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Disentangling effects of invasive species and habitat while accounting for observer error in a long-term amphibian study

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Abstract. The invasive American bullfrog (*Lithobates catesbeianus*) and a variety of non-native sport fish commonly co-occur in lowland lentic habitats of the western United States. Both invasive taxa are implicated in declines of native amphibians in this region, but few long-term studies of communities exist. Further, field studies of invasive–native interactions are complicated by confounding habitat modifications and observation errors. We surveyed amphibians and measured habitat characteristics for 12 yr across 38 wetland sites within the Willamette Valley, Oregon, USA. We assessed the influence of invasive species, habitat, and their interactions on the distributions of five native amphibian species using a multispecies dynamic occupancy model that accounted for false-negative and false-positive detections. In general, habitat characteristics—such as within-pond vegetation cover, surrounding forest, and drought severity—were important for local persistence of native species when bullfrogs co-occurred. We also found evidence of a cumulative negative effect of bullfrogs and non-native fish (families Centrarchidae and Ictaluridae) on northern red-legged frog (*Rana aurora*) local persistence that was mediated by the dominance of invasive reed canarygrass (*Phalaris arundinacea*). Non-native fish and bullfrogs had variable effects on native amphibian species, but neither invasive taxon appears to be causing declines in occupied sites within our study area. Moreover, species relationships with habitat differed when invaders were present, indicating that certain habitats may increase persistence of native amphibians in the invaded landscape.

Key words: bullfrog; coexistence; co-occurrence; habitat; non-native fish; occupancy dynamics; restoration.

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INTRODUCTION

Biological invasion is a major cause of ecosystem transformation and biodiversity loss (Wilcove et al. 1998, Simberloff et al. 2013, Gallardo et al. 2016, Ricca et al. 2016). The rise of anthropogenic transport pathways and habitat alteration mean that, increasingly, species communities assemble under environments or disturbance regimes that differ from the historical conditions in which they coevolved (Seastedt et al. 2008). In this era of novel ecosystems, it is common for communities to include multiple invasive species of different trophic levels that cause ecological and/or economic harm (Johnson et al. 2009, Ricciardi and MacIsaac 2011).

Interactions among invaders produce complex ecological responses that challenge management and restoration efforts (Strayer et al. 2006, Preston et al. 2012). Multi-invader interactions can exacerbate (i.e., facilitation; Adams et al. 2003, Heimpel et al. 2010) or mediate (i.e., exclusion or density control; La Pierre et al. 2010, Hudina et al. 2011) effects on native species through a variety of direct and indirect pathways. The habitats in which invasive and native species co-occur can also strongly influence the outcomes of their interactions. For example, in Atlantic Canada, native mud crab mortality was lowest in oyster bed habitats compared to unstructured (i.e., sandy sediment) habitats when invasive European green crabs (*Carcinus maenas*) were present, suggesting habitat complexity mediated predator–prey dynamics (Gehrels et al. 2016). These context-dependent interactions demonstrate the importance of considering invader impacts within the framework of community composition, habitat, and evolutionary relationships.

In the lowlands of the Pacific Northwest, the invasive American bullfrog (*Lithobates catesbeianus*) and non-native warm-water fishes (i.e., bluegill, bass, bullhead catfish, and others) are widely distributed and commonly co-occur with native amphibian species in lentic systems. Non-native fish can have negative effects on native amphibian distribution (Joseph et al. 2016), individual survival (Goodsell and Kats 1999, Adams 2000, Hamer and Parris 2013), somatic growth (Lawler et al. 1999, Nyström et al. 2001), and behavior (Lawler et al. 1999, Davis et al. 2012). The evidence linking bullfrogs to native amphibian declines, however, is more inconsistent. Bullfrogs in their invasive western range have been cited as a threat to native amphibians based on the observed inverse relationship between bullfrog and native amphibian abundance and distribution in some populations (e.g., *Rana boylii* and *Rana aurora* in Moyle 1973). However, conclusions are limited by confounding interrelated stressors such as non-native fish, disease, contaminants, or habitat alteration inducing niche partitioning (Hayes and Jennings 1986). Agonistic interactions between invasive bullfrogs and native species have been detected in experimental studies (Kiesecker and Blaustein 1997, Kupferberg 1997, Pearl et al. 2004), but field observational studies from the Northwest suggest bullfrogs alone are weak predictors of native amphibian occurrence patterns (Richter and Azous 1995, Adams 1999, Pearl et al. 2005, Cook and Jennings 2007, Adams et al. 2011, Rowe and Garcia 2014). Experimental studies exploring the combined effects of invasive bullfrogs and non-native fish on native amphibians have had mixed, species-specific outcomes (Kiesecker and Blaustein 1998, Lawler et al. 1999, Adams 2000, Preston et al. 2012).

Inconsistent reports of invasive bullfrog effects on native amphibians may also result from failure to study species interactions within a community context or over adequate time frames. Understanding invasion outcomes requires long-term monitoring to separate real spatiotemporal variation in species occurrence from observation error. Moreover, native–invasive interactions can be intensified or mediated by local and landscape habitat characteristics including climate (Melbourne et al. 2007, Ousterhout et al. 2015). Within-pond physical heterogeneity and vegetation structure can increase availability of refugia from predators and diffuse competition (Hartman et al. 2014, Anderson and Semlitsch 2016, Kenison et al. 2016). Dominant plant species, such as invasive reed canarygrass (*Phalaris arundinacea*), can affect both native and invasive amphibians by modifying wetland structure and function, prey resources, and water chemistry (Spyreas et al. 2010). Proximal forest cover can provide valuable habitat and movement corridors for terrestrial adults outside the breeding season and support population persistence (Trenham and Shaffer 2005). Hydroperiod alteration caused by drought, direct management, or evapotranspiration by aggressive plant invaders can influence amphibian exposure to predators and survival through metamorphosis (Walls et al. 2013, Hossack et al. 2017). Yet, under an optimal range of habitat conditions, subordinate native species may persist with harmful invaders (Cook and Jennings 2007). Thus, the direction and strength of native species habitat associations is expected to vary as a function of community composition and individual traits.

In addition to inherent complexities of natural systems, studies of invasive species' effects on native communities are complicated by observation error, particularly when species are part of an assemblage. False-positive (a species absent

from a site is incorrectly recorded as present) and false-negative (a species occupying a site is undetected) detections can both lead to biased estimates if not accounted for in the analysis of survey data. This is especially problematic when one species alters the behavior of another species, affecting its probability of detection. For example, California red-legged frogs (*Rana draytonii*) shifted habitat use from bare shore to willow-dominated banks when bullfrogs were present and created the illusion of reduced native abundance in the presence of bullfrogs (D'Amore et al. 2009). These potential observation biases must be addressed to reliably evaluate the relationship between invaders and population responses of native species.

Here, we report on a 12-yr study of amphibian occurrence dynamics in a multi-invader community in the Willamette Valley, Oregon, USA. Our objectives were to (1) determine the individual and cumulative effects of non-native fish and bullfrogs on native amphibians, (2) assess the influence of habitat, including the presence of another common wetland invader, reed canarygrass, on amphibian occurrence dynamics, and (3) evaluate whether habitat relationships differ for native species in the presence or absence of bullfrogs. We developed a multispecies dynamic occupancy model to derive estimates of colonization, persistence, and detection probabilities to understand the factors contributing to native amphibian population success in the presence and absence of invasive species. We also compared patterns in proportion of occupied sites for each species to assess population status over time.

Methods

Study system

The Willamette Valley is an agricultural and urbanizing lowland spanning north–south ~290 km between Eugene and Portland at a width of ~20–60 km along the Willamette River, Oregon, USA (Hulse et al. 1998). The region experiences a cool Mediterranean climate, with average annual precipitation of 100–125 cm (Jackson and Kimerling 1993). Amphibians native to this area include the Pacific chorus frog (*Pseudacris regilla*), northern red-legged frog (*R. aurora*), rough-skinned newt (*Taricha granulosa*), northwestern salamander (*Ambystoma gracile*), and long-toed salamander (*Ambystoma macrodactylum*). The red-legged frog is designated a species of concern in the Willamette Valley ecoregion (Oregon Conservation Strategy 2016). The Oregon spotted frog (*Rana pretiosa*) and western toad (*Anaxyrus [=Bufo] boreas*) are also native but appear to be extirpated from the valley floor. Bullfrogs and non-native fish were introduced to this area starting around the early 1920s and 1880s–1890s, respectively (Lampman 1945, Hayes 1994).

Our scope of inference was wetlands within the U.S. Fish and Wildlife Service Willamette Valley Wetlands Complex and the Bureau of Land Management West Eugene Wetlands Complex. We randomly selected 42 wetlands out of 69 that we thought remained inundated annually through June to support amphibian metamorphosis. We later omitted four wetlands that did not meet this criterion, resulting in 38 wetlands that were surveyed across five discrete National Wildlife Refuge or landownership boundaries (Fig. 1). We considered wetlands representative of independent populations because each site was separated from its nearest neighbor by a distance exceeding amphibian dispersal movements or by a physical barrier (e.g., paved road; Grand et al. 2017). Sites within the same landownership boundary were separated by a mean distance of 2.17 km (standard error = 0.08). Some wetlands received active hydrological or habitat management, but our study sites were relatively protected from agriculture and development compared to other wetlands in the valley.

Amphibian and fish surveys

We sampled sites annually from 2004 to 2015 between 8 April and 22 June. For wetlands >1 ha (N = 12), we selected an accessible area (<1 ha) with probable amphibian habitat to survey. We set 10 collapsible mesh minnow traps (5.8 cm funnel diameter) at evenly spaced intervals around the survey area; trap locations remained consistent among years. Traps were placed parallel to the shore on substrate in the shallow wetland margin so that at least 2.5 cm of airspace remained at the top. Traps were set after noon and were checked and removed within 24 h. In 2004 and 2005, we set traps during one annual visit to each site. Beginning in 2006, a subset of 10 sites was randomly selected for a second visit 1–3 weeks after the first sampling date. In 2006,

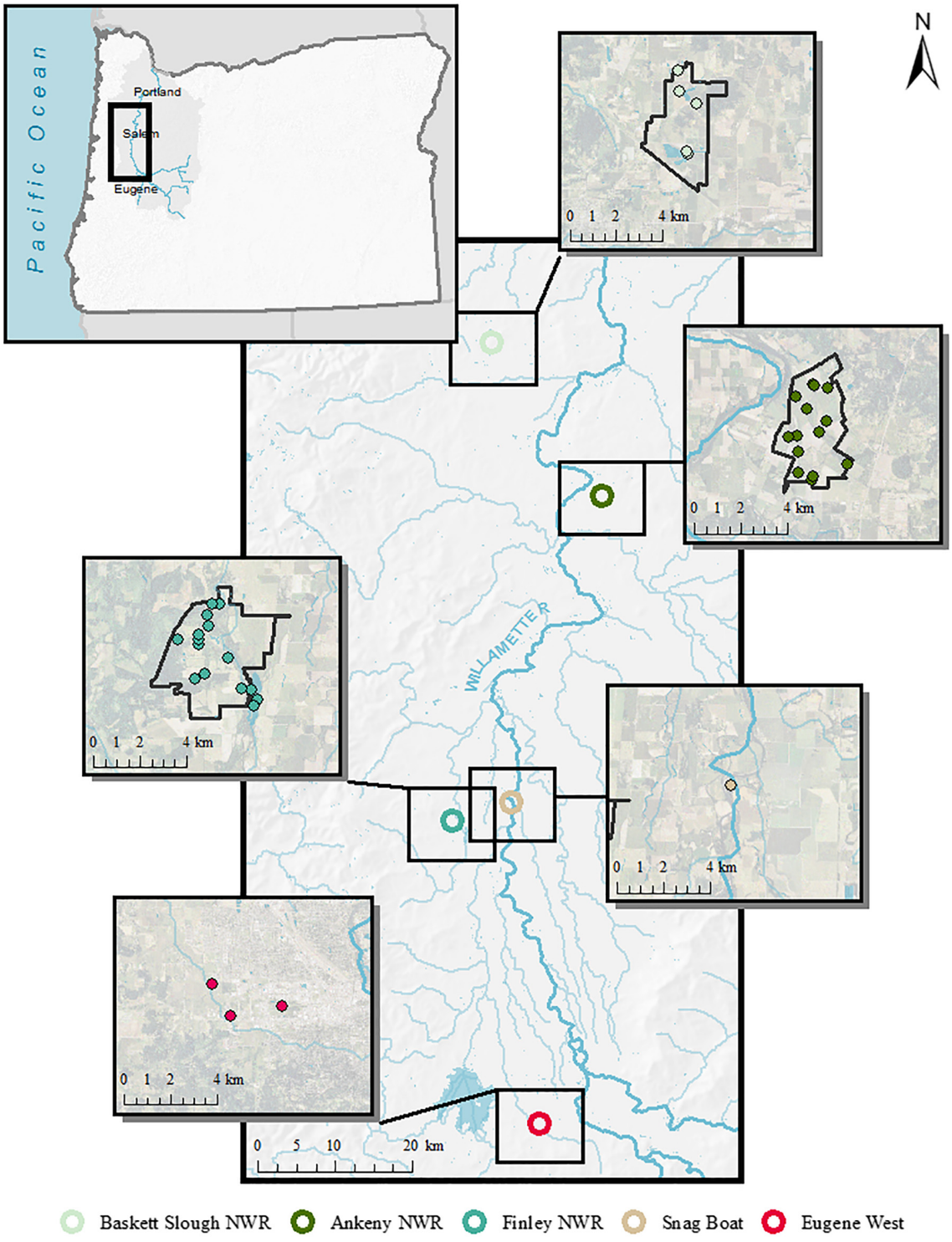


Fig. 1. Map of wetland complexes within the Willamette Valley, Oregon, USA, surveyed for amphibians. Insets show National Wildlife Refuge (NWR) boundaries and sampling locations at each complex. All coordinates are in Universal Transverse Mercator (UTM) Zone 10 in NAD 1983 datum.

we set 10 traps per site during the second sampling event, and in all subsequent years, we set five traps per site during the second sampling event due to logistical constraints. Because we were interested in understanding breeding population dynamics, we considered an amphibian species detected during a site visit if we found a life stage representing evidence of reproduction (larva, metamorph, or paedomorph) in at least one trap. From 2009 through 2015, we recorded data on fish detections, defined as any life stage captured in at least one trap during a sampling season. Our analysis of non-native fish is limited to the families Centrarchidae and Ictaluridae, taxa that are widespread in the region and that have high potential to predate and alter behavior of amphibians.

Habitat variables

We selected annual, site-level, and observation-level variables hypothesized to influence probabilities of detection, local persistence, and colonization for amphibians. During each site visit, we recorded the percent of inundated area covered by emergent vegetation (visually estimated to the nearest 5%), whether reed canarygrass was among the three emergent plant species with greatest coverage, and the percent of pond perimeter with trees >5 m tall within 5 m of high waterline (visually estimated to the nearest 5%). Percent emergent vegetation was expected to influence detection probability because dense cover can provide refugia for amphibians and influence trap effectiveness. Vegetation structure and function also influence the quality of breeding and rearing habitat (Richter and Azous 1995, Pearl et al. 2005, Adams et al. 2011), so we hypothesized percent emergent vegetation and dominance of reed canarygrass would be related to the probability of local persistence. Because reed canarygrass is common in amphibian habitats and often forms monotypic stands of exceptionally high biomass relative to native wetland plants, we were particularly interested in whether dominant reed canarygrass could alter invasive–native interactions at higher trophic levels. We expected percent forested perimeter to be related to amphibian persistence. Native lentic-breeding amphibians of the Willamette Valley use upland habitats outside the breeding season for foraging and overwintering (Nussbaum et al. 1983), and previous work using the first five years of this dataset indicated proximal forest is associated with reduced local extinction probabilities for red-legged frogs (Adams et al. 2011). Estimates of percent emergent vegetation and forested perimeter were averaged over surveys and years to create variables that varied by site but were static across time. We created a binary site-level variable for reed canarygrass dominance based on whether it was recorded as one of the top two dominant emergent species most years.

Landscape variables were derived using ArcMap 10.3 (ESRI 2014). We estimated the area of forest cover within a 1-km buffer of each site, extracted from the 2011 National Land Cover Database raster (Homer et al. 2015), to represent landscape permeability, which is linked to the probability a site is colonized. We selected the buffer distance of 1 km because there is previous research suggesting forest cover within 1 km from a breeding site is especially valuable to several species (Pearl et al. 2005, Guderyahn et al. 2016, Grand et al. 2017). Precipitation patterns can influence the availability of breeding habitats, developmental and breeding phenology, and dispersal and colonization dynamics (Petranka et al. 2004, Hossack et al. 2013, Walls et al. 2013, Anderson et al. 2015). Therefore, we derived two landscape variables to describe the availability of aquatic habitat during breeding and emergence. We hypothesized the amount of summer wetland inundation surrounding the site would represent availability of potential breeding habitats and affect probability of colonization. We estimated inundated area within a 1-km radius centered on each site from a National Wetlands Inventory polygon shapefile representing the typical surface water extent from June through August (U.S. Fish and Wildlife Service 2014). The shapefile was proofed for accuracy using 3-m digital elevation model contours, U.S. Department of Agriculture Oregon National Agriculture Imagery Program imagery, and expert site knowledge. We also derived wetland drawdown by calculating the percent difference between winter (January or February) and summer (August or September) inundated area for each study site because amphibian local extinction probability is often linked to hydroperiod (Cayuela et al. 2012, Salice 2012). We

estimated inundated area from aerial imagery, elevation contours, and light detection and ranging data collected during a typical water year, 2003 or 2015.

We used average monthly Palmer Drought Severity Index (PDSI) values for the Willamette Valley (Division 2) to describe drought severity each year (data downloaded from the National Climatic Data Center on 18 July 2016). The Palmer classification scale is centered on 0 and spans −4 (extremely dry) to 4 (extremely wet), with negative values indicating drought conditions and increasing positive values indicating greater water availability. We hypothesized the amount of water available from February to July would influence the probability of local persistence. Similarly, we hypothesized the same metric with a one-year lag would influence the probability a site is colonized because drought in year t could influence sites available to philopatric breeding adults in year $t + 1$.

Non-native fish occupancy model

We developed a single-season occupancy model for non-native fish, which allowed us to estimate fish occupancy (ψ^{fish}) and detection probabilities (p^{fish}; Appendix S1). We assumed any changes in occupancy state at a site over our study period were random and interpret the fish occupancy parameter as the probability of site use, or the probability non-native fish ever occupied a site over the study period (MacKenzie et al. 2017). We included covariates hypothesized to influence probability of fish site use, including percent emergent vegetation, site drawdown, area of inundation within a 1-km buffer during the winter (proxy for landscape permeability for dispersal), and maximum water depth at a site (factor: shallow <1 m, moderately deep 1–2 m, or deep >2 m). We hypothesized non-native fish detection probability was related to percent emergent vegetation.

Multispecies dynamic occupancy model

We developed a multispecies dynamic occupancy model to assess what factors governed occurrence of amphibians (MacKenzie et al. 2003, Royle and Kéry 2007). Dynamic occupancy models require repeated observations or surveys for each site over time. Survey data are separated into primary and secondary occasions. It is assumed the occupancy state is static across secondary occasions (i.e., within a primary occasion), but the species distributions can exhibit turnover between primary occasions. For our study, primary occasions were the sampling seasons (i.e., years), and secondary occasions were multiple visits within a season. For each amphibian species, the model estimates the initial probability a site was occupied (ψ_1), the probability a species was detected during a site visit given it was present (p), the probability an unoccupied site in year t was newly colonized in year $t + 1$ (γ), and the probability an occupied site in year t remained occupied in year $t + 1$ (i.e., local persistence, ϕ). We relied on covariate information and our 12 yr of monitoring data to estimate initial occupancy probability in year 0 (i.e., the year prior to our monitoring efforts), which was modeled as a constant using a beta distribution. This allowed us to use all 12 yr of monitoring data to estimate factors related to probabilities of colonization and local persistence, which were the focus of our study. All other parameters were modeled using logistic regressions. We first attempted to fit the model using a community structure (Kéry and Royle 2008, Zipkin et al. 2012), where predictor variables for native species share an additional hierarchical component (i.e., species-specific parameters as random effects drawn from a common distribution); however, this model could not converge. Therefore, we parameterized the model so that each native amphibian species had separate model intercepts and coefficients, except when modeling potential false-positive detections (Appendix S1).

In addition to the hypotheses outlined above, we investigated whether habitat and invaders influenced native amphibian dynamics. Specifically, we wanted to assess if bullfrog presence and non-native fish site use reduced probabilities of native amphibian detection, colonization, and local persistence; if the effect of habitat characteristics and non-native fish on native amphibian local persistence probabilities varied with bullfrog presence; and if there was evidence that reed canarygrass intensified or mediated a combined effect of bullfrogs and non-native fish on local persistence probabilities. To assess the effects of multispecies interactions on local persistence, we used the model parameterization of Waddle et al. (2010), where a different local persistence

model is applied based on bullfrog presence (latent occupancy). We modeled effects of fish site use on all parameters and bullfrog effects on probabilities of detection and colonization using factor variables representing fish and bullfrog presence (Appendix S1). The global model for local persistence of native amphibians when bullfrogs were absent included percent emergent vegetation, reed canarygrass dominance, percent forested pond perimeter, PDSI, site drawdown, and fish site use (Tables 1, 2; Appendix S1). The global model for local persistence of native amphibians when bullfrogs were present included the same factors as above, but we also incorporated an interaction between fish use and reed canarygrass dominance. The global model for native amphibian colonization included area of summer wetland inundation within 1 km, area of forest cover within 1 km, PDSI in previous year, fish use, and the presence of bullfrogs (Table 1, Fig. 2; Appendix S1). The global model for native amphibian detection included percent emergent vegetation, the number of traps set each site visit (trap effort), the ordinal day from the start of each survey year to capture variability in amphibian phenology, fish use, and the presence of bullfrogs (Tables 1, 2, Fig. 2; Appendix S1). The global detection, local persistence, and colonization models for bullfrogs contained the same parameters as described above, with the exclusion of the model intercepts and coefficients related to bullfrog effects.

Using the multispecies dynamic occupancy model allowed us to correct our monitoring data for false-negative detections. However, northwestern and long-toed salamanders are morphologically similar in early life stages (Tihen 1958), which can also potentially introduce false-positive detections when one species is mistaken for the other. Even a small number of false-positive detections (e.g., 5%) can lead to a significant bias in occupancy model parameter estimates (Royle and Link 2006, Miller et al. 2011). Therefore, we incorporated the site confirmation design to account for this process in our model (reviewed in Chambert et al. 2015). This approach avoids bias in estimates by accommodating both ambiguous and unambiguous species detections,

Table 1. Mean, standard deviations (SD), and upper and lower 95th percentile of measured predictor variables used in the multispecies dynamic occupancy model and the non-native fish occupancy model.

Variable	Range (or sample size)	Mean	SD	Lower percentile	Upper percentile	Varied by	Covariate for
Ordinal day	98–173	138.3	15.5	110.8	167.0	Site × Survey × Year	p
Trap effort	5–10	9.3	1.8	5.0	10.0	Site × Survey × Year	p
Emergent vegetation (%)	6.8–87.3	55.5	25.5	14.4	87.3	Site	p, ϕ, p^{fish}, ψ^{fish}
Forested perimeter (%)	0–87.7	21.7	25.6	0.0	83.1	Site	ϕ
Drawdown (%)	0–100	64.4	35.8	0.0	100.0	Site	ϕ, ψ^{fish}
PDSI survey window	−2.4 to 2.8	−0.3	1.7	−2.3	2.7	Year	ϕ
Reed canarygrass dominance	Dominant (n = 19), not dominant (n = 19)	–	–	–	–	Site	ϕ
Forest cover (ha)	0–104.3	20.3	29.9	0.0	95.7	Site	γ
Summer inundated area (ha)	3.9–52.3	22.6	15.8	4.2	51.9	Site	γ
PDSI recruitment window	−2.1 (dry) to 2.8 (wet)	−0.1	1.6	−2.0	2.7	Year	γ
Season	Early (n = 642), late (n = 270)	–	–	–	–	Site × Survey × Year	b, p_{10}
Depth	<1 m (n = 6), 1–2 m (n = 20), >2 m (n = 12)	–	–	–	–	Site	ψ^{fish}
Winter inundated area (ha)	6.3–100.9	47.3	20.4	20.2	90.8	Site	ψ^{fish}

Notes: PDSI, Palmer Drought Severity Index. Parameters estimated by the multispecies dynamic occupancy model included detection probability (p), probability of classifying an ambystomatid salamander detection as unambiguous (b), probability of an erroneous ambystomatid salamander detection (p_{10}), colonization probability (γ), and local persistence probability (ϕ). Parameters estimated for the non-native fish occupancy model included non-native fish detection probability (p^{fish}) and probability of non-native fish site use (ψ^{fish}). Summary statistics not relevant for factor variables are indicated by en dash.

Table 2. Parameter estimates, standard deviations (SD), upper and lower limits of the 90% credible intervals (CI), and odds ratios (OR) for non-native fish site use (ψ^{fish}) and detection probability (p^{fish}) from the best fitting single-season occupancy model.

Parameter	Mean	SD	Lower CI	Upper CI	OR
ψ^{fish}					
Intercept	0.161	0.698	−0.926	1.364	1.18↑
Emergent vegetation	−1.097	0.537	−2.018	−0.263	3.03↓
Winter inundated area	0.455	0.575	−0.401	1.481	1.58↑
Depth	1.745	0.861	0.368	3.195	5.73↑
p^{fish}					
Intercept	−1.833	0.286	−2.313	−1.372	6.25↓

Notes: Odds ratios are given as the absolute magnitude of the effect, with arrows indicating the direction of the relationship. The reference categories for depth are shallow (<1 m) or deep (>2 m) water depth (i.e., the effect shown is for moderate depth compared to shallow and deep, which had identical means).

where unambiguous detections are known with certainty and ambiguous detections could represent a false-positive detection. We defined a northwestern salamander or long-toed salamander detection as unambiguous if an expert (i.e., personnel with over 15 yr of experience identifying species in the field) was present to identify larvae or if readily distinguishable breeding life stages apart from larvae were detected. All other northwestern salamander or long-toed salamander detections were classified as ambiguous. Because both of these ambystomatids can be misidentified as the other, we modeled the probability a detection is classified as unambiguous given the site is occupied (b) and the probability of erroneously detecting the species given the site is unoccupied (p_{10}) using the same logistic regressions for both species, but allowed the probability to vary based on species using a factor variable. We hypothesized these parameters

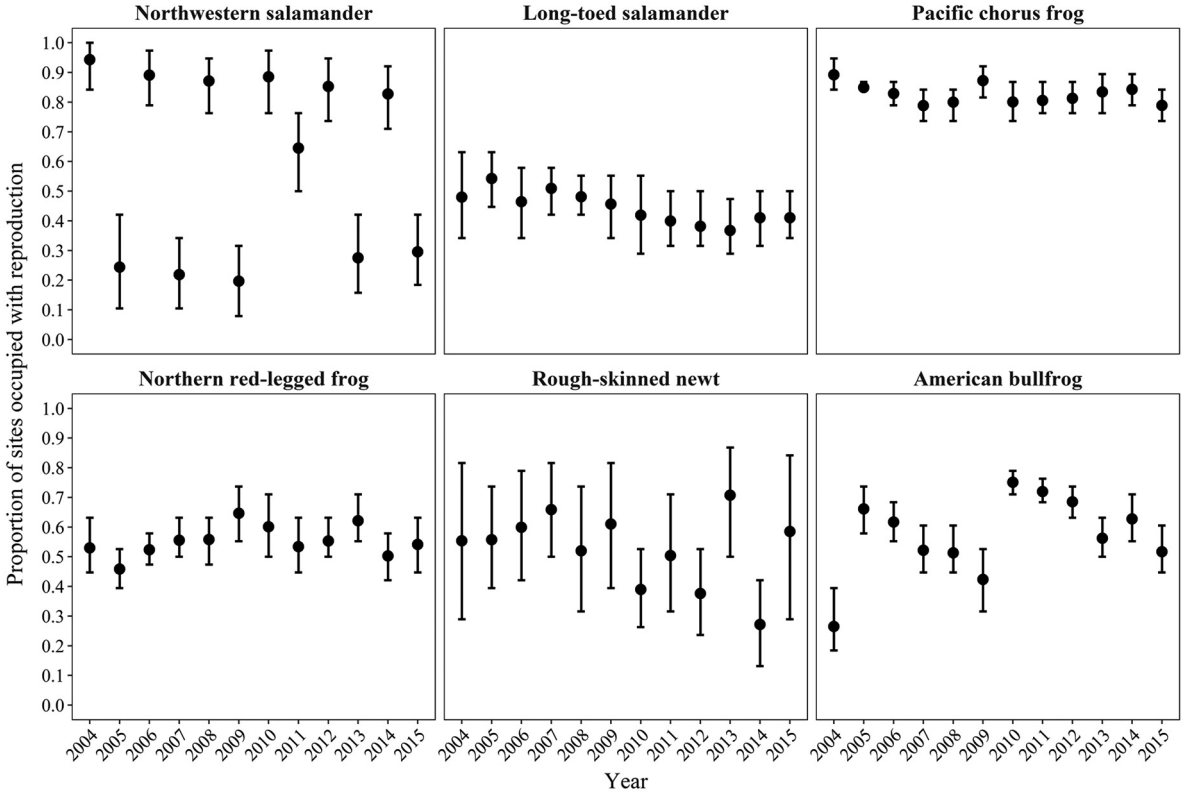


Fig. 2. Estimated proportion of sites occupied (with 90% credible intervals [CI]) with reproduction for each species within the Willamette Valley, Oregon, USA, 2004–2015.

are linked to developmental stage because the two species are more easily distinguished over ontogeny. Thus, we modeled both probabilities as a function of timing within the survey season using a factor variable to distinguish late-season or early-season periods (Appendix S1). Early-season detections were defined as those occurring prior to the median survey date for the year, and all other detections were classified as late-season.

The model was fit using Markov chain Monte Carlo (MCMC) and in JAGS (Plummer 2003) implemented in program R (version 3.2.2, R Core Team 2013) using the jagsUI package (Kellner 2016). Code used to fit the model is provided in Data S1. Diffuse prior distributions were used for all parameters. Specifically, all logit-scale model intercepts and coefficients had a normally distributed prior with a mean of zero and a precision of 0.37, and the priors for initial occupancy probabilities were drawn from a beta distribution with shape parameters set to 1. All continuous variables were assessed for collinearity (all had $|r| < 0.8$) and standardized to $\bar{x} = 0$ and standard deviation (SD) = 1 prior to model fitting. We fit the model with three independent chains, each consisting of 400,000 iterations, following a burn-in and adaption phase of 100,000 iterations each. This resulted in convergence for all parameter estimates based on the Brooks and Gelman diagnostic ($\hat{R} < 1.03$; Brooks and Gelman 1998) and visual inspection of trace and density plots of posterior distributions.

Given the large number of species and covariates included in our analysis, we implemented a multi-step approach to select a model for each species that included a reduced set of covariates. We a priori defined a strongly influential covariate as one with a coefficient estimate that had ≥0.90 of the posterior distribution mass on one side of zero (either positive or negative; see Fields et al. 2017); however, fitting global models can lead to inflated variance in the estimated parameters, and the posterior distribution of model parameters can shift based on the inclusion (and exclusion) of different covariates. Therefore, we first fit the global model to identify covariates that were moderately influential, which we defined as any coefficient estimate that had ≥0.80 of the posterior distribution mass on one side of zero. After removing all non-influential covariates, we refit the model to identify covariates that met our initial ≥0.90 threshold. Only the covariates that met this threshold were included in the selected model from which we based our inferences. Again, the posterior distribution of parameters can shift based on the set of covariates included in the model. Thus, we only considered covariates in the final selected model to be strongly influential if ≥0.90 of the posterior distribution mass continued to remain on one side of zero. We describe model parameters by their mean and 90% credible interval (90% CI). Odds ratios were also calculated for each coefficient estimate to facilitate interpretation (Hosmer and Lemeshow 2000), which should be interpreted as changes associated with a 1 SD change in the corresponding predictor variable because continuous predictor variables were standardized prior to model fitting. Furthermore, we estimated the proportion of sites occupied (PAO) with reproduction for each amphibian species to better understand occupancy dynamics.

Results

We sampled 8–38 (median = 37) sites annually at least once (Appendix S2: Table S1). On average, 11.5 (SD = 3.80) sites were classified as permanent (held water all year, every year), 14.75 (SD = 5.88) sites were classified as semi-permanent (held water though growing season most years), and 3.83 (SD = 1.70) sites were classified as temporary (rarely held water though entire growing season). Our sampling window between 2004 and 2015 did not capture any extreme drought events. Average February-to-July PDSI across all years was -0.28 ± 1.72 SD, with the driest years (moderate drought) being 2004 and 2015 and the wettest years (moderately wet) being 2011 and 2012.

Non-native fish occupancy

Non-native centrarchid and ictalurid fish were naively detected (prior to correcting for imperfect detection) at 23.7% of sites. The best fitting single-season occupancy model indicated the probability of site use by non-native fish was 0.846 (90% CI [0.665, 0.965]) at sites with moderate water depth (1–2 m), meaning the odds a non-native fish used a site of moderate depth was 5.73 times greater when compared to shallow or deep sites (Table 2). Although all three depth factor levels (shallow, moderately deep, and deep)

were considered in the analysis, there was no statistical support for a difference in the effect of shallow and deep on non-native fish occupancy probability. The probability non-native fish used a site was negatively related to percent emergent vegetation and positively related to area of winter inundation. Non-native fish detection probability was low (0.141, 90% CI [0.090, 0.202]; Table 2).

Amphibian detectability and false positives

The best fitting multispecies dynamic occupancy models for amphibians indicated that, on average, detection probability was high for the long-toed salamander (0.833, 90% CI [0.732, 0.920]), chorus frog (0.937, 90% CI [0.873, 0.982]), and red-legged frog (0.947, 90% CI [0.893, 0.982]) and much lower for the northwestern salamander (0.165, 90% CI [0.108, 0.230]), rough-skinned newt (0.327, 90% CI [0.190, 0.527]), and bullfrog (0.392, 90% CI [0.281, 0.517]). A non-native fish effect on detection probabilities was not supported for the northwestern salamander; however, the odds of detecting the other native amphibian species when present was 1.75–5.56 times lower when non-native fish used a site (Table 3). Conversely, the odds of detecting bullfrogs when present was 7.03 times higher when non-native fish used a site. Bullfrog presence had a strong effect on detection probabilities for the northwestern salamander, long-toed salamander, chorus frog, and red-legged frog, but the direction of the relationship varied by species. Surprisingly, the model only supported a trapping effort effect on detection probabilities for the chorus frog and red-legged frog. Nevertheless, the effect was pronounced, suggesting the odds of detecting these species when present was 3.70 and 6.25 times lower, respectively, when deploying 5 traps instead of 10. As expected, detection probabilities for most amphibians decreased with percent emergent vegetation and increased with ordinal day.

Results suggested the false-positive part of the model was needed to understand occupancy dynamics of the northwestern and long-toed salamanders (Table 4). The probability a detection was classified as unambiguous given the site was occupied varied by season and species. The odds of an unambiguous detection was 1.45 times higher late in the season compared to early

Table 3. Parameter estimates, standard deviations (SD), upper and lower limits of the 90% credible intervals (CI), and odds ratios (OR) for detection probability (p) from the best fitting multispecies dynamic occupancy models for amphibians.

Parameter	Mean	SD	Lower CI	Upper CI	OR
Northwestern salamander					
Intercept	−1.647	0.276	−2.115	−1.207	5.26↓
Bullfrog	0.420	0.348	−0.143	1.001	1.52↑
Ordinal day	−0.189	0.149	−0.435	0.054	1.20↓
Emergent vegetation	0.239	0.162	−0.025	0.509	1.27↑
Long-toed salamander					
Intercept	1.669	0.44	1.005	2.441	5.31↑
Bullfrog	−1.247	0.784	−2.352	0.206	3.45↓
Emergent vegetation	−0.552	0.272	−1.013	−0.127	1.72↓
Non-native fish	−0.567	0.532	−1.445	0.292	1.75↓
Pacific chorus frog					
Intercept	2.871	0.643	1.928	4.024	17.65↑
Bullfrog	0.818	0.439	0.094	1.536	2.27↑
Trap effort	−1.311	0.647	−2.355	−0.233	3.70↓
Ordinal day	1.496	0.293	1.031	1.993	4.46↑
Non-native fish	−1.369	0.66	−2.543	−0.390	4.00↓
Northern red-legged frog					
Intercept	3.026	0.582	2.117	4.027	20.61↑
Bullfrog	−0.925	0.514	−1.767	−0.078	2.50↓
Trap effort	−1.829	0.559	−2.742	−0.909	6.25↓
Ordinal day	0.906	0.232	0.538	1.298	2.47↑
Emergent vegetation	−0.614	0.262	−1.053	−0.194	1.85↓
Non-native fish	−1.689	0.534	−2.590	−0.837	5.56↓
Rough-skinned newt					
Intercept	−0.758	0.477	−1.447	0.110	2.13↓
Ordinal day	0.768	0.189	0.474	1.091	2.16↑
Emergent vegetation	−0.430	0.203	−0.778	−0.114	1.54↓
Non-native fish	−0.812	0.541	−1.768	0.002	2.27↓
American bullfrog					
Intercept	−0.448	0.307	−0.939	0.069	1.56↓
Ordinal day	−0.256	0.161	−0.523	0.005	1.30↓
Emergent vegetation	0.424	0.200	0.101	0.757	1.53↑
Non-native fish	1.950	0.474	1.173	2.726	7.03↑

Notes: Odds ratios are given as the absolute magnitude of the effect, with arrows indicating the direction of the relationship. The reference category for non-native fish indicates a site not used by non-native fish. The reference category for bullfrog indicates a site unoccupied by bullfrogs. The reference category for trap effort indicates a visit in which 10 traps were deployed.

Table 4. Parameter estimates, standard deviations (SD), upper and lower limits of the 90% credible intervals (CI), and odds ratios (OR) for the probability that a detection is classified as unambiguous given that the site is occupied (b) and the probability of erroneously detecting the species given that the site is unoccupied (p_{10}) from the best fitting multispecies dynamic occupancy models for northwestern and long-toed salamanders.

Parameter	Mean	SD	Lower CI	Upper CI	OR
b					
Intercept	0.300	0.263	−0.126	0.737	1.35↑
Season	0.373	0.332	−0.173	0.919	1.45↑
Species	2.617	0.816	1.480	4.129	13.7↑
p_{10}					
Intercept	−3.179	0.378	−3.843	−2.612	25.00↓
Species	1.011	0.441	0.321	1.763	2.75↑

Notes: Odds ratios are given as the absolute magnitude of the effect, with arrows indicating the direction of the relationship. The reference category for species is long-toed salamander. The reference category for season represents early-season detections.

in the season. For long-toed salamanders, the probability of an unambiguous detection was 0.573 (90% CI [0.469, 0.676]) early in the season, while the odds of an unambiguous northwestern salamander detection was 13.7 times higher (0.935, 90% CI [0.857, 0.989]). Although this indicates northwestern salamander detections were more likely to be classified with certainty than long-toed salamander detections, the odds of an uncertain northwestern salamander detection being a false positive was 2.75 times higher. Specifically, the probabilities of erroneously detecting the species given a site was unoccupied were 0.042 (90% CI [0.021, 0.068]) and 0.105 (90% CI [0.071, 0.143]) for long-toed and northwestern salamanders, respectively.

Amphibian occurrence patterns

The proportion of sites occupied with reproduction was high for chorus frogs and moderately high for long-toed salamanders and red-legged frogs, and relatively consistent across years (Fig. 2). Rough-skinned newts, bullfrogs, and especially northwestern salamanders showed marked flux in the proportion of sites that were occupied among years (Fig. 2). The proportion of bullfrog-occupied sites increased sharply between 2004 and 2005, after which site use remained relatively consistent for the remainder of our study period. Proportion of sites occupied by the northwestern salamander remained highly dynamic over the 12-yr study.

Amphibian dynamics as a function of invasive species and habitat

Northwestern salamander, red-legged frog, and rough-skinned newt colonization probabilities were unrelated to covariates in our models (Table 5). For chorus frogs and long-toed salamanders, the odds of a colonization event were 4.35 and 4.76 times lower, respectively, when breeding bullfrogs were present compared to when bullfrogs were absent. Long-toed salamander colonization probability was also 6.25 times lower when non-native fish used a site. Colonization probability for long-toed salamanders was

Table 5. Parameter estimates, standard deviations (SD), upper and lower limits of the 90% credible intervals (CI), and odds ratios (OR) for colonization probability (γ) from the best fitting multispecies dynamic occupancy models for amphibians.

Parameter	Mean	SD	Lower CI	Upper CI	OR
Northwestern salamander					
Intercept	3.668	0.879	2.327	5.193	39.17↑
Long-toed salamander					
Intercept	−0.886	0.892	−2.454	0.457	2.44↓
Bullfrog	−1.572	0.944	−3.113	−0.028	4.76↓
Non-native fish	−1.838	0.887	−3.311	−0.411	6.25↓
Forest cover	1.286	0.496	0.553	2.143	3.62↑
PDSI	−1.396	0.843	−2.934	−0.199	4.00↓
Pacific chorus frog					
Intercept	0.706	0.74	−0.439	1.983	2.03↑
Bullfrog	−1.464	0.849	−2.905	−0.116	4.35↓
Northern red-legged frog					
Intercept	−1.175	0.207	−1.520	−0.840	3.23↓
Rough-skinned newt					
Intercept	1.223	0.972	−0.106	3.044	3.40↑
American bullfrog					
Intercept	−2.235	0.577	−3.261	−1.382	9.09↓
PDSI	−1.959	0.629	−3.040	−0.975	7.14↓

Notes: PDSI, Palmer Drought Severity Index. Odds ratios are given as the absolute magnitude of the effect, with arrows indicating the direction of the relationship. The reference category for non-native fish indicates a site not used by non-native fish. The reference category for bullfrog indicates a site unoccupied by bullfrogs.

strongly, positively related to forest cover, and negatively related to PDSI (wet conditions) the previous year. Bullfrog colonization probability was also negatively related to previous year's PDSI.

Bullfrog presence had a strong negative effect on probability of local persistence for two native species, the long-toed salamander and chorus frog (Table 6). The odds of local persistence when bullfrogs occupied a site was 7.80 times lower and 5.14 times lower for long-toed salamanders and chorus frogs, respectively, compared to when bullfrogs were absent. The odds of local persistence for red-legged frogs was 1.83 times lower when bullfrogs were present compared to when they were absent, but this effect was relatively weak based on our a priori criterion for the distribution of posterior mass (≥0.90). There was a positive effect of bullfrog presence on local persistence probabilities for the northwestern salamander and rough-skinned newt. The effect was not strong for the rough-skinned newt, based on the distribution of the posterior mass.

The relationship between probability of local persistence and habitat characteristics differed as a function of bullfrog occupancy for some native

Table 6. Parameter estimates, standard deviations (SD), upper and lower limits of the 90% credible intervals (CI), and odds ratios (OR) for local persistence probability (ϕ) from the best fitting multispecies dynamic occupancy models for amphibians.

	Invasive bullfrog absent					Invasive bullfrog present				
Parameter	Mean	SD	Lower CI	Upper CI	OR	Mean	SD	Lower CI	Upper CI	OR
Northwestern salamander										
Intercept	−3.287	0.962	−4.913	−1.798	25.00↓	−0.582	0.817	−1.854	0.807	1.79↓
Emergent vegetation						1.386	0.987	−0.023	3.163	4.00↑
PDSI						1.725	0.691	0.783	3.030	5.61↑
Long-toed salamander										
Intercept	3.143	0.880	1.827	4.703	23.16↑	1.088	0.805	−0.066	2.528	2.97↑
Reed canarygrass dominant†	1.796	1.231	−0.205	3.841	6.03↑					
Forest perimeter	−1.039	0.878	−2.268	0.628	2.86↓	0.654	0.733	−0.276	2.081	1.92↑
Pacific chorus frog										
Intercept	3.449	0.759	2.385	4.846	31.47↑	1.813	0.281	1.377	2.295	6.13↑
Forest perimeter						0.361	0.268	−0.047	0.823	1.43↑
No non-native fish, reed canarygrass dominant‡						0.625	1.083	−0.867	2.667	1.87↑
Northern red-legged frog										
Intercept	2.196	0.569	1.385	3.221	8.99↑	1.592	0.606	0.680	2.659	4.91↑
PDSI						−0.561	0.408	−1.261	0.077	1.75↓
Forest perimeter						0.949	0.507	0.203	1.851	2.58↑
Non-native fish, reed canarygrass not dominant‡						−1.241	0.817	−2.624	0.054	3.45↓
No non-native fish, reed canarygrass dominant‡						1.065	1.178	−0.766	3.096	2.90↑
Rough-skinned newt										
Intercept	−0.945	0.836	−2.305	0.393	2.56↓	−0.426	0.914	−1.853	1.140	1.54↓
PDSI						−2.393	1.246	−4.486	−0.377	11.11↓
American bullfrog										
Intercept						2.145	0.379	1.559	2.801	8.54↑
Reed canarygrass dominant†						−0.674	0.462	−1.440	0.077	1.96↓
PDSI						0.636	0.291	0.175	1.129	1.89↑

Notes: PDSI, Palmer Drought Severity Index. Odds ratios are given as the absolute magnitude of the effect, with arrows indicating the direction of the relationship. The reference category for non-native fish indicates a site not used by non-native fish. The reference category for reed canarygrass dominant indicates a site not dominated by reed canarygrass.

† Reed canarygrass dominance as an offset term was only included when bullfrogs were absent and when modeling American bullfrog local persistence probability.

‡ Interaction between non-native fish presence and reed canarygrass dominance was only included when bullfrogs were present.

amphibians (Table 6). When bullfrogs were absent, the long-toed salamander was the only species associated with a local persistence model containing influential predictor variables. Here, local persistence was negatively related to percent of forested pond perimeter and positively related to reed canarygrass dominance, with the odds of local persistence being 6.03 times more likely when reed canarygrass was dominant compared to when it was not dominant. When bullfrogs were present, reed canarygrass no longer influenced long-toed salamander local persistence. Generally, however, models for local persistence of native amphibians contained a greater number of influential habitat and climatic predictor variables when bullfrogs were present compared to when they were absent. Forested pond perimeter became positively related to long-toed salamander, chorus frog, and red-legged frog local persistence when bullfrogs were present. Likewise, local persistence for the northwestern salamander was positively associated with percent emergent vegetation at bullfrog-occupied sites. Average monthly PDSI was an influential predictor of local persistence for some species in the presence of bullfrogs, with red-legged frogs and rough-skinned newts exhibiting a negative relationship and northwestern salamanders exhibiting a positive relationship. The probability of local persistence for bullfrogs was also positively related to average monthly PDSI.

An interaction between reed canarygrass dominance and vertebrate invaders was supported for the chorus frog and red-legged frog (Table 6). For chorus frogs, reed canarygrass dominance was associated with increased local persistence at bullfrog-occupied, fishless sites. However, this effect was weak based on our posterior mass criterion for classifying covariates as influential. For red-legged frogs, reed canarygrass dominance offset the combined negative effect of bullfrogs and non-native fish (Fig. 3). That is, at sites with both vertebrate invaders, the odds of red-legged frog local persistence was 3.45 times more likely when reed canarygrass was dominant compared to when reed canarygrass was not dominant. At sites with bullfrogs and no fish, the odds of red-legged frog local persistence was 2.90 times more likely when reed canarygrass was dominant compared to when reed canarygrass was not dominant. The probability of local persistence for red-legged frogs was lowest, on average, at bullfrog-occupied, fish-used sites without dominant reed canarygrass (0.578, 90% CI [0.315, 0.822]). However, when there was dominant reed canarygrass at a site used by non-native fish, the probability of red-legged frog local persistence was equal to when fish and reed canarygrass were absent. The only amphibian showing a negative relationship with reed canarygrass was the invasive bullfrog; the odds of bullfrog local persistence was 1.96 times less likely when reed canarygrass was dominant.

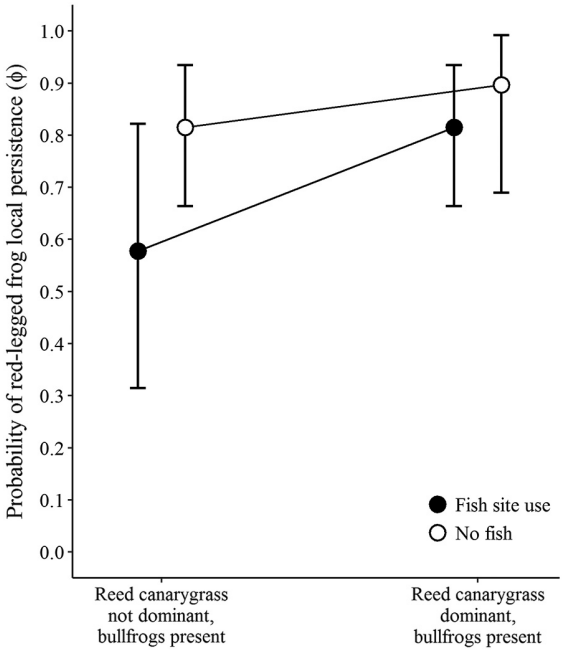


Fig. 3. Estimated local persistence probabilities for the northern red-legged frog (*Rana aurora*) as a function of the interaction between reed canarygrass dominance and non-native fish in the presence of bullfrogs. We investigated all combinations of reed canarygrass, non-native fish, and bullfrog factor levels; however, some interactions (Table 6) were not supported by model selection and thus are represented as the intercept for the probability of local persistence when covariates are set to their means.

Discussion

We demonstrate that although occurrence and distribution patterns vary through time,

native amphibians may be capable of coexisting with bullfrogs in the Willamette Valley, especially when favorable habitat conditions exist. For most native species except northwestern salamanders, the proportion of sites with reproduction remained relatively stable over our study period. Bullfrogs reduced colonization and local persistence probabilities for long-toed salamanders and chorus frogs, and the direction and magnitude of the bullfrog effect was influenced by habitat. When both bullfrogs and fish co-occurred, they had a stronger cumulative negative impact on red-legged frog persistence compared to when only one invader occurred, but this negative effect was offset by dominant reed canarygrass. In the absence of invasive bullfrogs, few habitat variables explained patterns of local persistence. However, habitat variables had greater relative importance when bullfrogs were present, suggesting the value of habitat increases for native species co-occurring with invaders. In this system, it appears habitat can regulate the strength of the indirect influence bullfrogs have on native species local persistence.

Amphibian occurrence patterns

It was common for amphibians in our study area to show interannual variability in proportion of sites occupied, and given we only considered aquatic life stages in our analysis, this metric is an indication of the variability in the number of sites used for reproduction. Despite fluctuation in individual sites used for breeding on an annual basis, we did not detect any declines in the overall number of breeding sites over the 12-yr survey. Furthermore, long-term trends in the proportion of sites with reproduction by native species appeared independent of the proportion of sites with reproduction by bullfrogs, suggesting bullfrog expansion in our study region does not correspond to range contraction by natives.

The proportion of sites used for reproduction was highly unstable across years for northwestern salamanders and unconnected to regional climate patterns like drought severity. It is worth noting that our ability to detect this species when it was present at a site was relatively low. This resulted in more uncertainty in occupancy dynamics for this species, which may partially explain the observed patterns. However, model diagnostics suggest there were no issues with model convergence or parameter identifiability. Thus, although the high variation in the proportion of sites with reproduction seems extreme, it is important to consider possible biological mechanisms for this pattern. Large population fluctuations in amphibians are well documented (Pechmann et al. 1991, Semlitsch et al. 1996, Alford and Richards 1999, Trenham et al. 2003). For example, in a 12-yr study of *Ambystoma tigrinum*, *A. talpoideum*, and *A. opacum*, Pechmann et al. (1991) found that breeding populations cycled between years of complete recruitment failure and years of high counts of breeding females. Local persistence of amphibians is generally driven by the number of animals successfully metamorphosing and recruiting into the adult population. In *A. tigrinum*, recruitment of young-of-the-year individuals is strongly regulated by older paedomorphs through cannibalism, and populations can undergo cyclic fluctuations based on age structure (Wissinger et al. 2010). In other cases, population size is highly sensitive to survival of postmetamorphic life stages (Trenham and Shaffer 2005, Taylor et al. 2006). Our sampling methods only detected northwestern salamander larvae and, rarely, paedomorphs, so the occupancy dynamics we encountered could be driven largely by reproductive success of unobserved adults. Because temporal variability in proportion of area occupied could also be related to unmodeled temporal variability in detection probability, we conducted a post hoc analysis where we fit models that included a random year effect on detectability of all amphibian species. However, the patterns in the proportion of sites occupied remained consistent for all species, validating our results. Despite the uncertainties in the underlying mechanism, our long-term dataset reveals an interesting pattern of overall stability despite extreme interannual variability in sites used for breeding by northwestern salamanders, a pattern that would be mischaracterized as population losses or gains using a short time series (Alford and Richards 1999).

Invader effects on native amphibians

We observed a strong negative effect of bullfrogs on long-toed salamander and chorus frog

local persistence and colonization probabilities. This suggests bullfrogs represent a threat, and these two native species may preferentially avoid breeding at invaded sites. Many amphibians demonstrate selective egg deposition based on predator presence (Kats and Sih 1992, reviewed in Buxton and Sperry 2017). Learned, innate, or plastic antipredator responses could represent a strategy by which long-toed salamanders and chorus frogs persist in the landscape despite aquatic invaders. These species are also strongly associated with vernal and temporary waterbodies (Nussbaum et al. 1983), and the negative relationship between colonization and bullfrogs may also be a function of conflicting hydroperiod needs not considered a priori in the colonization model. Local persistence of other native species was unaffected by bullfrogs or, in the case of northwestern salamanders, increased with bullfrog presence.

In addition to the singular effects of bullfrogs on some native species, we also observed an additive negative effect of non-native fish and bullfrogs on northern red-legged frog local persistence. Previous studies have also found this species and the closely related California red-legged frog to be susceptible to bullfrogs and fish (Kiesecker and Blaustein 1997, 1998, Lawler et al. 1999). Bullfrog presence may induce habitat partitioning by red-legged frogs that increases their exposure to fish and reduces resource acquisition. These results provide further evidence of a multi-invader interaction that exacerbates the threat to a species of special concern.

Amphibian dynamics as a function of invasive species and habitat

For native amphibian species, especially those most vulnerable to invasive predators, habitat conditions became stronger predictors of local persistence when bullfrogs were present compared to when they were absent. We pose several hypotheses for why local persistence of native species showed different relationships with habitat as a function of bullfrog presence. First, insufficient variation in habitat conditions across bullfrog-invaded and uninvaded sites could skew the results. That is, if habitat conditions are relatively constant at sites without bullfrogs but diverse at bullfrog-occupied sites, we would expect to only see habitat effects when bullfrogs are present. This explanation is implausible because the ranges of values for our site-level covariates were very similar between sites with and without bullfrogs (Appendix S3: Table S1). We also consider the potential for cumulative negative effects of habitat stressors and invaders leading native species to persist in marginal habitats unless an invader is present. Finally, habitat mediation could occur if predatory or competitive outcomes are altered under certain habitat conditions. In this case, a native species capable of occupying a broad range of invader-free habitats can only persist with invaders when habitat conditions afford the native species protection from the invader. The resolution of our approach does not allow us to reconcile whether the patterns we found in our analysis result from cumulative effects or from habitat mediation. To disentangle these hypotheses would likely require a manipulative experiment to isolate habitat effects and determine the mechanism that results in the observed pattern. In either case, our analysis suggests certain habitat qualities are favorable for some natives in the presence of bullfrogs.

Perimeter forest cover was important for local persistence of long-toed salamanders, chorus frogs, and red-legged frogs when bullfrogs were present. These species typically have low larval survival and adults visit wetlands briefly during their breeding seasons, so local persistence of populations may be strongly regulated by survival of terrestrial adults in forested uplands (Trenham and Shaffer 2005, Harper et al. 2008). Perimeter forest could compensate for reduced habitat suitability due to bullfrog presence by mediating within-pond interactions, perhaps via increased nutrient input that diffuses interspecific competition or via microclimate changes favoring native species. Forest cover may also enhance quality of terrestrial adult habitat and maintain inter-site movements, thus ensuring future breeding opportunities (Pearl et al. 2005, Olson et al. 2007). The long-toed salamander, a species showing a shift from a negative to positive relationship with surrounding forest when bullfrogs were present, may display broad ecological tolerances in the absence of bullfrogs that become narrower when bullfrogs are present.

Vegetation was important for several species. Local persistence of northwestern salamanders increased with emergent vegetation when they

were syntopic with bullfrogs, with which they had a positive association. This suggests that although northwestern salamanders had higher local persistence at bullfrog-occupied sites, they may benefit from greater vegetation cover for breeding and oviposition when bullfrogs are present. Long-toed salamander, chorus frog, and red-legged frog local persistence was positively associated with dominance of invasive reed canarygrass, whereas bullfrog local persistence was negatively associated with dominance of reed canarygrass. These findings contrast with Guderyahn et al.'s (2016) observations of a negative association between non-native vegetation and several native species in urbanized areas of this region, and they add to the growing body of literature on the nuanced and species-specific effects of reed canarygrass on amphibians. In experimental mesocosms, Rittenhouse (2011) determined that low dissolved oxygen created by excessive reed canarygrass biomass caused reduced survivorship of some amphibian larvae. However, decomposing leaf litter and resulting eutrophication also enhanced larval growth, suggesting the interplay between reed canarygrass dominance and site hydrology has important implications for survival. Holzer and Lawler (2015) found Pacific chorus frog larvae had higher survival in reed canarygrass experimental treatments, and adults of this and other species (e.g., *Lithobates pipiens*; Gilbert et al. 1994) may preferentially use this invasive plant for breeding and oviposition microhabitat. The protective (larvae and adults) and supportive (eggs) structure of this plant may offer some value to native amphibians, especially in the presence of non-native predators.

We found evidence that reed canarygrass can mediate the cumulative negative effect of bullfrogs and non-native fish on red-legged frog local persistence, and to a lesser extent, the singular effect of bullfrogs on chorus frog local persistence. Heavy reed canarygrass cover could reduce open water and thus habitat quality for bullfrogs, as well as decreasing their efficiency as predators. Dense growth in pond margins may cause bullfrogs to shift microhabitat use to deeper water, making fishless shallows available to red-legged frog larvae (Kiesecker and Blaustein 1998). Despite this plant invader's propensity to achieve high biomass, there was no correlation between reed canarygrass dominance and overall percent emergent vegetation at our sites, leading us to conclude reed canarygrass may fulfill a functional role that is not captured by the general cover variable. Still, our measure of reed canarygrass dominance is coarse-grain in that it was limited to a single measurement for each site across years, and it did not represent the proportion of the site dominated by this plant species nor the growth habit (i.e., evenly interspersed or patchy). Further work is needed to disentangle the structural, chemical, and functional effects of this plant on different amphibian life stages in the context of multi-invader communities.

The effects of water availability on pond-breeding amphibians reflect life history tradeoffs related to phenology and predator avoidance (Wellborn et al. 1996). Long-toed salamander and bullfrog colonization probabilities were positively associated with drought conditions (negative PDSI) the previous year, suggesting limited water availability in the previous season may stimulate colonization the following year. This could indicate pond-switching by the two species in the event that previously suitable breeding habitats were lost. For example, 2004 was a moderately dry year that corresponded with a substantial increase in the proportion of sites occupied by bullfrogs the following year. Water drawdown rate at a site was not an influential predictor of local persistence for any species; however, wet conditions (positive PDSI) during the developmental and emergence window were important for several species. We found that local persistence for habitat generalists that transform earlier in summer (e.g., the long-toed salamander and chorus frog) was unaffected by or even negatively related (e.g., rough-skinned newt) to PDSI. Local persistence of the northwestern salamander and bullfrog, species that typically have a multi-year larval period, was highest in wet years with positive PDSI. Although these species are thought to predominantly breed in permanent ponds (Snyder 1956, Snow and Witmer 2010), we found they broadly occurred across a gradient of hydroperiods within our study area. In fact, we detected northwestern salamander and bullfrog breeding life stages with certainty at 58.3% and 75% of the 12 sites that dried in late summer during a typical water year, respectively. These temporary sites lack strong connectivity to

other breeding habitats, suggesting these species can reach metamorphosis in one year or that they expend appreciable breeding effort in ponds that often dry.

Implications of this work

Our analysis offers improved inferences on previously documented amphibian occupancy dynamics and habitat associations in the Willamette Valley. We used 12 yr of data to estimate occupancy dynamics as a function of invaders and habitat, rather than drawing conclusions from species overlap during snapshots in time. We also accounted for sources of bias that are not always considered in observational studies. Because we focused on sites that are relatively buffered from landscape alterations associated with intensive land use, we were better able to isolate the effects of invasive predators from environmental changes. Still, it is worth noting that these sites are located on public lands managed by refuges, and unaltered wetlands are exceedingly rare across our study region (Kentula et al. 2004). Species-specific differences in detection probabilities underscore the importance of using methods that account for imperfect detection. Moreover, our results from modeling potential species misidentifications (i.e., false-positive detections) highlight the value of accounting for this often overlooked source of observer error. We found that the probability of erroneously detecting ambystomatid salamanders given the site is unoccupied was 0.042–0.105 when detections were classified as uncertain, which exceeds the rates determined to severely bias estimates of occupancy dynamics if not accounted for (Royle and Link 2006, Miller et al. 2011).

Although our analysis has advantages over previous work, challenges remain. The lack of a singular effect of non-native fish on native amphibian local persistence was surprising given the literature on the negative effects of centrarchids on amphibian distributions in this region (Richter and Azous 1995, Adams 1999, Pearl et al. 2005). Our field methods were better suited for sampling amphibians than fish, and despite correcting for imperfect detection using occupancy modeling, our estimates of non-native fish effects (i.e., from a covariate describing whether non-native fish *ever* used a site) are not directly comparable to our estimates of bullfrog effects (i.e., from a covariate allowing for annual changes in occupancy), and fish are therefore less thoroughly examined. Fish captures were restricted to the shallow margins of ponds where traps could be placed, which may explain the estimated relationship between fish probability of site use and water depth. In some cases, non-native fish could have been present at a site but unavailable for sampling because they used deep microhabitats where traps were not set. This analysis could have also been improved by characterizing the effects of the entire fish community, including native species and non-native gape-limited western mosquitofish (*Gambusia affinis*).

Conclusion

Invasive species management often focuses on population-level control of invaders (Myers et al. 2000). Although examples of successful eradication programs exist (Anderson 2005, Griffiths et al. 2015, but see Rout et al. 2014), removal efforts can be costly and impractical, especially when sustained monitoring and intervention are required to prevent reinvasion (Hobbs and Cramer 2008, Bucciarelli et al. 2014). Worse yet, they can have negative or unexpected outcomes (Doubledee et al. 2003, Simberloff et al. 2013). In the Willamette Valley, high landscape permeability due to regular flooding makes permanent eradication of aquatic invaders intractable in many systems (Adams and Pearl 2007 and citations therein, Pearl et al. 2005, Pilliod et al. 2013). Here, non-native fish and bullfrogs have variable effects on different native amphibian species, but do not appear to be causing declines in our study area. Instead, habitat may play the strongest role in regulating native amphibian persistence in this system, allowing natives to coexist with invaders under favorable habitat conditions. This study provides new insight into the relative strength of these synergistic factors influencing native amphibian occupancy dynamics.

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Data Availability

Data are available at https://doi.org/10.5066/p9xdebob.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2674/full