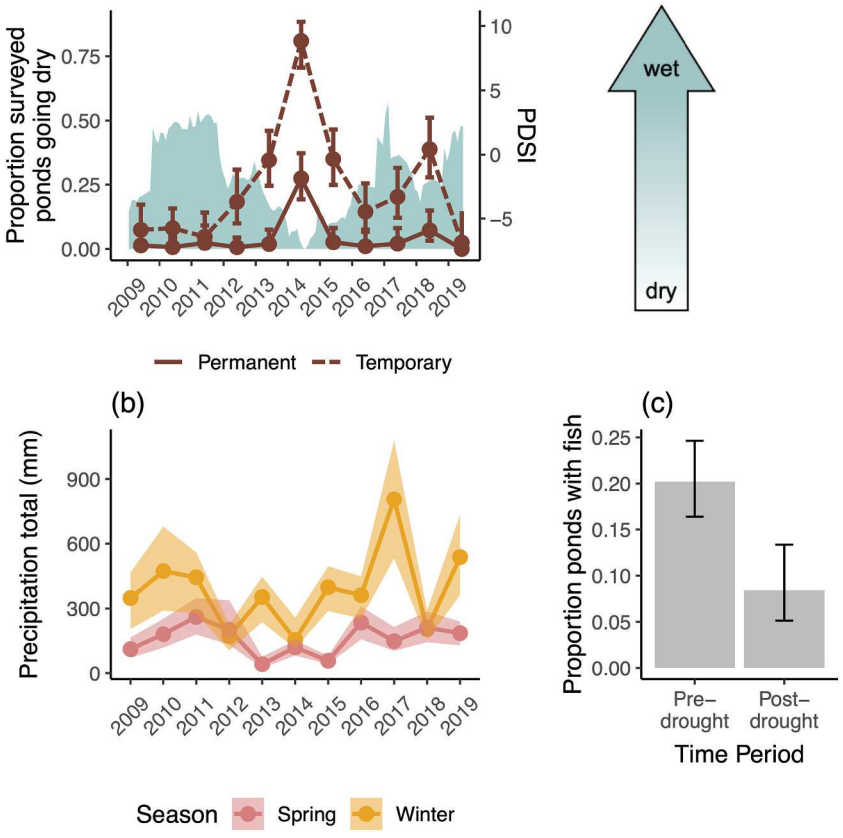

Fig. 2. Impacts of drought on precipitation, pond drying, and fish invasion. (a) The proportion of permanent (solid red) and temporary (dashed red) ponds observed going dry in each summer was inversely related to the Palmer Drought Severity Index (PDSI, in blue; lower values = drier conditions). (b) Precipitation totals in winter (October–February) and spring (March–June), averaged across sites. (c) The proportion of all ponds with fish decreased from pre-drought (2009–2012) to post-drought (2016–2019). Error bars show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

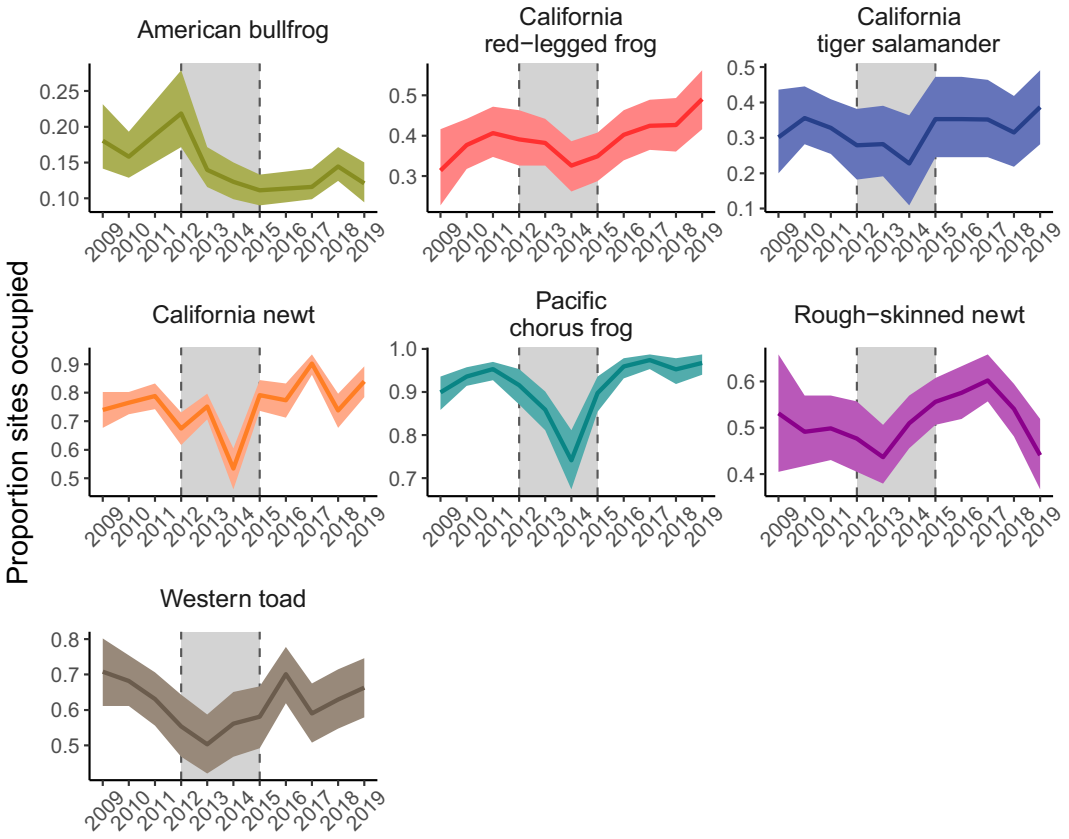

Fig. 3. Proportion of sites occupied by juvenile forms of each amphibian species across the past decade. Plots show mean (solid line) and 95% posterior credibility intervals (ribbon), derived from dynamic occupancy models. Several species exhibited reduced occupancy during the most severe years of drought (gray box). Note that the y-axis differs among species and that proportions are calculated out of only those sites within a species' range (Appendix A).

Pond permanence also interacted with drought to influence persistence. For four species (California red-legged frogs, California newts, Pacific chorus frogs, and California tiger salamanders), persistence was reduced when spring drought was severe, but the effect was larger in temporary relative to permanent ponds (significant interaction between spring PDSI and pond permanence; Fig. 4). Higher winter precipitation was associated with increased persistence for California newts and Pacific chorus frogs ($\beta_{winter\_precip} = 1.33$, SD = 0.49 and $\beta_{winter\_precip} = 0.86$, SD = 0.43 respectively).

Colonization probability was also associated with drought conditions, particularly the amount of precipitation (Fig. A.3). The probability of colonization was positively related to spring precipitation for Pacific chorus frogs ($\beta_{spring\_precip} = 1.08$, SD = 0.55), and positively related to winter precipitation for California newts ($\beta_{winter\_precip} = 1.58$, SD = 0.38). Thus, for these species, drought conditions (lower precipitation) were associated with reduced colonization, although the timing of precipitation was an important component.

Five of the six native species showed reduced persistence or colonization in the presence of invasive species (Fig. A.2, Fig. A.3). Specifically, fish presence was associated with lower persistence for Pacific chorus frogs ($\beta_{fish} = -0.99$, SD = 0.45), California newts ($\beta_{fish} = -2.16$, SD = 0.44), and western toads ($\beta_{fish} = -1.71$, SD = 0.57); translating into a 2.7, 8.7, and 5.5 times greater odds of persisting in the absence of fish, respectively. Colonization probability was lower in the presence of fish for California tiger salamanders ($\beta_{fish} = -2.07$, SD = 0.80; 8 times more likely to colonize a site without fish), Pacific chorus frogs ($\beta_{fish} = -1.86$, SD = 0.67; 6.5 times more likely), and rough-skinned newts ($\beta_{fish} = -2.87$, SD = 0.76; 17 times more likely). While fish presence appeared to affect five of the native species, bullfrogs were only negatively associated with two native species. Rough-skinned newts had reduced persistence in bullfrog-occupied ponds ($\beta_{bullfrog} = -3.80$, SD = 0.64) and California newts had reduced colonization ($\beta_{bullfrog} = -1.59$, SD = 0.55).

Finally, land cover type was an important predictor of colonization probability (Fig. A.3). Western toads and California red-legged frogs were more likely to colonize ponds surrounded by grassland (toads: $\beta_{SSG} = 1.00$, SD = 0.36; frogs: $\beta_{SSG} = 0.55$, SD = 0.21), whereas rough-skinned newts, California newts, and bullfrogs were less likely and thus were expected to benefit from increased forest cover (rough-skinned newts: $\beta_{SSG} = -0.94$, SD = 0.34; California newts: $\beta_{SSG} = -0.63$, SD = 0.31; bullfrogs: $\beta_{SSG} = -0.70$, SD = 0.35; Appendix A). Ponds surrounded by a higher proportion of developed land had reduced rates of colonization for three of the seven species (California tiger salamanders: $\beta_{DEV} = -2.51$, SD = 0.65, bullfrogs: $\beta_{DEV} = -0.68$, SD = 0.36, California red-legged frogs: $\beta_{DEV} = -0.46$, SD = 0.27).

3.5. Detection probabilities

The use of seines, which sample large volumes of open water, increased the probability of detection for nearly all species (6/7 species; Table A.4), whereas dipnet sweeps and visual encounter surveys had variable effects (Table A.4). Surveys conducted later in the summer were associated with decreased detection for California tiger salamanders ($\beta_{day} = -0.59$, SD = 0.24), western toads ($\beta_{day} = -0.43$, SD = 0.12) and Pacific chorus frogs ($\beta_{day} = -0.41$, SD = 0.11), all of which lay eggs early or develop quickly (Table A.2). Later surveys increased detection probabilities for California newts ($\beta_{day} = 0.79$, SD = 0.15), and California red-legged frogs ($\beta_{day} = 0.57$, SD = 0.12), which both take longer to develop.

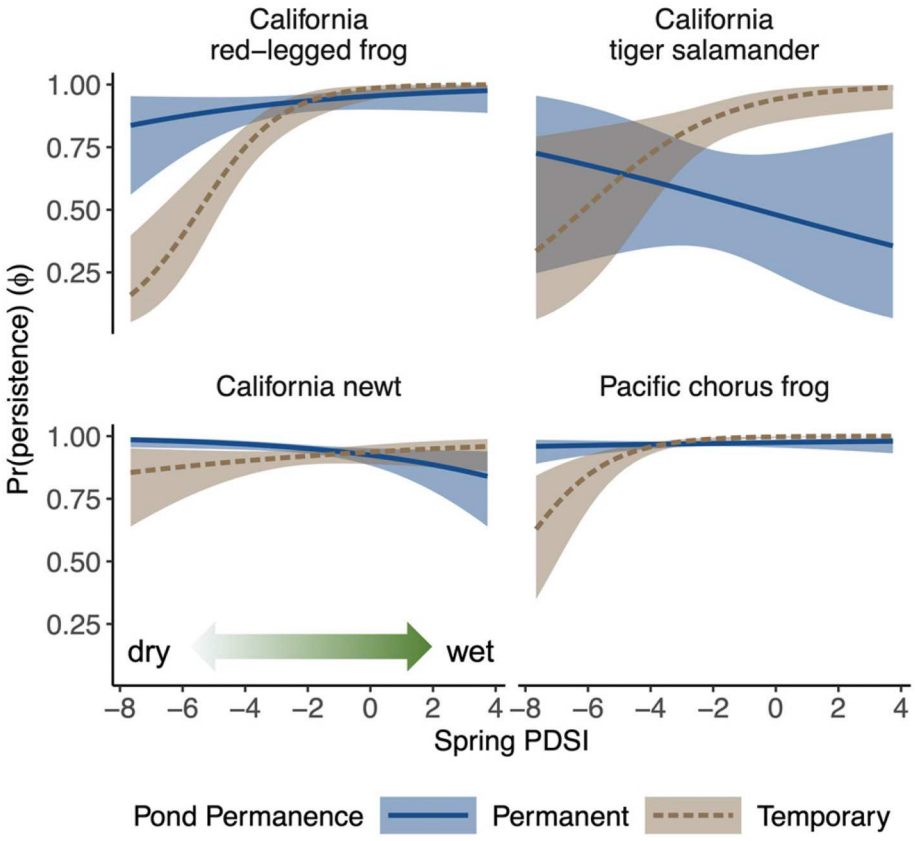

Fig. 4. Relationship between amphibian persistence probability (ϕ), pond permanence, and spring drought (Palmer Drought Severity Index (PDSI); lower values = drier conditions). Lines illustrate predictions (mean ± SD) derived from occupancy models. We show only those species for which the interaction between pond permanence and PDSI was significant; in these species, drought was associated with reduced persistence in temporary ponds.

4. Discussion

By synthesizing over 2000 survey events collected over an extensive geographic range and temporal duration (2009–2019), the current study provides enhanced resolution on how native and invasive species in aquatic ecosystems respond to extreme drought. This dataset coincided with California's most severe drought in more than 1000 years (Griffin and Anchukaitis, 2014), providing a unique opportunity to quantify both the initial responses and subsequent recovery of an entire community to this large disturbance. Using dynamic occupancy models, we linked drought conditions to changes in juvenile occupancy through extinction and colonization dynamics. Although amphibians were sensitive to drought in general, the management of more permanent waterbodies appeared to contribute to population persistence, and native amphibians recovered to pre-drought occupancy levels in the years following drought. On the other hand, non-native fish and bullfrogs were lost from several permanent ponds that dried during drought, and did not appear to recover by the time of this writing. These findings indicate that even in a system facing extraordinary variation in climate and multiple concurrent threats, native species can display high resilience and long-term stability.

4.1. Drought and recovery

A major impact of the 2012–2015 severe drought was the loss of breeding sites, with more than half of monitored ponds failing to hold water throughout the developmental season in 2014 – including many sites previously considered "permanent" (Fig. 2). The reduced availability of breeding sites was a major mechanism by which drought affected amphibian species, as evidenced by sharply reduced occupancy in 2014 (Fig. 3) and the relationship between hydroperiod, drought, and persistence for several species (Fig. A.2). Our finding agrees with other studies demonstrating that wetland dry-downs severely lower amphibian occupancy (e.g. McMenamin et al., 2008; Werner et al., 2009; Zylstra et al., 2019). Reduced precipitation was also linked to lower colonization and persistence rates for a number of species, suggesting that drought likely affected amphibians not only through loss of breeding sites, but also by altering important cues for breeding and dispersal, such as seasonal precipitation (Cayuela et al., 2014).

Two species (the rough-skinned newt and western toad) showed no significant relationships between drought variables and persistence or colonization– an interesting pattern given their different life histories. Western toads may be relatively drought-tolerant due to their short development times (the fastest of any species in this study system; Table A.2), which could allow them to complete metamorphosis prior to ponds drying. Rough-skinned newts were more likely to occur in permanent sites (Fig. A.2, Fig. A.3), and can also use streams, lakes, and reservoirs as refugia (Stebbins and McGinnis, 2012), which perhaps explains their insensitivity to the drought variables modeled herein. The differences in the timing and magnitude of drought-induced declines across species (Fig. 3) indicate that habitat preferences or demographic traits are likely to moderate drought resilience in amphibians and which specific variables are useful in predicting breeding success.

Only one amphibian, the invasive American bullfrog, failed to recover quickly following drought (Fig. 3). Bullfrogs have the longest larval development of any species in this study (Table A.2), and are less able to modify developmental rates in response to drying (Cook et al., 2013). As expected, bullfrogs relied on permanent ponds, with the odds of persistence 15 times higher in permanent relative to temporary ponds. Moreover, the probability of a bullfrog colonizing a previously unoccupied site was only 0.01, the lowest of any species (Fig. A.3). While bullfrogs have high dispersal potential, it is strongly mediated by

landscape features, including the distribution of wetland "stepping stones" (Peterson et al., 2013). Wetland landcover was rare within the study area (Fig. 1), with 40% of ponds containing no wetland cover within 1 km. Thus, recruitment failure during drought, paired with low colonization rates, likely inhibited bullfrog recovery following drought.

The associations between landcover type surrounding each pond and occupancy dynamics reinforce the importance of both upland and wetland habitats for amphibian population persistence (Trenham and Shaffer, 2005). For example, developed landcover was associated with lower colonization probability for three of seven species (including both protected species). The mechanisms by which habitat development reduces colonization include physical barriers to movement, lack of cover, and insufficient moisture (Hamer and McDonnell, 2008). Alternatively, grassland and scrub habitat were associated with higher colonization for western toads and California red legged frogs, whereas the two newt species were more likely to colonize where forest cover was high, consistent with previous studies and reflecting species-specific habitat relationships (Pearl et al., 2005; Fellers and Kleeman, 2007; Searcy et al., 2013). Resilience to disturbances such as disease, drought, and invasions are typically moderated by the ability of amphibians to recolonize following local extinctions (e.g. metapopulation dynamics, Cosentino et al., 2011; Heard et al., 2015). Similarly, we identified a strong relationship between colonization probability and land cover type, confirming the importance of landscape context to recovery.

4.2. Invasive species and hydroperiod

Promoting amphibian resilience to future climate conditions poses a challenging compromise, in that creating more permanent waterbodies provides refugia during drought, but may also facilitate species invasions (Shoo et al., 2011). The influence of invasive species in permanent ponds was notable, particularly for fishes, which reduced the persistence or colonization of several native amphibian species. In contrast, bullfrogs did not appear to limit the occupancy of native amphibians broadly, a finding in line with other studies in the western United States that revealed fish to be a more detrimental invader (Pearl et al., 2005; Adams et al., 2011). However, we acknowledge that by focusing on amphibian occupancy, rather than density, we may have underestimated the impacts of bullfrogs on native amphibians.

Interactions between pond hydroperiod and drought (Fig. 4) indicated that permanent ponds were more effective at maintaining amphibian persistence during dry years than were temporary ponds. Thus, permanent ponds were valuable to native and not just invasive taxa. The interaction between pond permanence and drought was particularly notable for the endangered California tiger salamander, which had higher persistence in temporary ponds during normal to wet years (perhaps due to the presence of invasive taxa in permanent ponds) but reduced persistence in temporary ponds in dry years, likely from drying (Fig. 4). Altogether, this suggests that the value of a given hydroperiod is modified by climatic conditions. The potential value of permanent waterbodies was also enhanced by the extinction and lack of re-colonization by invasive fishes (Fig. 2) and bullfrogs (Fig. 3) at several sites. While sample sizes prevented us from explicitly testing the impact of this decline in invasive species, we note that in locations that gained red-legged frogs over the past decade ($n = 21$), six were sites where invaders were lost. More than half (59%) of the ponds in the study area were classified as permanent, perhaps explaining why, despite severe drought, populations were more resilient than in other systems in the western United States (McMenamin et al., 2008; Zylstra et al., 2019). This study contributes to a growing body of literature emphasizing that a complex of lentic waterbodies with diverse hydroperiods can buffer against the concurrent threats of invasions and climate change, especially when species display plasticity in habitat use (Shoo et al., 2011; Lannoo and Stiles, 2020).

4.3. Conclusions and recommendations

Our study locations – primarily stock ponds situated within a highly urbanizing region – represent a departure from the ephemeral vernal pools that once occurred throughout the California Bay Area (Grossinger et al., 2007). Native species within these systems face concurrent threats of species invasions, climate change, and habitat modification both at the local (e.g., pond hydroperiod) and regional (land use change) scales. Despite expectations that these threats would strongly reduce amphibian viability, native amphibians showed no evidence of declines in occupancy over the past decade. The threatened California red-legged frog additionally showed evidence of a long-term increase in occupancy. These findings highlight the importance of managed ponds in providing breeding habitat for native amphibian species and facilitating their persistence following the loss of their original aquatic habitats. Our research additionally suggests that episodic drought can provide momentum for invader eradication efforts, including draining specific ponds to disproportionately eliminate non-native taxa. However, we note that as of 2021, California was again experiencing an exceptional drought, and the increasing frequency of such events may mean that amphibian populations cannot fully recover before the next drought begins. Considering this, our work provides further support for the benefit of managing for hydroperiod diversity. Maintaining a network of closely located ponds along a hydroperiod gradient is likely to enhance regional-scale resilience for multiple species as climate variability increases.

Authorship contribution statement for BIOCON-D-21-00256

Monitoring programs were supervised by SB, JP, and PTJJ. TM-G, JP, SB, WEM, and PTJJ collected amphibian survey data. PTJJ, WEM, TM-G, and EM contributed to design of the study. WEM analyzed data and wrote the initial manuscript. All authors contributed to reviewing and editing the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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