

Floodplains provide important amphibian habitat despite multiple ecological threats

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Abstract. Floodplain ponds and wetlands are productive and biodiverse ecosystems, yet they face multiple threats including altered hydrology, land use change, and non-native species. Protecting and restoring important floodplain ecosystems requires understanding how organisms use these habitats and respond to altered environmental conditions. We developed Bayesian models to evaluate occupancy of six amphibian species across 103 off-channel aquatic habitats in the Chehalis River floodplain, Washington State, USA. The basin has been altered by changes in land use, reduced river–wetland connections, and the establishment of non-native American bullfrogs (*Rana catesbeiana* = *Lithobates catesbeianus*) and centrarchid fishes, all of which we hypothesized could influence native amphibian occupancy. Despite potential threats, the floodplain habitats had relatively high rates of native amphibian occupancy, particularly when compared to studies from non-floodplain habitats within the species' native ranges. The biggest challenge for native amphibians appears to be non-native centrarchid fishes, which strongly reduced occupancy of two native amphibians: the northern red-legged frog (*Rana aurora*) and the northwestern salamander (*Ambystoma gracile*). Emergent vegetative cover increased occupancy probability for all five native amphibian species, indicating that plant management may offer a strategy to counter the negative effect of centrarchids by providing refuge from predation. We found that temporary and permanent hydroperiod sites supported different species; hence, both should be conserved on the landscape. Lastly, human-created and natural ponds had similar amphibian occupancy patterns, suggesting that pond construction offers a viable strategy for adding habitats to the floodplain landscape. Overall, floodplain ponds and wetlands provide important amphibian habitat, and we offer management strategies that will bolster amphibian occupancy in an altered floodplain landscape.

Key words: amphibians; centrarchid; floodplain; occupancy; pond; threats; wetland.

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INTRODUCTION

Freshwater floodplains are among the most biodiverse and productive ecosystems on the planet (Junk et al. 1989, Ward et al. 1999, Tockner and Stanford 2002), providing ecosystem services valued at \$1.5 trillion annually (de Groot et al. 2012, Costanza et al. 2014). Unaltered floodplains include a mosaic of aquatic habitats, ranging from the lotic mainstem river to slow-moving side channels to lentic oxbows, ponds, and seasonally flooded fields and forests (Ward et al. 2002). These systems provide critical habitat for myriad aquatic and semi-aquatic taxa, including fish, birds, amphibians, and invertebrates. Many of these organisms exhibit life history adaptations to unaltered hydrological regimes for feeding, breeding, and rearing, and their life cycles are often synchronized to match seasonal flood pulses (Junk et al. 1989, Bunn and Arthington 2002, Lytle and Poff 2004, Kupferberg et al. 2012). Despite the ecological importance of unaltered riverine floodplains and hydrological regimes, these systems are globally threatened by altered habitat, flow and flood control, invasive species, and pollution (Tockner and Stanford 2002). For example, North America and Europe have altered significant portions of their river floodplains, with estimates of floodplain development and cultivation reaching as high as 90% (Tockner and Stanford 2002). Loss of intact flood regimes, coupled with additional stressors from land use, invasive species, and pollution, underscore that floodplains face significant ecological stress and potential loss of ecological function (Tockner et al. 2010). To combat these stressors and enhance critical floodplain habitats, restoration efforts have been initiated worldwide with billions of dollars spent on projects in the United States alone (Bernhardt et al. 2005, Palmer et al. 2005).

Successful restoration projects require understanding the effects of multiple stressors on ecological function, including the responses of multiple, interacting species (Lake et al. 2007, Naiman et al. 2012). Amphibians, for example, are affected by threats to floodplains as they make extensive use of diverse aquatic and terrestrial floodplain habitats (Joly and Morand 1994, Henning and Schirato 2006, Tockner et al. 2006) and are adapted to seasonal inundation (Kupferberg et al. 2012). Amphibians are important components of aquatic

and terrestrial ecosystems, providing a critical energy link in the food web and exchanging resources between these systems (Pough 1980, Fritz and Whiles 2018, Ocock et al. 2018). Additionally, amphibian declines are occurring globally due to multiple threats that mirror floodplain losses: altered habitat and the introduction of non-native species, with climate change, disease, contaminants, and commercial use acting as additional stressors (Collins 2010, Grant et al. 2016). Multiple threats often act synergistically to create novel ecosystems where ecological responses are difficult to predict (Hobbs et al. 2006, Strayer 2010).

Multiple stressors that threaten floodplain aquatic habitat may influence amphibian distribution on the landscape. For instance, if a mainstem river is disconnected from its floodplain, off-channel ponds and wetlands could face reduced nutrient loading from upstream (Noe and Hupp 2005), lowered productivity (Junk et al. 1989, Tockner et al. 2000), and reduced habitat complexity (Tockner et al. 2006). Altered hydrology can also favor non-native and generalist species (Bunn and Arthington 2002, Kupferberg et al. 2012). Converting forests for agriculture or development can reduce terrestrial habitat critical to amphibians, introduce contaminants, alter hydrology, and facilitate invasion of non-native species (Hamer and McDonnell 2008). The introduction of non-native species, such as fishes and the American bullfrog (*Rana catesbeiana* = *Lithobates catesbeianus*), has been correlated with fewer native amphibians in isolated wetlands (Hayes and Jennings 1986, Adams 1999, Rowe and Garcia 2014), potentially due to direct predation (Kiesecker and Blaustein 1998) or competition for food (Kupferberg 1997, Kiesecker et al. 2001). However, amphibian occupancy patterns in floodplain wetlands have seldom been examined and the role of stressors may differ from isolated wetlands.

In addition to floodplain ponds and wetlands potentially operating differently than isolated water bodies, floodplain habitats require special attention for the complex management challenges they pose. For example, it is nearly impossible to remove non-native species in riverine systems where aquatic connectivity increases invasion opportunities. In cases where eradication is not feasible, the only currently viable option may be to facilitate coexistence through habitat manipulation (Adams and Pearl 2007).

For instance, manipulating hydroperiod to promote seasonal pond drying can eliminate fish and bullfrogs that require permanent waters (Adams and Pearl 2007). However, that option may not be feasible for water bodies that are larger or lack a way of altering water level (Adams and Pearl 2007), nor may it be suitable for native species that require permanent waters, such as the threatened Oregon spotted frog (*Rana pretiosa*; Hallock 2013). Planting emergent vegetation may provide habitat refuge for native amphibians and reduce encounter rates with non-native predators (Adams and Pearl 2007, Rowe et al. 2019), but this approach is untested. Managing for native amphibians and restoring functional floodplain ecosystems requires an understanding of how native amphibians respond to diverse threats, including introduced species, land use change, and altered hydrology.

In this study, we evaluated how multiple threats and habitat characteristics influence amphibian occupancy along the Chehalis River floodplain in Washington State, USA. The Chehalis River Basin hosts diverse land uses, including unmanaged and harvested forests, agriculture, and urban and residential development. Additionally, non-native fishes and bullfrogs introduced to the basin have potentially negative but unstudied ecological consequences. To study this system, we developed Bayesian occupancy models for the six amphibian species currently found within the floodplain and allowed for predator–prey interactions among amphibian species. Occupancy models are an effective tool for evaluating relationships between species occurrence and environmental conditions at the landscape scale. A notable strength of occupancy models is their ability to account for imperfect species detection (i.e., false-negative detections in the monitoring data; Mackenzie et al. 2017). Detection bias is a major concern in systems where environmental conditions and species competition may influence both the probability of detecting a species (e.g., due to behavioral changes by the target species) and the probability that a species occurs at a site (Mackenzie et al. 2017). We fit these models to three years of survey data from 103 off-channel habitats that represent oxbows, ponds, and seasonal wetlands. We predicted that non-native fishes and bullfrogs would reduce amphibian occupancy, whereas certain habitat features, such as emergent vegetation,

nearby forest cover, and river connectivity, would increase amphibian occupancy. Our study was designed to inform aquatic restoration and management options for native amphibians in alluvial floodplains.

METHODS

Study area: Chehalis River Basin

The Chehalis River Basin is the largest river basin entirely within Washington State, draining 6890 km² from three geographical regions: the Cascades Mountains foothills, the Olympic Mountains, and the Willapa Hills (Fig. 1). The basin is largely rain-fed; annual precipitation in Grand Mound, Washington, ranged from 108 to 164 cm during the study period (2015–2017). The Chehalis River mainstem travels 201 km before emptying into Grays Harbor and the Pacific Ocean. The upper mainstem (above river km 174) has a largely confined channel, and land use is primarily forestry. Between the cities of Pe Ell (river km 174) and Chehalis (river km 121), the floodplain broadens and is dominated by agriculture. As the river approaches Interstate-5 and the cities of Chehalis and Centralia, both river confinement and urbanized land uses increase. Below Centralia (river km 105), the floodplain broadens again and land use returns to primarily agriculture until the confluence with the Satsop River (river km 33). Between the Satsop River confluence and Chehalis River mouth at Grays Harbor is tidal surge floodplain, which is dominated by riparian forest (Smith and Wenger 2001).

Study sites

We identified off-channel habitats with GIS using 2011 and 2013 NAIP aerial photographs taken in late summer. We selected habitats with surface water and within the Federal Emergency Management Agency (FEMA)-specified 100-yr floodplain with an additional 100 m width on each side of the Chehalis River. This process identified 324 off-channel habitats; however, map review coupled with ground-truthing efforts removed 25 sites that were not appropriate to sample (e.g., manure lagoons, wastewater pond) and added eight sites, including depressional wetlands in seasonally inundated fields. We stratified these 307 sites across 10 segments

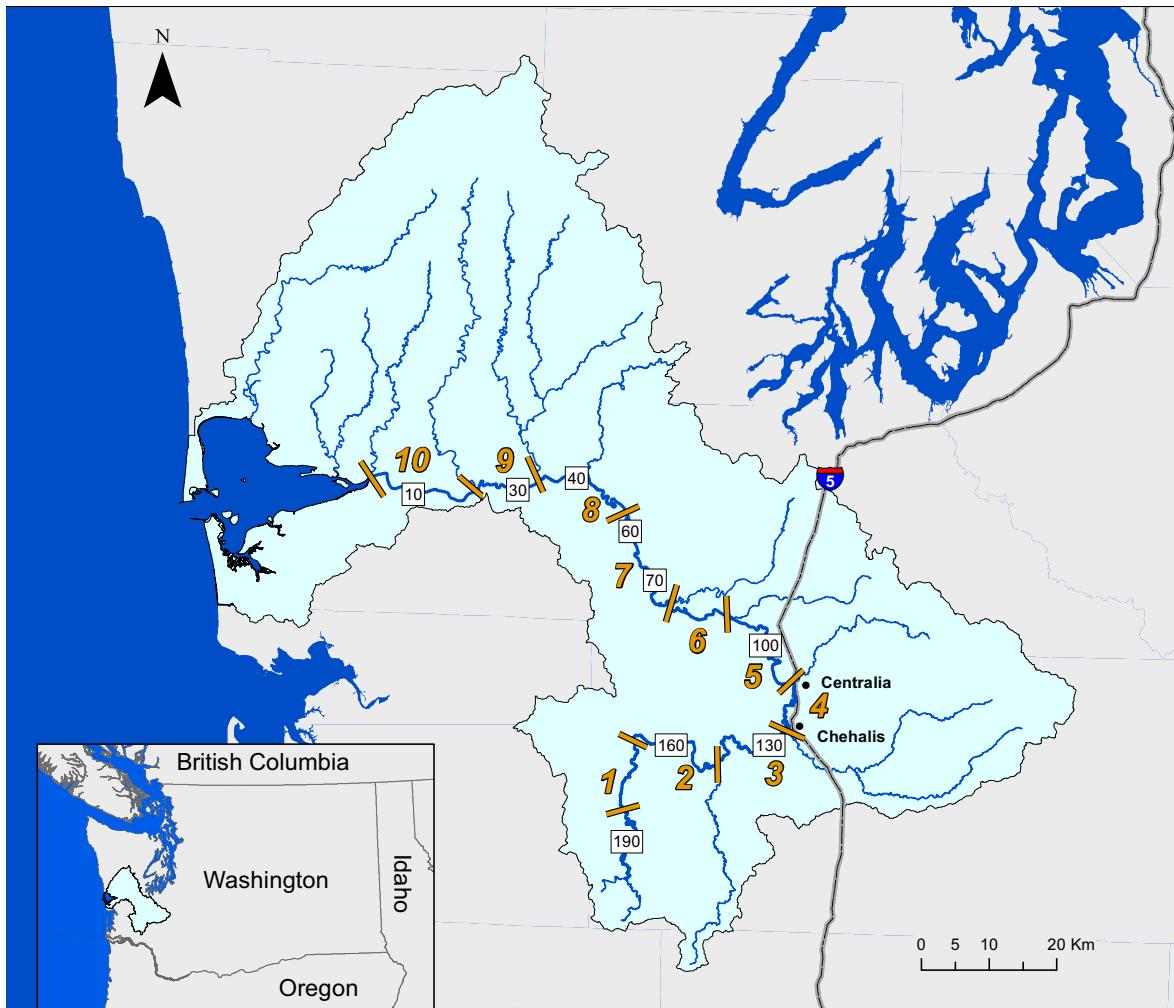


Fig. 1. The Chehalis River Basin (pale blue), with inset showing the study basin within Washington, USA. Gold bars along the river indicate river section (1–10), and white boxes indicate river kilometer.

of the Chehalis mainstem (Fig. 1). We sampled all available sites (contingent upon landowner permission) in the first two river segments (most upstream) due to the few sites present and because this area encompasses locations most likely affected by a proposed dam and reservoir; the ecological effects of such a dam are of interest to the State of Washington because the entire basin is the focus of an aquatic species restoration plan (CBS 2017). In the next downstream river segment, we sampled 50% of its sites, and we sampled about 36% of sites in the remaining river segments. In each river segment, we selected sites randomly and sampled them conditional upon access permission from private

landowners. Overall, we obtained permission to access 83% of sites where access was requested.

Over each of three years (2015–2017), Washington Department of Fish and Wildlife field crews surveyed sites three times between mid-January and early June, within the breeding season for the suite of native pond-breeding amphibians that utilize floodplain off-channel habitats (2015: $n = 49$; 2016: $n = 54$; 2017: $n = 50$). We sampled 38 sites across multiple years, yielding 103 unique sites sampled across three years.

Amphibian and fish sampling

Our study included six pond-breeding amphibians: the northern red-legged frog (*Rana aurora*),

Pacific treefrog (*Pseudacris regilla*), long-toed salamander (*A. macrodactylum*), northwestern salamander (*Ambystoma gracile*), rough-skinned newt (*Taricha granulosa*), and the non-native American bullfrog. We observed 12 native and eight non-native fish species during the surveys (Appendix S1).

We used visual encounter surveys (VES) where surveyors conducted a slow walk within aquatic habitats in depths up to 1 m. We used kayaks where sites had limited access. The VES effort focused on observing amphibian egg masses, larval or adult amphibians, and fish. We augmented VES with 50 dip net samples that were widely distributed across sample sites. Additionally, we used electrofishing during one of the three site visits in each of 2016 and 2017. We identified all amphibian and fish species and their life stages, and archived photographic vouchers. For most amphibians, we considered a species detected at a site if we encountered life history stages evident of successful breeding (i.e., eggs, larvae, recent metamorphs). For newts, we also included the adult life stage in our detection histories because adult newts are largely aquatic during the native amphibian breeding season and often prey on the eggs and larvae of other amphibian species (Marks and Doyle 2005). Timing of surveys (mid-January–early May) preceded the local American bullfrog breeding season (typically late May–July; *personal observation*); therefore, we only included bullfrog larvae in our analyses (i.e., these individuals had successfully overwintered as larvae).

Habitat characteristics

During field surveys, we took representative site photos that we used to classify sites into one of three categories for emergent vegetation cover: low (0–33% surface area), medium (34–66%), or high (>66%). In 2017, we recorded emergent vegetative cover to the nearest 10% of surface area, which was later assigned to either the low, medium, or high category for analysis.

We marked rough delineations of pond or wetland area at each site on a map, which was digitized to polygons using ArcMap (ESRI 2011). We measured polygon surface area on the first of three sampling occasions when water bodies were typically at their largest. We then used the 2011 National Land Cover Database (Homer

et al. 2015) to determine land cover within a 1-km buffer of each water body. We were particularly interested in forest cover within the buffer as many of these species have a terrestrial adult life cycle, where they rely upon undeveloped, often forested, landscapes.

We classified pond hydrology characteristics, including hydroperiod (permanent or temporary), origin (natural or human-made), and surface water connection to a river. While river connectivity typically referred to the Chehalis River, some sites were connected to another tributary entering the floodplain. We assigned sites into one of four connectivity categories: never connected, rarely connected (only every few years during a major flood), seasonally connected (typically every winter), or permanently connected. We determined hydrologic classifications from field crew notes, conversations with landowners, and visual assessment of current and historical aerial photographs. Connectivity was also informed by Hydrologic Engineering Center's River Analysis System (HEC-RAS) one-dimensional hydrological inundation model outputs, which was developed cooperatively between Washington Department of Fish and Wildlife and Anchor QEA (CBS 2017).

Statistical analysis

We modeled the probability of detecting a species when it is present (hereafter “detection probability”) and the probability of site occupancy for all six amphibian species using a Bayesian hierarchical framework (Kéry and Royle 2016). Specifically, we developed multi-species, single-season occupancy models using survey data collected at all 103 unique sites, with environmental covariates on both detection and occupancy probabilities. First, we selected the study sites for analysis. We had 38 sites that were sampled across multiple years; for these sites, we selected one study year to include in the analysis to avoid assuming that occupancy across years at a site was independent. To select which study year to include, we prioritized the study year when a site had been sampled three times (occasionally water bodies dried or access was retracted before three surveys were completed). If a site was sampled three times in multiple years, we randomly selected a study year to include in the analysis.

Table 1. Predictor variables examined in the detection and occupancy models of the amphibian species.

Predictor variable	Type	Summary	Explanation
Detection (p)			
Day of year	Continuous	25–161; 87.1 (34.0); first visit: 52.0 (16.1); second visit: 82.0 (10.6); third visit: 127.2 (15.0)	Day of year for survey date across three site visits
Centrarchids presence	Categorical	0: 62 sites; 1: 41 sites	Absence (0) or presence (1) of non-native centrarchids based on observations compiled from all three site visits
Bullfrogs presence	Categorical		Modeled bullfrog occupancy (used as covariate for the four prey species)
Occupancy (ψ)			
Bullfrog presence	Categorical		Modeled bullfrog occupancy (used as covariate for the four prey species)
Newt presence	Categorical		Modeled newt occupancy (used as covariate for the four prey species)
Centrarchid presence	Categorical	0: 62 sites; 1: 41 sites	Absence (0) or presence (1) of non-native centrarchids based on observations compiled from all three site visits (included in model for all native species)
Emergent vegetation	Categorical	Low: 38 sites; medium: 30 sites; high: 35 sites	Maximum amount of emergent vegetation cover at the site across three site visits: low (0–33%), medium (34–66%), or high (>66%)
Hydroperiod	Categorical	Temporary: 39 sites; permanent: 64 sites	Temporary or permanent hydroperiod
Forest cover	Continuous	0–67%; 17.7 (16.0)	Percent of forest cover in a 1-km buffer around each site
Connectivity	Categorical	Never: 12 sites; rarely: 37 sites; seasonally: 47 sites; permanently: 7 sites	Extent to which a site is connected to a river/stream: never, rarely, seasonally, or permanently
Origin	Categorical	Human-made: 19 sites; natural: 84 sites	Human-made or natural origin
Year	Categorical	2015: 40 sites; 2016: 30 sites; 2017: 33 sites	Year the site was visited (2015, 2016, or 2017)
Surface area	Continuous	128–171,813; 25,707.8 (31,684.5)	Surface area (m ²) at first site visit of the year

Note: Summary statistics include range and mean (standard deviation) for continuous variables and sample size for each level of categorical variables.

We then created detection and occupancy models starting with single-species, single-season occupancy models for the bullfrog and newt monitoring data. These two species potentially prey upon or compete with the other four native amphibian species; therefore, we developed their models first so that their modeled occupancy could be used in the detection and occupancy models for the other native species (e.g., create multi-species models). We used two covariates on detection probability: day of year and centrarchid presence (Table 1). While emergent vegetation may also influence detection probability, it was collinear with day of year (i.e., more emergent vegetation later in the season) and therefore excluded from the detection models. We decided to use day of year as opposed to emergent vegetation because it was a finer resolution than the emergent vegetation categories (low, medium, and high). For centrarchids, we used naïve observations and did not model occupancy because

fish sampling methods differed (e.g., VES and dipnets vs. electrofishing) and we cannot assume closed fish populations across our study period. We did not include native fish species in our models because they co-evolved with our amphibian species and are unlikely to lower occupancy probabilities.

We used covariates on occupancy probability, including surface area, emergent vegetation, forest cover (% in a 1-km buffer), river connectivity, hydroperiod, site origin (natural vs. human-made), and study year (Table 1). For newts, we also included naïve centrarchid presence as a covariate because we are uncertain on the extent to which newt larvae in our study region are toxic to fish. We included study year to account for environmental differences across years that were not accounted for with the covariates we considered. For instance, total precipitation in nearby Grand Mound, Washington, was 71, 116, and 101 cm between November and March

of the 2015, 2016, and 2017 sampling seasons, respectively.

After building global models with all possible covariates for detection and occupancy probabilities for the bullfrog and newt, we evaluated the importance of each environmental covariate using an indicator variable approach (Kuo and Mallick 1998). Specifically, for each species, we multiplied the model coefficient for each covariate by a latent, binary inclusion parameter (w_v for all covariates in the model). During this process, a covariate is included in the estimates when the associated inclusion parameter is 1, and not included in the estimates when the associated inclusion parameter is 0. This model selection approach allows for the evaluation of all possible combinations of predictor variables simultaneously, where each unique sequence of inclusion parameters is a candidate model (Royle et al. 2014). After fitting global models with the inclusion parameters, we took the top 100 models and considered a covariate important if at least 50% of the 100 top models included that covariate (Table 2). We based our inferences on the best-approximated model for each species (Appendix S2).

After selecting the best-approximated model for bullfrogs and newts, we created detection and occupancy probability models for the remaining four potential prey species: red-legged frogs, Pacific treefrogs, long-toed salamanders, and northwestern salamanders. Detection covariates included the following: day of year, centrarchid presence (naïve), and bullfrog presence (modeled) (Table 1). Occupancy covariates included the following: surface area, emergent vegetation, forest cover (% in a 1-km buffer), river connectivity, hydroperiod, site origin (natural vs. human-made), study year, centrarchids (naïve), bullfrogs (modeled), and newts (modeled; Table 1). We used the same indicator variable approach described above to infer the best-approximated model (Appendix S2).

We fit models using a Monte Carlo-Markov chain (MCMC) algorithm implemented in the program JAGS (Plummer 2003). Within the program R (R Core Team 2017), we used the rjags package (Plummer et al. 2016) to run JAGS. We used diffuse prior distributions 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 inclusion parameters had uninformative prior probabilities of 0.5 (i.e., equal probability of model inclusion or exclusion). The top ten models for each species can be seen in Appendix S2. Prior to model fitting, we standardized all continuous variables with a mean of zero and standard deviation (SD) of one. We drew inferences from 60,000 posterior samples taken from three chains of 150,000 samples thinned to every five, with a burn-in of 50,000 samples. This resulted in convergence for all parameter estimates based on the Brooks and Gelman diagnostic ($R < 1.1$; Brooks and Gelman 1998) and visual inspection of trace and density plots of posterior distributions. We describe the posterior distributions for detection probability and occupancy probability by their mean, SD, and 95% credible interval. We calculated odds ratios for each coefficient estimate to facilitate interpretation (Hosmer et al. 2013). We also report the proportion of area occupied, which is the estimated number of sites occupied divided by the total number of sites.

RESULTS

We analyzed survey data from 103 sites, representing a diversity of water bodies (Table 1). Sites ranged in surface area from 128 to 171,813 m² (mean = 25,707.8 m²; SD = 31,684.5); 64 sites were permanent and 39 were temporary. There was no relationship between surface area and hydroperiod (t -test, $t = 1.12$, $df = 94.1$, $P = 0.27$), reflecting that there were small, permanent water bodies as well as large, ephemeral sites. In terms of river connectivity, 12 sites were never connected, 37 rarely connected, 47 seasonally connected, and seven permanently connected. Connectivity was independent of hydroperiod: There were permanent, isolated water bodies as well as temporary sites with river connections. The exception was that all sites with permanent river connections had a permanent hydroperiod. We naively detected centrarchids at 41 sites and bullfrogs at 55 sites.

Detection probability

The mean detection probability (p) ranged from 0.37 (± 0.06 SD) for bullfrogs to 0.87 (± 0.04 SD) for red-legged frogs (Fig. 2B). Detection probabilities increased with day of year for three

Table 2. Parameter weights ($\times 100$) of predictor variables based on their probability of occurring in top 100 models.

Predictor Variable	American bullfrog	Rough-skinned newt	Northern red-legged frog	Pacific treefrog	Long-toed salamander	Northwestern salamander
Detection (p)						
Bullfrog presence	na	na	72	42	100	9
Day of year	67	56	29	100	8	0
Centrarchid presence	88	17	7	100	20	1
Occupancy (ψ)						
Bullfrog presence	na	na	63	30	40	65
Newt presence	na	na	25	25	37	40
Forest	34	85	10	5	17	19
Surface area	62	9	31	41	40	15
Centrarchid presence	na	37	100	29	34	56
Year	65	64	95	84	86	83
Origin	42	60	46	49	80	57
Connected	97	88	100	100	99	100
Emergent vegetation	64	73	95	97	84	93
Hydroperiod	62	17	31	64	100	29

Note: Predictor variables are included in the best-approximated model if they are retained in at least 50% of the 100 top models for each species (indicated with bold type).

species: American bullfrogs, rough-skinned newts, and Pacific treefrogs. Centrarchids were associated with increased detectability for American bullfrogs and reduced detectability for Pacific treefrogs: Bullfrogs were 2.8 times more likely and treefrogs 2.6 times less likely to be detected when centrarchids were present (Table 3). American bullfrogs were associated with reduced detectability for both northern red-legged frogs and long-toed salamanders, which, when present, were 2.6 and 4.2 times less likely to be detected, respectively, when bullfrogs were present (Table 3). None of the three covariates influenced detection probability for northwestern salamanders (Table 3).

Occupancy probability

The proportion of area occupied ranged from 0.43 (± 0.04 SD) for rough-skinned newts to 0.92 (± 0.02 SD) for northwestern salamanders (Fig. 2B). Medium levels of emergent vegetation (34–66% cover) increased occupancy probability (ψ) for all six species, with the odds of occupying a site being 1.5 times (rough-skinned newts) to 6.3 times (long-toed salamanders) more likely when a site had medium levels of emergent vegetation compared to a site with low amounts of emergent vegetation (Table 4, Fig. 3B). Centrarchids reduced occupancy probability for two

species: Northern red-legged frogs and northwestern salamanders were 8.4 and 3.6 times less likely to occupy a site where centrarchids were present (Table 4, Fig. 3A). American bullfrogs did not negatively influence the probability of occupancy for any of the four potential prey species and were actually positively associated with occupancy probability for northern red-legged frogs and northwestern salamanders, although estimates included zero (Table 4).

River connectivity had the strongest effect when the connection was permanent: Sites that were permanently connected to a stream or river had lower occupancy probability for northern red-legged frogs, Pacific treefrogs, long-toed salamanders, and northwestern salamanders (odds ratios range: 4.1–7.8), and only rough-skinned newt probability of occupancy increased with permanent connections (Table 4). Hydroperiod also influenced occupancy probabilities for three species: American bullfrogs were 3.5 times more likely to occupy a permanently wet site, whereas Pacific treefrogs and long-toed salamanders were 2.9 and 12.4 times more likely to occupy an ephemeral site, respectively (Table 4). Study year affected occupancy probabilities for all species: Relative to 2015, long-toed salamanders were more likely to occupy a site in 2016; newts, northern red-legged frogs, and

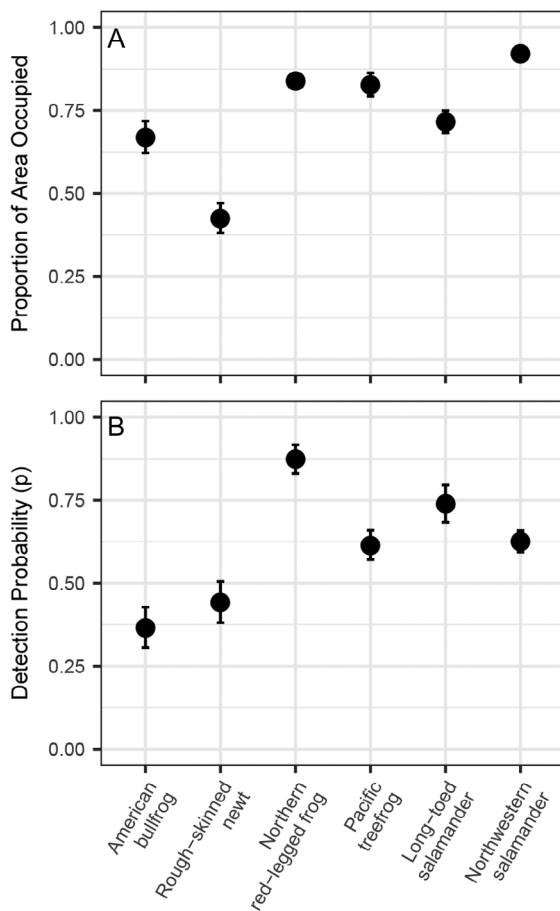


Fig. 2. The mean \pm standard deviation for the (A) proportion of area occupied and (B) detection probability based on the best-approximated occupancy model for each species. We calculated detection probability from the back-transformed intercept, which assumes the average value for continuous predictor variables (e.g., day of year) and baseline level for factor variables (e.g., absence of centrarchids and American bullfrogs).

northwestern salamanders were more likely to occupy a site in 2017; and American bullfrogs and Pacific treefrogs were less likely to occupy a site in 2017 (Table 4). Rough-skinned newts were the only species where occupancy probability increased with forest cover; newts were also 4.6 times more likely to occupy a human-made vs. natural site (Table 4). Newts had no effects on detection or occupancy for the four potential prey amphibian species. Surface area only affected American bullfrog occupancy probability: Bullfrogs

were more likely to occupy a smaller site than a larger one.

DISCUSSION

This study demonstrates the importance of floodplain off-channel ponds and wetlands to native amphibians, even in a highly altered landscape. To date, most research on habitat use by stillwater-breeding amphibians largely focuses on isolated water bodies, with only a few examples of floodplain studies (Joly and Morand 1994, Jansen and Healey 2003, Henning and Schirato 2006, Tockner et al. 2006, Ocock et al. 2016). However, the unique hydrology of floodplain systems may mean that traditional ideas about habitat use and landscape dynamics may not apply (e.g., “ponds as patches,” Marsh and Trenham 2001). Overall, we show that occupancy rates for the four amphibian prey species were generally higher in the floodplain habitats we studied than in non-floodplain habitats within the species’ native ranges (Appendix S3), we identify non-native centrarchid fishes as the major threat to this set of native amphibians, and we provide management and restoration recommendations that will bolster amphibian occupancy across the landscape.

Occupancy was relatively high (≥ 0.72) for the four amphibian prey species (northern red-legged frog, Pacific treefrog, northwestern salamander, and long-toed salamander) when compared to studies focusing on the same suite of amphibians in their native range (Appendix S3). For instance, we estimated that the proportion of area occupied was 1.5–1.6 times higher for three of the four potential prey species in the Chehalis River Basin compared to non-floodplain systems in the Willamette Valley of Oregon (Appendix S3; Rowe et al. 2019). Our occupancy estimates were most similar to a study conducted in the Puget Sound Basin, Washington, which may partially reflect geography as well as the fact that many of their sites were also river-connected (Appendix S3; Richter and Azous 1995, Azous and Horner 1997). While we cannot determine the exact mechanism for our study’s high occupancy estimates, the fact that we observed similar occupancy patterns between isolated and seasonally connected water bodies suggests that the high occupancy rates within the floodplain

Table 3. Best-approximating detection probability (p) models for the six amphibian species, including parameter estimates, standard deviations (SDs, in parentheses), upper and lower 95% credibility intervals (CI), and odds ratios (with direction of the relationship indicated using an arrow).

Species	Parameter	Estimate	95% CI		Odds ratio
			Lower	Upper	
American bullfrog	Intercept	-0.557 (0.268)	-1.073	-0.019	
	Day of year	0.403 (0.155)	0.102	0.711	↑ 1.50
Rough-skinned newt	Centrarchids: present	1.026 (0.344)	0.351	1.697	↑ 2.79
	Intercept	-0.232 (0.255)	-0.747	0.256	
Northern red-legged frog	Day of year	0.400 (0.186)	0.042	0.774	↑ 1.49
	Intercept	2.000 (0.418)	1.270	2.916	
Pacific treefrog	Bullfrog: present	-0.945 (0.478)	-1.946	-0.067	↓ 2.57
	Intercept	0.474 (0.189)	0.108	0.847	
Long-toed salamander	Day of year	0.479 (0.140)	0.212	0.759	↑ 1.61
	Centrarchids: present	-0.941 (0.301)	-1.526	-0.346	↓ 2.56
Northwestern salamander	Intercept	1.066 (0.303)	0.514	1.715	
	Bullfrog: present	-1.437 (0.373)	-2.193	-0.729	↓ 4.21
	Intercept	0.518 (0.137)	0.253	0.790	

Notes: Estimates are in the logit-scale. Continuous predictor variables were fit with standardized data; estimates and odds ratios should be interpreted for a one SD change in predictor variable.

may be due to landscape-level patterns. For instance, floodplain ponds and wetlands may be more productive due to nutrient-rich groundwater (Tockner et al. 2000, Tockner and Stanford 2002) and the more spatially complex floodplain landscape may support a food web mosaic (Bellmore et al. 2013) that increases community stability (Bellmore et al. 2015). A greater proportion of wet areas on the landscape may also facilitate colonization. Regardless of mechanism, the Chehalis River floodplain provides important habitat for native amphibian species despite numerous threats, at least over the three-year period we sampled. It appears that floodplains are worthwhile locations for amphibian conservation and restoration efforts.

We identified non-native centrarchids as the greatest threat to native amphibian occupancy. Centrarchids reduced occupancy for the northern red-legged frog and northwestern salamander and reduced detection of the Pacific treefrog but had no effect on either the long-toed salamander or rough-skinned newt. The different species responses were likely a factor of life history traits influencing which amphibian species routinely encounter centrarchids. In particular, the northern red-legged frog and northwestern salamander have long developmental intervals (typically 11–14 weeks and 12–14 months to reach

metamorphosis, respectively) and often breed in permanent water, where there is greater likelihood of spatial overlap with centrarchid fishes (Lannoo 2005). In contrast, the Pacific treefrog and long-toed salamander metamorphose relatively rapidly (in eight weeks or less; Lannoo 2005) and were, respectively, 2.9 and 12.4 times more likely to occupy temporary hydroperiod sites, which reduces interactions with centrarchids. Indeed, we detected centrarchids in 53% (34/64) of permanent hydroperiod sites, but in only 17% (7/41) of temporary hydroperiod sites.

In contrast to our findings, other studies have found that non-native fishes negatively influenced both the Pacific treefrog (Monello and Wright 1999, Pearl et al. 2005, Joseph et al. 2016) and long-toed salamander (Pearl et al. 2005, Pilioid et al. 2010) occupancy. Two of the three studies evaluating the effect of centrarchids on Pacific treefrogs did not estimate detection (for which we found a negative effect), which could generate false negatives (i.e., centrarchids may reduce treefrog detectability, which may be interpreted as an absence and incorrectly reduce occupancy estimates). Long-toed salamanders were the native amphibian species least likely to occupy permanent hydroperiod sites, so the overlap between centrarchid and long-toed salamander utilization of sites may be too sparse to

Table 4. Best-approximating occupancy probability (ψ) models for the six amphibian species, including parameter estimates, standard deviations (SDs, in parentheses), upper and lower 95% credibility intervals (CI), and odds ratios.

Parameter	Estimate	95% CI		Odds ratio
		Lower	Upper	
American bullfrog				
Intercept	0.296 (0.995)	-1.585	2.336	
Surface area	-0.888 (0.384)	-1.688	-0.181	↓ 2.43
Year: 2016	0.625 (0.874)	-0.989	2.456	↑ 1.87
Year: 2017	-1.003 (0.752)	-2.493	0.451	↓ 2.73
Connection: rare	-1.278 (0.880)	-3.063	0.405	↓ 3.59
Connection: seasonal	0.848 (0.889)	-0.854	2.623	↑ 2.34
Connection: permanent	0.253 (1.229)	-2.043	2.773	↑ 1.29
Emergent vegetation: medium	1.168 (0.904)	-0.532	3.029	↑ 3.22
Emergent vegetation: high	-0.324 (0.820)	-1.947	1.282	↓ 1.38
Hydroperiod: permanent	1.243 (0.736)	-0.180	2.723	↑ 3.47
Rough-skinned newt				
Intercept	-0.178 (0.765)	-1.593	1.408	
Forest	0.728 (0.338)	0.134	1.433	↑ 2.07
Year: 2016	0.199 (0.663)	-1.079	1.521	↑ 1.22
Year: 2017	0.894 (0.642)	-0.358	2.160	↑ 2.45
Origin: natural	-1.521 (0.755)	-3.045	-0.077	↓ 4.58
Connection: rare	0.658 (0.783)	-0.889	2.194	↑ 1.93
Connection: seasonal	1.015 (0.805)	-0.576	2.590	↑ 2.76
Connection: permanent	1.755 (1.070)	-0.276	3.973	↑ 5.78
Emergent vegetation: medium	0.384 (0.663)	-0.879	1.723	↑ 1.47
Emergent vegetation: high	-0.576 (0.647)	-1.860	0.688	↓ 1.78
Northern red-legged frog				
Intercept	1.199 (0.906)	-0.560	3.000	
Bullfrog: present	1.176 (0.810)	-0.381	2.812	↑ 3.24
Centrarchids: present	-2.131 (0.763)	-3.694	-0.703	↓ 8.43
Year: 2016	-0.159 (0.719)	-1.576	1.262	↓ 1.17
Year: 2017	1.440 (0.855)	-0.137	3.220	↑ 4.22
Connection: rare	-0.190 (0.844)	-1.848	1.469	↓ 1.21
Connection: seasonal	0.511 (0.906)	-1.260	2.298	↑ 1.67
Connection: permanent	-1.710 (1.030)	-3.728	0.319	↓ 5.53
Emergent vegetation: medium	1.791 (0.855)	0.221	3.580	↑ 6.00
Emergent vegetation: high	1.074 (0.793)	-0.410	2.710	↑ 2.93
Pacific treefrog				
Intercept	1.959 (1.024)	0.024	4.053	
Year: 2016	0.225 (0.946)	-1.519	2.207	↑ 1.25
Year: 2017	-0.771 (0.831)	-2.409	0.871	↓ 2.16
Connection: rare	0.849 (0.992)	-1.000	2.921	↑ 2.34
Connection: seasonal	0.278 (0.904)	-1.471	2.094	↑ 1.32
Connection: permanent	-1.411 (1.098)	-3.544	0.777	↓ 4.10
Emergent vegetation: medium	1.620 (1.002)	-0.152	3.812	↑ 5.05
Emergent vegetation: high	1.030 (0.931)	-0.639	3.060	↑ 2.80
Hydroperiod: permanent	-1.064 (0.885)	-2.831	0.666	↓ 2.90
Long-toed salamander				
Intercept	2.091 (0.944)	0.290	3.991	
Year: 2016	1.481 (0.832)	-0.055	3.235	↑ 4.40
Year: 2017	0.153 (0.729)	-1.285	1.588	↑ 1.17
Connection: rare	0.358 (0.824)	-1.257	1.971	↑ 1.43
Connection: seasonal	0.077 (0.841)	-1.555	1.743	↑ 1.08
Connection: permanent	-1.969 (1.112)	-4.205	0.186	↓ 7.16

(Table 4. Continued.)

Parameter	Estimate	95% CI		Odds ratio
		Lower	Upper	
Emergent vegetation: medium	1.839 (0.955)	0.138	3.884	↑ 6.29
Emergent vegetation: high	0.090 (0.770)	-1.365	1.656	↑ 1.09
Hydroperiod: permanent	-2.519 (0.851)	-4.237	-0.893	↓ 12.41
Northwestern salamander				
Intercept	1.002 (1.112)	-1.112	3.268	
Bullfrog: present	1.403 (1.061)	-0.669	3.505	↑ 4.07
Centrarchids: present	-1.284 (0.991)	-3.257	0.663	↓ 3.61
Year: 2016	-0.262 (1.084)	-2.287	2.016	↓ 1.30
Year: 2017	1.291 (1.211)	-0.929	3.828	↑ 3.64
Origin: natural	0.849 (1.033)	-1.138	2.935	↑ 2.34
Connection: rare	1.230 (1.148)	-0.927	3.582	↑ 3.42
Connection: seasonal	0.857 (1.129)	-1.304	3.161	↑ 2.36
Connection: permanent	-2.052 (1.204)	-4.378	0.336	↓ 7.78
Emergent vegetation: medium	1.321 (1.096)	-0.776	3.548	↑ 3.75
Emergent vegetation: high	1.351 (1.214)	-0.902	3.878	↑ 3.86

Notes: Estimates are in the logit-scale. Continuous predictor variables were fit with standardized data; estimates and odds ratios should be interpreted for a one SD change in predictor variable.

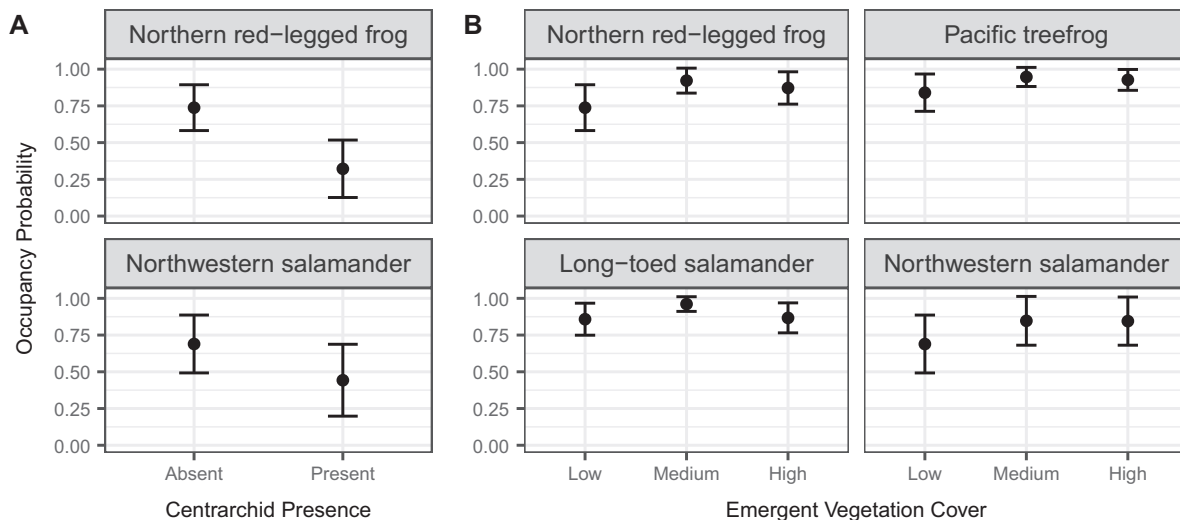


Fig. 3. Relationship between (A) centrarchid presence and (B) emergent vegetation cover (when centrarchids are absent) on the mean \pm standard deviation occupancy probability of the four prey species for which these variables are included in the best-approximated models.

identify an effect. Long-toed salamanders may simply avoid permanent hydroperiod sites with fish in a manner similar to that described for wood frogs (*Rana sylvatica*; Hopey and Petranka 1994). Alternatively, long-toed salamanders may select breeding habitat based on other variables; for instance, temperature is a major proximal factor in determining amphibian growth and

differentiation (Smith-Gill and Berven 1979) and short hydroperiod habitats frequently have thermal regimes that favor rapid development (Bancroft et al. 2008). Our approach cannot distinguish among these alternatives, but we can state that a negative centrarchid effect was evident among native amphibians that tend to utilize permanent sites where centrarchids and

native amphibians have the greatest opportunity to interact.

Unlike centrarchids, we found little evidence that American bullfrogs adversely impacted native amphibian occupancy. Bullfrogs reduced detection of the northern red-legged frog and the long-toed salamander, which might reflect these two species altering their behavior, such as habitat switching when bullfrogs were present (Kiesecker and Blaustein 1998). Nonetheless, bullfrogs did not negatively affect native species occupancy. In fact, the pattern was opposite: The northern red-legged frog and northwestern salamander had occupancy probabilities three to four times higher when bullfrogs were present, perhaps reflecting their use of hydrologically or structurally similar water bodies. While bullfrogs have been implicated with amphibian declines, much of this work was correlative and potentially explained by confounding variables, such as non-native fish or disease (Hayes and Jennings 1986), or was experimental (Lawler et al. 1999, Adams 2000), which may amplify effects not seen in the wild. In field studies within the Pacific Northwest, most studies have found no effect of bullfrog presence on native amphibian species occurrence (Richter and Azous 1995, Adams et al. 1998, 2011, Adams 1999, Pearl et al. 2005, but see Rowe et al. 2019). It is possible that our native amphibian assemblage was not as susceptible to bullfrogs due to their use of terrestrial habitats post-metamorphosis. Where native amphibian species are more reliant on aquatic habitats, such as in desert or Mediterranean climates, they may be more vulnerable to bullfrog predation or competition (Bissattini et al. 2019). Bullfrogs may also be more problematic where they transmit deadly amphibian pathogens, which pose a serious threat for native amphibians in Brazil and Europe (Garner et al. 2006, Carvalho et al. 2017). For the Pacific Northwest, however, our study provides additional support to long-standing evidence that if a bullfrog effect exists, it is minor when contrasted to effects by exotic fishes (Hayes and Jennings 1986) or habitat (Adams et al. 1998).

The results strongly supported our prediction that emergent vegetation would increase native amphibian occupancy. Based on areal cover, intermediate levels of emergent vegetation cover increased occupancy for all native amphibian

species. A number of other studies have highlighted emergent vegetation as important to the same suite of native amphibians (Monello and Wright 1999, Pearl et al. 2005, Adams et al. 2011, Rowe et al. 2019). Emergent vegetation can provide refuge by reducing the foraging efficiency of fish predators (Diehl 1988, Sass et al. 2006) or maintaining cooler water temperatures (Miller and Fujii 2010) and can support abundant high-quality food resources (Cattaneo and Kalff 1980, James et al. 2000). Experimentally exploring the relative importance of these different mechanisms would be worthwhile, especially in a restoration and management context. Managers can design wetland and pond bathymetry to promote emergent vegetation by creating a low-gradient aquatic margin with shallow waters (Zedler 2000). However, there is a management concern that creating shallow pond margins will encourage the spread of reed canary grass (*Phalaris arundinacea*), an already common invasive exotic. Some research suggests that reed canary grass may not negatively affect this amphibian assemblage (Pearl et al. 2005, Holzer and Lawler 2015) and could actually benefit native amphibians by providing refuge habitat from non-native predators (Rowe et al. 2019). Yet other effects of reed canary grass on wetland ecosystems remain unknown; for instance, selected plant traits (e.g., lignin, phenolics, and nutrient ratios) may affect amphibian performance (Cohen et al. 2012, Holzer and Lawler 2015). Overall, emergent vegetation appears to be important for mediating negative effects of non-native predators on native amphibians.

Counter to our expectations, we found little evidence that river connectivity increased native amphibian occupancy. We predicted that intermittent river connectivity might reflect a more historical inundation regime, which could bolster nutrients and food resources (Junk et al. 1989). However, we found that both isolated sites and those with intermittent connections were indistinguishable in quality, at least in context of our high-level connectivity classification. It is possible that the floodplain landscape is more important than actual flood connectivity in affecting amphibian occupancy, particularly in wet climates that do not rely on surface river connectivity as a water source (as opposed to more arid landscapes, Ocock et al. 2016). Future research

evaluating the mechanisms behind this pattern would be fruitful, such as examining amphibian metacommunities, groundwater inputs, and ecosystem dynamics along the connectivity gradient. Further, we found that sites permanently connected to the river strongly favored rough-skinned newts and reduced occupancy for the four remaining native amphibian species. Permanently connected sites may be subject to more regular flows and fish access and should be avoided when restoring habitats for native amphibians.

Our study has two additional findings that will inform aquatic restoration within a floodplain landscape. First, we found no strong effects of forest cover (at the 1-km scale) on occupancy for the four amphibian prey species. Greater forest cover increased occupancy only for the rough-skinned newt, consistent with Pearl et al. (2005) who studied the same suite of species in the Willamette Valley, Oregon. In more urban areas, distance to nearest forest patch may be more important for the same suite of amphibians (Guderyahn et al. 2016, Grand et al. 2017). But in this floodplain landscape, the land cover (e.g., mostly forest and farmland) appears to be permeable enough to support the native amphibian assemblage. Future studies should explore amphibian movement in agricultural floodplains, particularly as agriculture has reduced amphibian use in other (non-floodplain) agricultural regions (Gray et al. 2004, Piha et al. 2007). Secondly, we found that water body origin (human-built or natural) had little influence on amphibian occupancy. This finding is similar to that of Guderyahn et al. (2016) for an area with greater urbanization. Rough-skinned newts favored human-built ponds, but pond origin lacked a clear relationship to the other species. This finding suggests that management and restoration in which construction of new water bodies is involved may benefit this set of native amphibians.

To close, our study within the Chehalis River floodplain is pertinent to active efforts to restore the watershed's aquatic habitats and informs management of other river floodplains facing threats from agriculture, development, reduced wetland-river connections, and established non-native predators. We found that native amphibians remain widespread across off-channel

habitats within this modified floodplain. Yet, amphibians face clear challenges from the altered environment. The largest challenge we identified was the negative effect of centrarchid fishes. Restoration alternatives to reduce the negative effects of centrarchids are twofold. First, maintaining both permanent and temporary water bodies on the landscape may permit amphibians with faster development times to use temporary habitats with fewer centrarchid fishes. Secondly, in permanent water bodies where centrarchid removal is currently not feasible, managing for intermediate levels of emergent vegetation may reduce the negative centrarchid effect. The primary challenge with this option is establishing desired native emergent vegetation levels where a constant reed canary grass reinvasion pressure exists. Interestingly, reconnecting wetlands to the river may not increase habitats occupied by native amphibians, but it also may not reduce them unless the connection is permanent. In conclusion, restoring off-channel ponds and wetlands within a floodplain landscape appears promising and warrants further experimentation and adaptive management.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.md243j3>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2853/full>