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Identification of habitat controls on northern red-legged frog populations: implications for habitat conservation on an urbanizing landscape in the Pacific Northwest

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Abstract

Introduction: In the Pacific Northwest of North America, research addressing lentic-breeding amphibian population vulnerability has emphasized aquatic habitats, frequently neglecting terrestrial habitats. Consequently, wetland protection and restoration often fails to preserve or restore adjacent uplands required by lentic-breeding amphibians. Inattention to the juxtaposition and connectivity of uplands to wetlands could locally extirpate lentic-breeding amphibians. The objective of this research is to identify the relative importance of juxtaposed terrestrial and aquatic habitats in a lentic-breeding amphibian, the northern red-legged frog (*Rana aurora*), by evaluating the relationship between its occurrence and abundance with its aquatic and terrestrial habitats. To accomplish this, egg mass counts were used to quantify *R. aurora* populations in 30 stillwater habitats across an urbanization gradient. Using a Geographic Information System, seven descriptors of aquatic and surrounding terrestrial habitats were measured to evaluate their relationships to *R. aurora* occurrence and abundance.

Results: *Rana aurora* occurrence and breeding abundance both reflect the forested area around wetland breeding sites and forest connectivity to those sites. *Rana aurora* breeding abundance also strongly reflects the percent of forested perimeter around wetland breeding sites. The forest habitat most important for *R. aurora* breeding abundance seems to be > 200 m from the breeding wetlands. The American bullfrog presence and the two aquatic parameters measured, wetland area and vegetated area, were unrelated to *R. aurora* occurrence and breeding abundance.

Conclusions: Area and connectivity of juxtaposed forested terrestrial habitat may represent a basic control on *R. aurora* presence and population size. Urban development policies should consider preservation and restoration of upland forest habitats beyond current fixed-width buffers and wetland habitat area at landscape scales.

Keywords: Northern red-legged frog, Amphibian habitat, *Rana aurora*, Land use, Landscape planning, Urban landscapes, Amphibian population

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Introduction

Maintaining populations of species with complex life histories that migrate between different habitats is challenging in human-altered landscapes. Terrestrial upland habitats are fragmented by roads (Trombulak and Frissell 2000) or replaced by buildings (Lehtinen et al. 1999), and wetland breeding sites may be altered or eliminated entirely (Dodd and Smith 2003). Outside of the US Pacific Northwest (PNW), such habitat alteration has been linked to declines in amphibian species richness (Lehtinen et al. 1999) or declines in the local populations of lentic-breeding amphibians that require terrestrial habitat juxtaposed to wetlands (Pope et al. 2000; Semlitsch 2000; Semlitsch and Bodie 2003). In the PNW, because most lentic-breeding amphibians require both terrestrial and aquatic habitats to complete their lifecycles, connectivity between these habitats is critical for maintaining local populations. Consequently, lentic-breeding amphibians may be threatened to varying degrees in human-altered landscapes featuring loss of breeding wetlands, adjacent non-breeding forested habitats, and landscape connectivity (Gibbs 2000).

The PNW has one of the fastest growing conurbations in North America (Pivo 1996). In Washington State, human population density increased by 13% between 2000 (2116 persons/km^2) and 2012 (2395 persons/km^2) (US Census Bureau 2015). Washington State's most populous county, King County, reached a total population of 2,044,449 in 2013 (US Census Bureau 2015) and is predicted to double by 2040 (WOFM [Washington Office of Financial Management] 2012). This extraordinary growth raises concerns that the forested landscape will be further fragmented as urbanization increases (Pivo 1996, Butler et al. 2004, McKee et al. 2004, Luck 2007). Attendant rapid changes in forested landscapes threaten the viability of wildlife dependent upon forest habitat for part of their lifecycle.

Over a decade has elapsed since McKinney (2002) emphasized the paucity of studies addressing urbanization impacts on native animal species (Scheffers and Paszkowski 2012). This statement is particularly relevant for amphibians in the PNW (Hayes et al. 2008). Accordingly, the goal of the present research was to examine how loss of forested terrestrial habitat due to urbanization is impacting the northern red-legged frog (*Rana aurora*), a lentic-breeding amphibian widespread in the mesic PNW. *Rana aurora* is the ideal amphibian to assess urbanization impacts because it is seasonally dependent on coupled aquatic (reproductive) and terrestrial (non-breeding active season) habitats and migrates seasonally long distances (to at least 5 km) utilizing a mosaic of aquatic and terrestrial habitats (Hayes et al. 2008). Habitat loss and fragmentation are more likely to affect migrating lentic-breeding amphibians such as *R.*

aurora compared to other amphibians whose life history phases are predominantly within aquatic habitats and/or are strongly riparian associated (Hayes et al. 2008).

Although diverse studies of amphibian assemblages report strong associations between amphibian richness and composition of the surrounding landscape (Laan and Verboom 1990; Knutson et al. 1999; Lehtinen et al. 1999), projects designed to protect and restore wetlands infrequently consider the surrounding uplands also needed by amphibians. This issue may be critically important in maintaining the population levels of lentic-breeding amphibians in the PNW—where forests are the primary upland habitat utilized during their lengthy non-breeding active season (Nussbaum et al. 1983; Martin and McComb 2003; Pearl et al. 2005; Hayes et al. 2008). If specific connectivity needs exist between the terrestrial and aquatic habitats that these amphibians require, then projecting how future land-use change might affect amphibian population dynamics may be facilitated (Cole et al. 1997; White et al. 1997).

The quantity and distribution of forested habitat needed to sustain *R. aurora* in the PNW is largely undocumented (Hayes et al. 2008). This study was designed to assess the habitat needs of *R. aurora* and to identify relationships as well as possible threshold criteria that exist between the jutxaposed mosaic landscape of aquatic and terrestrial habitats and *R. aurora* population levels. The present research describes the relationship between *R. aurora* occurrence and abundance and the terrestrial habitat (including forested area, its connectivity, and percent of forested wetland perimeter), as well as wetland characteristics (including wetland size and emergent vegetation). These data should help to identify conservation needs and strategies for lentic-breeding amphibians requiring both aquatic and terrestrial habitats at spatial scales within the seasonal habitat footprint used by *R. aurora*.

Methods

Site description and selection

Rana aurora populations were surveyed across selected wetlands within the greater Seattle area of western King County, Washington State, USA. King County is bordered by Puget Sound on the west and the Cascade Mountains on the east. Temperate moist forests dominate the less developed (eastern) portion of the study area (Franklin and Dyrness 1973). Wetlands diverse in size, shape, and type are imbedded across this landscape.

Geographic Information System (GIS) spatial tools were used to identify which wetlands within the water body dataset from the King County data portal meet the criteria for our survey (ESRI 2011; King County 2010). Initially, all open water wetlands below 800 m in elevation were located to minimize the likelihood of selecting

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wetlands above *R. aurora's* local elevation range (Nussbaum et al. 1983; Dvornich et al. 1997). Wetlands within 200 m of another wetland were excluded from the survey to ensure that independent breeding populations of *R. aurora* were being considered. *Rana aurora* adults are known to make exploratory movements among potential breeding sites during the post-winter thaw pre-breeding period, but such movements are not known to exceed 150 m (M. Hayes, unpublished data). Such movements are distinguishable from the back-and-forth migrations adults make between aquatic breeding habitat to which adults return annually with high site fidelity, and upland forested habitat where the non-breeding active season is spent (Licht 1974, Hayes et al. 2008). Human-constructed stormwater ponds were also excluded from this study.

In total, 1006 wetlands fulfilled the aforementioned selection criteria. Wetlands larger than 1.5 ha were excluded to ensure sampling effectiveness. Also, larger wetlands are more likely to be permanently flooded and have a higher predominance of exotic-invasive predators which negatively affect the occurrence of *R. aurora* (Adams 1999; M. Hayes, unpublished data). Wetlands under 1.5 ha encompass over 93% (2582 total wetlands and 2406 < 1.5 ha) of the total number of wetlands in *R. aurora's* local breeding range, and 88% (1006 total wetlands and 883 < 1.5 ha) of the wetlands that fell within the parameters of this study. For the remaining 883 wetlands, the percentage of surrounding forest area was determined within a 5-km footprint perpendicular from the edges of each wetland. A maximum distance of 5 km was used because *R. aurora* adults have been recaptured at straight-line distances of 5 km from their breeding ponds (Hayes et al. 2001; Hayes et al. 2007). Wetlands were then categorized across two strata to adequately characterize the variability in forest cover and wetland size for site selection. These strata included: (1) five categories of surrounding forest cover (≤ 17%, > 17–33%, > 33–50%, > 50–66%, > 66–100%) and (2) three evenly distributed categories of wetland size (≤ 0.50 ha, > 0.5–1.0 ha, and > 1.0–1.5 ha). The greatest forest cover category was twice the size of other categories because few wetlands existed where forest cover values were > 66%. Combined strata resulted in 15 different categories.

From this pool of wetlands, two categories within each of the 15 habitat categories were randomly chosen for this study, totaling 30 habitat categories (Fig. 1). Wetlands were then visited to ensure that they satisfied the selection criteria and that they had not been altered after the GIS dataset was created. Wetlands less than 0.6 m deep, and/or with vegetation that shaded them for most of the day, were excluded from the study database as being either too ephemeral or too shaded to be used by *R. aurora* (Licht 1969, 1971). Excluded wetlands were

replaced by the next wetland in the random sequence within the same habitat category.

Data collection
Landscape and aquatic habitat
All aquatic habitat and landscape features were estimated in ArcGIS 10.0 (ESRI 2011). Wetland area was estimated using the Geometry Field Calculator. Percent forest cover was estimated using the 2006-era classification of the US West Coast Region, zone 1 Landsat raster data with an accuracy of 86.1% and grain size of 90 × 90 m (DOC et al. 2008). These Landsat data were differentiated into 21 class types, but four classes (Deciduous Forest, Evergreen Forest, Mixed Forest, and Palustrine Forested Wetland) were collapsed into one "Forest" category.

Following this reclassification, percent forest area of the landscape surrounding each wetland was calculated using FRAGSTATS (v4.0) (McGarigal et al. 2012). Percent forest was calculated at 19 different distances from the wetlands in cumulative concentric footprints extending outward from the wetland edge every 50 m up to a distance of 500 m and subsequently every 500 m up to 5 km (Fig. 2). These nested footprints were used to characterize different habitat configurations across *R. aurora's* migratory pathway.

For each wetland, the following calculations were made: percent forested perimeter (PFP), area of emergent vegetation, and connectivity. Percent forested perimeter was calculated to evaluate wetland access to *R. aurora*. Perimeter was estimated using both the geometry calculator and the intersect functions (ESRI 2011). The percentage of forested perimeter was calculated by dividing the length of the wetland edge by the total distance of wetland edge that came into direct contact with the "Forest" category described above. The area of emergent vegetation within the wetland was calculated to evaluate the availability of potential breeding habitat because *R. aurora* oviposits on a vegetation brace (Licht 1971). Google imagery base map (2010) and GIS Editor were used to develop emergent vegetation polygons that included only the area within the wetland that might be used as an oviposition brace. Connectivity was calculated to evaluate the effects of fragmentation on the occurrence and abundance of *R. aurora* within study wetlands using the COHESION metric in FRAGSTATS (v4.0) (McGarigal et al. 2012). COHESION estimates the connectivity of habitat potentially used by *R. aurora* dispersing through the landscape classified in a forest/non-forest binary fashion (Schumaker 1996; see Supplementary file FRAGSTATS_COHESION information).

Amphibian presence and abundance
Rana aurora occurrence and abundance were estimated from visual encounter surveys of egg masses (Heyer et

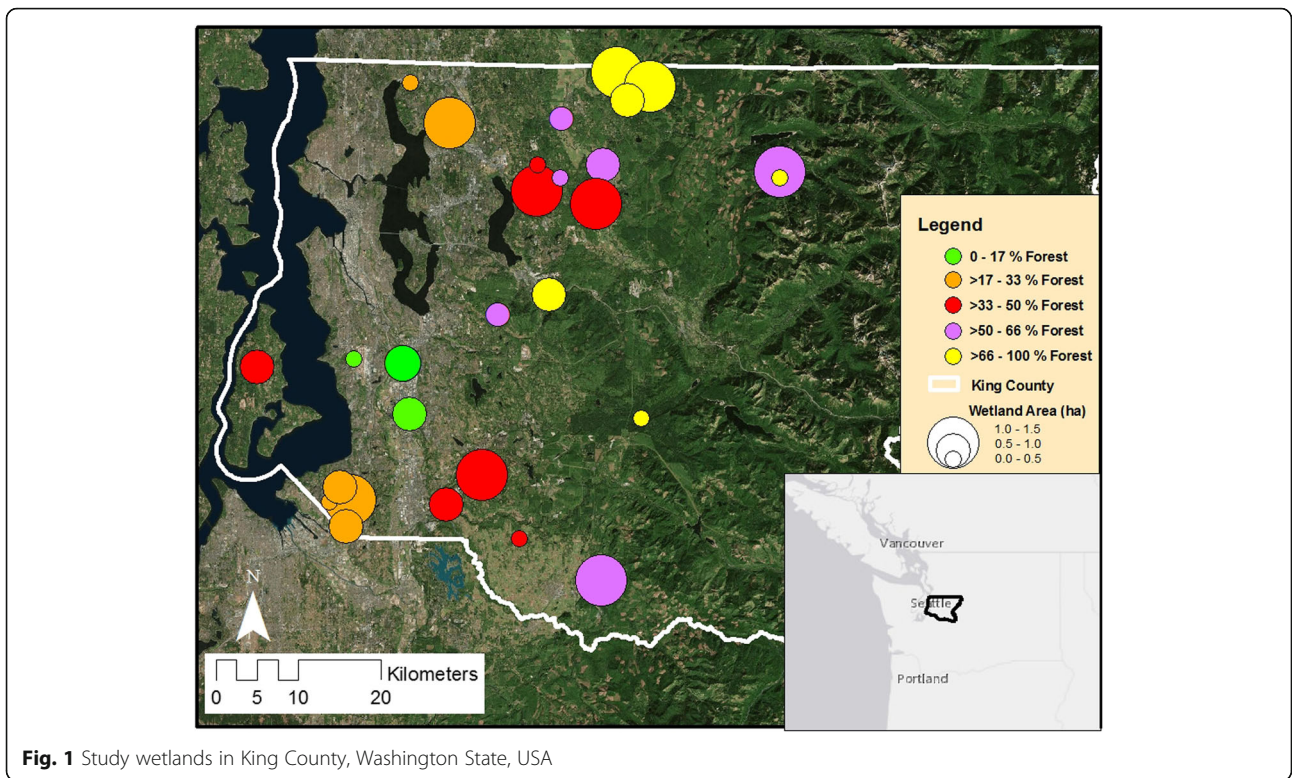Grand *et al. Ecological Processes* (2017) 6:44

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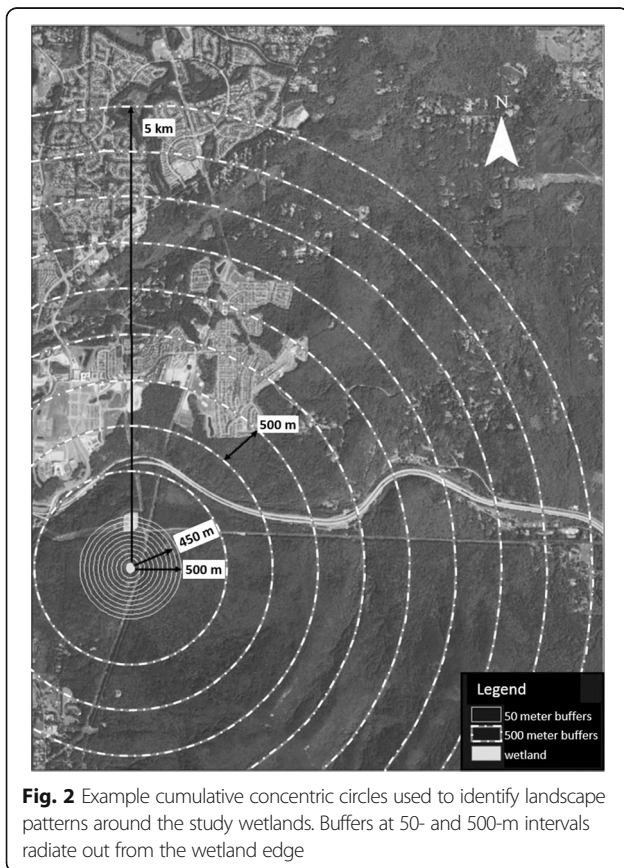**Fig. 1** Study wetlands in King County, Washington State, USA

Fig. 2 Example cumulative concentric circles used to identify landscape patterns around the study wetlands. Buffers at 50- and 500-m intervals radiate out from the wetland edge

al. 1994) completed between 17 February and 9 May 2012. For *R. aurora*, one egg mass corresponds to one breeding female as multiple clutching is not known and unlikely to occur given oviposition seasonality (see Licht 1969, 1971); hence, egg mass numbers effectively estimate the breeding population size of females and are a good surrogate for breeding population size (e.g., Richter and Azous 2001).

Citizen science volunteers were trained on egg mass identification and survey procedures by the Woodland Park Zoo (Seattle, WA, USA) and by Washington Department of Fish and Wildlife (WDFW) researchers (MPH and CDA). Citizen science volunteers surveyed seven of the wetlands while accompanied by an experienced surveyor. The other 23 wetland surveys utilized the double-observer approach published by Grant et al. (2005) where one experienced observer led the team. Surveys were completed by walking around each wetland to a water depth of 1 m. A flotation device was used to navigate around wetlands where thick woody vegetation and/or deep water impeded effective monitoring from the shore. One site was resurveyed the following year, February and March 2013, due to uncertainty in the quality of the original survey. Given that adult *R. aurora* have an estimated longevity of 10–12 years (Licht 1974), research has shown that the variation in egg mass numbers is typically very low from year to year (Adams 1999; M. Hayes, unpublished data), which supports the

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inclusion of the resurvey data. Additionally, climatic conditions between 2012 and 2013 were very similar and 2013 was not a severe drought year (NOAA 2012 and 2013; NIDIS 2017)—which otherwise might have affected the egg mass production rates of breeding females.

The species identity of each egg mass found was documented. Each wetland was surveyed at least twice to ensure obtaining the maximum estimate of egg mass numbers. If, on the second survey, a wetland still showed signs of recently deposited egg masses (i.e., based on their containing round embryos) adjacent to older egg masses (i.e., containing elongated embryos), the wetland was resurveyed until all egg masses contained elongated embryos that signified the end of ovipositiong. For each wetland, the maximum egg mass count was recorded. Due to evidence that most *R. aurora* breeding females lays eggs within 2 weeks of each other (Licht 1971), the extent of the wetland covered, and the number of surveys conducted, the detection rate was assumed to be 100%. Therefore, if no egg masses were found, occurrence was assumed to be zero.

During egg mass surveys, the presence of aquatic predators including the exotic American bullfrog (*Rana (Lithobates) catesbeiana)* and fish were recorded.

Two wetlands were excluded from analysis due to the ambiguity in egg mass identification. Both wetlands were from the lowest forest cover category and medium wetland size category.

Data analyses

Descriptive summaries of the recorded data are presented for the sample of observations investigated in this study. Associations of habitat variables [i.e., percent forest (PCF), connectivity (CON), area of emergent vegetation (EMG), forested perimeter (FRP), wetland area (AREA), bullfrog occurrence (BULL), and fish occurrence (FISH)] and *R. aurora* breeding abundance and occurrence were evaluated using the optimal discriminant analysis (ODA) machine-learning algorithm (Yarnold and Soltysik 1991). The ODA algorithm identifies the threshold value (cutpoint) for an ordered attribute (independent variable)—or the assignment rule for a categorical attribute—that most accurately (optimally) discriminates the different categories (or levels) of the class (dependent) variable for the sample. Identifying the maximum-accuracy (optimal) model involves computing the effect strength for sensitivity (ESS) that is obtained by using every possible cut-point (or assignment rule) to classify sample observations. The ESS is the mean sensitivity obtained by the model across class categories which standardizes, using a 0–100% scale, where 0% is the level of accuracy expected by chance and 100% is the perfect accuracy; negative values indicate lower accuracy than expected by chance. By definition, the optimal model yields the greatest ESS. The following ESS groups

are formed based on levels of accuracy: values < 25% reflect a relatively weak effect; values < 50% are moderate effects; values < 75% are relatively strong effects; and values < 90% are strong effects. Exact statistical significance is computed as a permutation probability, and validity analysis (e.g., single-sample jackknife, called leave-one-out or LOO analysis) is used to assess potential cross-generalizability of the model in correctly classifying new subjects that may differ in their characteristics relative to subjects in the original sample (Yarnold and Soltysik 2005; Yarnold 2017).

Applications involving two or more attributes are analyzed using classification tree analysis (CTA), which constructs optimal models by chaining multiple ODA models together (Yarnold 1996a; Linden and Yarnold 2016). Because of the small sample, in conjunction with the relatively strong effects identified for some attributes (i.e., that produced few misclassifications), CTA models were not possible for the present sample (Yarnold and Soltysik 2016).

A Spearman's rank correlation was used to identify the relationship between percent forest and *R. aurora* breeding abundance within each of the 19 cumulative concentric areas. The non-parametric coefficient was used because abundance data was strongly negatively skewed in a scatterplot matrix of predictor and response variables. To reduce the risk of type I errors where multiple statistical tests were run on different distance ratios measured on the same dataset, the significance limit ($\alpha \leq 0.05$) was adjusted downwards according to Šidák (1967).

Results

Rana aurora egg masses were recorded at 21 of the 28 wetlands. Between one and 367 *R. aurora* egg masses were recorded at occupied sites (Figs. 3 and 4). Bullfrogs and fish were recorded in nine wetlands, but bullfrogs and fish co-occurred in only three wetlands (Table 1).

Rana aurora occurrence

Only two variables, connectivity (CON) and percent forest (PCF), of the seven variables examined to predict *R. aurora* occurrence had at least a relatively strong effect using the ODA algorithm; these results were further supported by a LOO analysis (Table 2). The best model for the CON metric, which predicted occurrence at higher values (> 96.26), had the stronger effect of the two variables but the PCF metric was only modestly weaker; PCF resulted in the best model when predicted occurrence values were above 28.0%. Training analysis found a third variable, forested perimeter (FRP), with a relatively strong effect, but a LOO analysis did not support this finding ($p > 0.05$). No statistically significant association was found between the occurrence of *R. aurora* and remaining variables examined (all $p > 0.05$; Table 2).
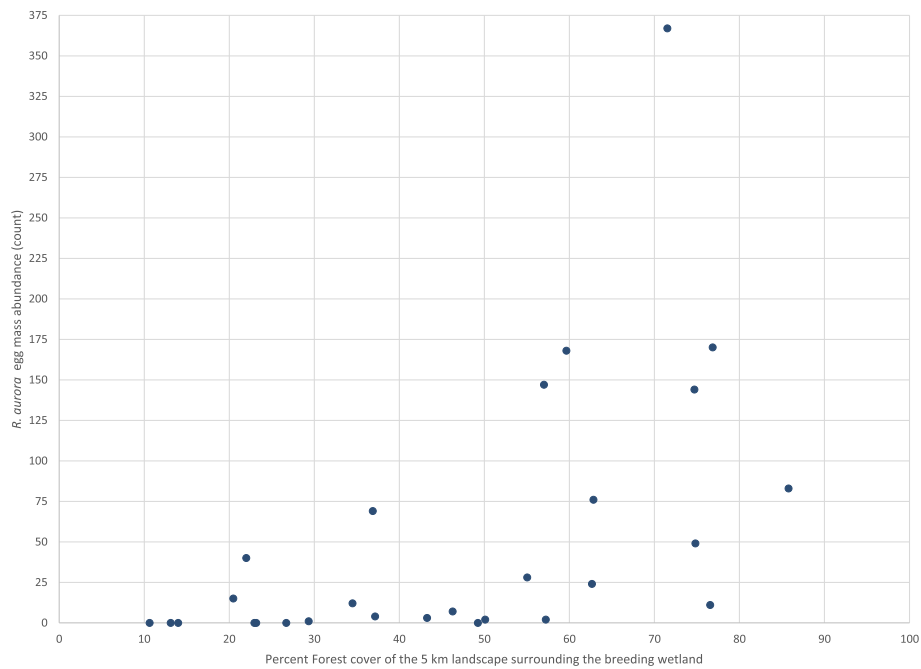
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Fig. 3 Relationship of *R. aurora* abundance with percent forest within 5 km of the wetland edge (*n* = 28)

Rana aurora abundance

Parallel to findings for *R. aurora* occurrence, CON and PCF yielded best models for *R. aurora* abundance with the strongest levels of accuracy for CON followed by a slightly lower level of accuracy with PCF; these results were supported by LOO analysis (Table 3). Notably, the best CON model predicting *R. aurora* abundance had the same cutpoint, > 96.26, as the best CON model for occurrence. Further, the best PCF model for abundance predicted large *R. aurora* populations (> 69 egg masses)
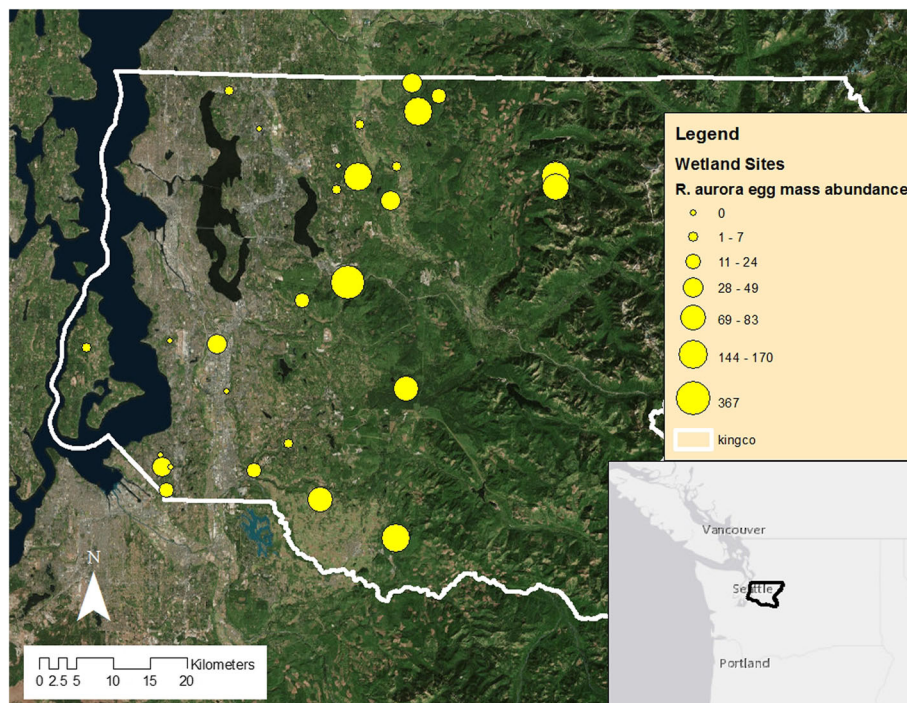

Fig. 4 Study wetland locations with symbol size proportional to the number of egg masses detected at that site

Table 1 Variables used in *R. aurora* occurrence and abundance models and their descriptive variation

Abbreviation	Description (units)	$\bar{\chi}$	$\tilde{\chi}$	SD	IQR	CV	Range
AREA	Wetland area (ha)	0.75	0.80	0.51	1.02	0.68	0.02–1.49
BULL	Bullfrog presence (bullfrog occupied or not)	0.32	0.00	0.48	1.00	1.48	0–1
CON	Aquatic/terrestrial landscape connectivity	98.19	99.58	2.46	3.63	0.03	90.28–99.98
EMG	Wetland area in emergent vegetation (m^2)	2565	1464	2493	3458	0.97	61–9482
FISH	Fish presence (fish occupied or not)	0.32	0.00	0.48	1.00	1.48	0–1
FRP	Perimeter of wetland adjacent to forest (%)	46.28	48.10	32.75	54.41	0.71	0–100
PCF	Percent forest within 5 km of wetland (ln[%])	46.23	47.76	22.33	37.81	0.48	10.64–85.77

Descriptive variables are the mean ($\bar{\chi}$), median ($\tilde{\chi}$), standard deviation (SD), interquartile range (IQR), and coefficient of variation (CV)

at forest cover values > 56.0%. However, the strongest effect, based on how it held up in LOO analysis, was for FRP where larger *R. aurora* populations (> 40 egg masses) were found when forest occurred on > 58.6% of the wetland perimeter. Also, consistent with the findings for *R. aurora* occurrence, no association emerged for abundance (number of egg masses) and wetland area (AREA) or bullfrog occurrence (BULL).

In contrast to the occurrence findings, a moderate strength effect emerged in training and LOO analysis for fish occurrence (FISH). If fish were present, *R. aurora* populations with at least five egg masses were found. Lastly, although a relatively strong effect was identified for the area of emergent aquatic vegetation (EMG) in training, this effect was not confirmed in LOO analysis (Table 3).

Spatial extent of forest influence on *R. aurora* breeding abundance

Percent forest (PCF) was positively correlated with *R. aurora* breeding abundance at distances ≥ 200 m ($r_s = 0.683$) using the Šidák-corrected rejection criterion ($\alpha' = 0.002$). The strength of the correlation between *R. aurora breeding abundance* initially increased relatively sharply with distance from the breeding site, peaking at a distance of 450 m ($r_s =$

0.778) and thereafter generally declining slightly but remaining high ($r_s > 0.7$) out to the 5-km distance (Fig. 5).

Discussion/conclusions

Rana aurora Occurrence and abundance in the terrestrial habitat

Landscape habitat association research has increasingly identified a positive relationship between forest area and amphibian occurrence (Porej et al. 2004; Cushman 2006). In this study, both *R. aurora* occurrence and breeding abundance had strong to very strong associations with all three forest-linked variables measured around wetlands that *R. aurora* utilized for breeding: the percentage of undeveloped upland forest habitat; the forested perimeter around the wetland; and the connectivity of that forest to the breeding wetland. Response consistency for the forest-linked variables underscores the importance of a forest-related effect for *R. aurora*. Moreover, the fact that all best forest-linked variable models were more robust for breeding abundance than for occurrence suggests that the focus of forest habitat control is linked to *R. aurora* abundance.

Rana aurora has been recaptured in the same season up to 5 km from their aquatic breeding sites (Hayes et

Table 2 Optimal discriminate analysis models for *R. aurora* occurrence addressing the seven variables examined

	Training analysis[a]					LOO analysis[b]		
Variable	Model	Number	Accuracy (%)	p<	ESS	Accuracy (%)	p<	ESS
AREA	–	–	–	0.9696	19.1	–	–	–
BULL	–	–	–	0.9999	4.8	–	–	–
CON	If CON ≤ 96.26 predict no occurrence	7	85.7	0.0009	81.0	71.4	0.0039	61.9
	If CON > 96.26 predict occurrence	21	95.2			90.5	–	–
EMG	–	–	–	0.0921	52.4	–	–	–
FISH	–	–	–	0.0615	42.9	–	–	–
FRP	If FRP ≤ 50.1% predict no occurrence	7	100.0	0.0238	61.9	–		
	If FRP > 50.1% predict occurrence	21	61.9				0.0604	42.9
PCF	If PCF ≤ 28.0% predict no occurrence	7	85.7	0.0025	76.2	71.4	0.0095	57.1
	If PCF > 28.0% predict occurrence	21	90.5			85.7		

[a]Training analysis reveals the maximum-accuracy (optimal) model by using every possible cut-point (or assignment rule) to classify sample observations
[b]Leave-one-out or LOO analysis is used to assess potential cross-generalizability of the model. See text for details
Cut points, group sample sizes, and accuracy are shown only for the best models considered significant ($p < 0.05$)

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Table 3 Optimal discriminate analysis models for *R. aurora* breeding abundance addressing the seven variables examined. Presentation is identical to Table 2

Variable	Training analysis[a]					LOO analysis[b]		
	Model	Number	Accuracy (%)	*p<*	ESS	Accuracy (%)	*p<*	ESS
AREA	–	–	–	0.1082	43.8	–	–	–
BULL	–	–	–	0.5757	20.8	–	–	–
CON	If CON ≤ 96.26 predict ≤ 1 egg mass	8	87.5	0.0001	87.5	75.0	0.0005	70.0
	If CON > 96.26 predict > 1 egg mass	20	100.0			95.0		
EMG	If EMG ≤ 2526 predict ≤ 1 egg mass	8	100.0	0.0448	55.0	–	0.2184	25.0
	If EMG > 2526 predict > 1 egg mass	20	55.0			25.0		
FISH	If FISH = 0 predict ≤ 4 egg masses	12	91.7	0.0390	41.7	91.7	0.0241	41.7
	If FISH = 1 predict > 4 egg masses	16	50.0			50.0		
FRP	If FRP ≤ 58.6% predict ≤ 40 egg masses	19	84.2	0.0012	73.1	84.2	0.0005	73.1
	If FRP > 58.6% predict > 40 egg masses	21	88.9					
PCF	If PCF ≤ 56.0% predict ≤ 69 egg masses	21	90.00	0.0006	81.0	76.2	0.0070	61.9
	If PCF > 56.0% predict > 69 egg masses	7	100.00			85.7		

[a]Training analysis reveals the maximum-accuracy (optimal) model by using every possible cut-point (or assignment rule) to classify sample observations
[b]Leave-one-out or LOO analysis is used to assess potential cross-generalizability of the model. See text for details

al. 2007). However, little is known about their dispersal patterns. Our spatial analysis revealed that the relationship between *R. aurora* breeding population size and percent forest becomes important at 200 m, peaks at 450 m, but remains high to 5 km which was the furthest distance examined in this study. Since the correlation between breeding population size and percent forest becomes significant at 200 m, along with the marked increase in the correlation coefficient up to 450 m, this suggests that the forest habitat further from the wetlands maybe more important habitat for *R. aurora* during its migration than the forests bordering the wetlands. During the non-breeding active season, this analysis also supports the importance of forested upland habitat located more than 450 m from a wetland as food, cover,

and migration corridors for *R. aurora*. Telemetry research on the connectivity of the forest patches within 450 m of wetland margins could help confirm whether the first few hundred meters are mainly used as corridors for *R. aurora* migrating to more distant forest patches. This finding is not unique. Richter and Azous (2001) analyzed the proportion of native amphibian species richness at a wetland and the area of forest land within cumulative concentric circles of 10, 100, 500, and 1000 m from the wetland edge in King County, Washington State. The relationship was weakest at 10 m ($R = 0.57$, $P = 0.01$) and strongest at 500 m ($R = 0.66$, $P = 0.004$) (Richter and Azous 2001).

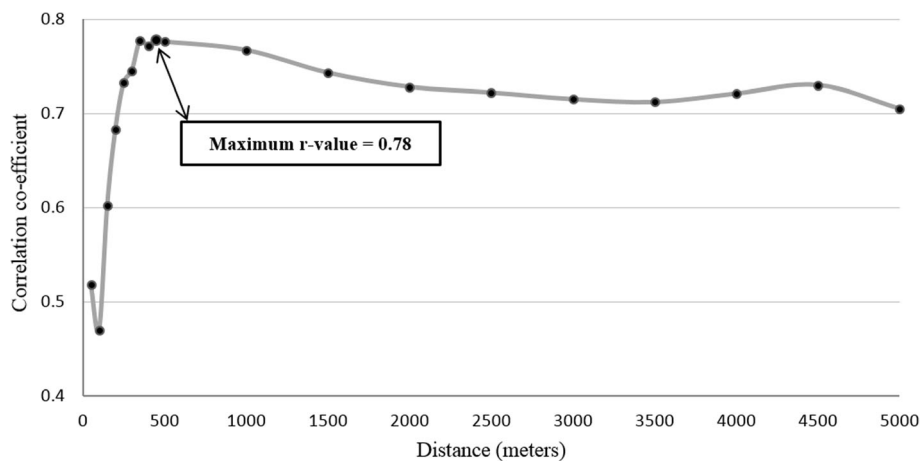Elsewhere, the most parsimonious models for overall salamander diversity and individual models for the

Fig. 5 Relationship between *R. aurora* abundance and percent forest as a function of distance from wetland

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presence of frogs and salamanders included land-use characteristics found beyond habitat proximate to breeding wetlands (within 200 m) (Porej et al. 2004; Semlitsch and Bodie 1998). However, why *R. aurora* travels such long distances is unclear. Habitat further from breeding wetlands may have some positive advantage, either greater food resources or fewer conspecifics to compete with for shelter and food (Haggard 2000). Alternatively, remaining too close to wetlands may pose some disadvantage, such as greater risk of predation (Licht 1974, 1986). Nonetheless, collective study results suggest that persistence of local amphibian populations depend on both wetland-adjacent and more distant upland landscapes. More research on the specific movements and behaviors of local amphibian species could better explain why the relationship of *R. aurora* egg mass counts is more important with forests located at farther distances from the breeding wetland.

A broad consensus exists that broadly dispersing species are adapted to habitat fragmentation (Kareiva and Wennergren 1995) and that such species disperse more easily across unsuitable habitat. However, this study showed connectivity was positively associated with *R. aurora* occurrence and abundance. This suggests it may be necessary to identify alternative causal relationships by which fragmentation exacerbates population declines as a result of habitat loss (Fahrig and Merriam 1985), i.e., adults are unable to utilize non-connected breeding habitat. One way to explore this possibility is to further research the existence of thresholds in forest area and how they may impact *R. aurora* occurrence. If such thresholds exist, identifying them is fundamental to understanding extinction processes and critical to landscape management and conservation design.

This research suggests that a threshold exists between forest cover and *R. aurora* breeding abundance within a range of 5 km from a wetland (Fig. 4). The cut point for the best ODA model for percent forested habitat identified a threshold at 56.0% forest cover, i.e., forest covers higher than 56% resulting in higher *R. aurora* breeding abundance. While this study sample size was too small to claim a definitive threshold, previous research on thresholds of forest fragmentation identified similar thresholds below which the former forest structure and function would no longer be maintained. Franklin and Forman (1987) predicted that major thresholds in fragmentation of the landscape would occur when about 50% of the forest was converted to non-forest as a result of clear-cutting in the PNW (i.e., amount of edge exceeds interior forest). Vogelmann (1995) reported the greatest increase in forest fragmentation as the landscape cover changed from 100 to ~ 80% forest area, with a threshold occurring at 60%. Thresholds of 50–60% forest cover have also been observed in a few studies on

migrating amphibians (Gibbs 1998; Homan et al. 2004). Spotted salamander occurrence at breeding wetlands diminishes at a threshold of 50–60% forest at both 100 and 1000-m distances (Gibbs 1998; Homan et al. 2004). Lastly, amphibian richness was found to be highest in the Puget Sound basin within wetlands that retain at least 60% of adjacent area in forestland up to and exceeding 500 m (Richter and Azous 2001). Critical thresholds are likely to be species-specific, but far-migrating species with a positive association with forest cover and negative association with road density like *R. aurora* are likely to be sensitive biotic indicators to urbanization; urbanization impacts are frequently detected as effects occurring on habitat fragmentation and loss (Pearl et al. 2005).

Rana aurora aquatic habitat relationships

A commonly preconceived notion of a positive wetland size-amphibian abundance relationship may carry more weight than it should, at least for *R. aurora*. Currently, no research indicates a positive association between *R. aurora* occurrence or abundance with wetland size. Richter and Azous (1995, 2001) reported amphibian richness was unrelated to wetland size, whereas Adams (1999) and Pearl et al. (2005) found *R. aurora* abundance and occurrence negatively associated with wetland open water.

This study also found no association between *R. aurora* occurrence or abundance and wetland size for wetlands less than 1.5 ha in size. Lack of association may reflect *R. aurora's* ability to lay multiple egg masses on one oviposition brace (per observation). Other research identifying negative associations with wetland size and *R. aurora* may reflect the secondary effects of exotic predators, i.e., smaller wetlands are less likely to maintain fishes or bullfrogs (Richter and Azous 1995; Adams 1999; Pearl et al. 2005). Additionally, *R. aurora* spend little time seasonally in wetlands, so finding a relationship with wetland size may not be a sensitive variable to measure. Lastly, males do not feed during breeding, so wetland food resources are likely unimportant for them (Licht 1969; Hayes et al. 2008).

If wetland size is less important in *R. aurora* occurrence and abundance, this may provide critical information needed for maintaining this species. Concerns for amphibian species commonly rely more on the status of the breeding wetlands and less on the upland terrestrial habitats (Hayes et al. 2008, Richter and Azous 2001). While wetlands are necessary for *R. aurora* survival, choosing them based on location within the landscape forest matrix may supersede size considerations.

Emergent vegetation was moderately associated with *R. aurora* abundance, but this habitat characteristic did not hold up in LOO. Other studies have shown positive associations with emergent vegetation, but the sample size was too small to explore this relationship in this

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study (Adams 1999; Hazell et al. 2004; Cary 2010). This needs further research at the study sites. Greater area of emergent vegetation may be important for several reasons: *R. aurora* attaching their egg masses to vegetation keep them from floating away or sinking, both of which contribute to mortality (per observation), and vegetation provides larval refuges (Kiesecker et al. 2001).

Aquatic predators and *R. aurora*

Bullfrog occurrence was unrelated to *R. aurora* occurrence and abundance. This pattern is not particularly surprising since several efforts at addressing *R. aurora* occurrence in the Pacific Northwest have failed to demonstrate a bullfrog effect (Adams 1999, 2000; Curry 2007). Wetlands with fish were expected to show the greatest difference in egg mass abundance because fish effects have been demonstrated on PNW amphibians elsewhere (Adams 1999, 2000; Kiesecker and Blaustein 1998; Monello and Wright 2001). Several factors may contribute to this contradiction that may explain these different results. The two most likely explanations are that in this study fishes were scored collectively (not all fish species are amphibian predators) and neither fish (nor bullfrog) detectability was estimated. Both factors are important limitations for a mobile sometimes cryptic organism.

Habitat protection and land-use planning in urban environments

Since urbanization can directly eliminate terrestrial habitat, it threatens amphibian persistence and ultimately the ecosystem services they provide. Except for research by Richter and Azous (2001), Pearl et al. (2005), and Ostergaard et al. (2008), studies have not addressed the reliance of PNW lentic-breeding amphibians on terrestrial habitats associated with their aquatic breeding habitat. This study provides the initial context for understanding the nature of the urbanizing threat on *R. aurora*, a species that makes long seasonal movements into forested terrestrial habitats. Importantly, the pivotal findings of this study are that the forested terrestrial habitat and its connectedness to the aquatic habitat, rather than aspects of the aquatic habitat per se, seem to be a fundamental determinant of *R. aurora*'s occurrence and abundance. These findings are consistent with what is currently known of *R. aurora* life history, where adults typically spend 8–10 months annually in forested terrestrial habitat and males may not feed at aquatic breeding sites (Hayes et al. 2008). These findings provide a clear rationale for managing wetland resources in concert with available juxtaposed forested uplands to maintain *R. aurora* and potentially other lentic-breeding amphibians on the landscape.

Most conservation policies concerning lentic-breeding amphibians, including those in King County, WA, are focused on wetland protection through fixed-width buffers (Hayes et al. 2008, Richter et al. 2008). These are typically determined based on wetland size, type, function, and surrounding vegetation types (Hayes et al. 2008, Richter and Azous 2001). These policies undervalue the condition of adjacent terrestrial habitat types for amphibians or other wildlife. Regulatory wetland buffers in Washington ranged from 15.2 to 91.4 m in width (McMillan 1998), but such buffers are much smaller than the 200 m to 5+ km distance that *R. aurora* may need to migrate in order to access its necessary resources. Despite the fact that King County's regulations are acknowledged to be effective within *R. aurora* habitat range, they are still unlikely to maintain landscape-level connectivity needed by *R. aurora* in the face of rapid population growth (Hayes et al. 2008, Richter et al. 2008). Therefore, if the goal is to avoid extirpation of *R. aurora* populations in urbanizing areas of the PNW, jurisdictions should consider protecting sufficiently large-scale terrestrial and breeding habitat connectivity that can facilitate inter-population dispersal and migration across broader landscapes (Semlitsch and Bodie 1998, Hayes et al. 2008).

This study identified multiple aquatic and terrestrial variables that are essential features required by *R. aurora*. This suggests that conservation plans for amphibians should perceive wetlands and the surrounding terrestrial habitat as one ecological unit that needs to be replicated to form a network across a landscape. Such an approach requires the land's governing bodies to plan early in the urbanization process. The feasibility of retaining the minimum amount of terrestrial habitat needed by *R. aurora* is challenging since decisions are made on a managed parcel-by-parcel basis in an urbanizing landscape (Baldwin et al. 2006). For example, the current King County buffer system may limit *R. aurora* from accessing breeding wetlands and other water and upland terrestrial resources beyond those buffers.

Rana aurora makes long annual migrations to and from breeding sites. With extensive travel distances, *R. aurora* is more likely to come into contact with unsuitable habitat and therefore increase the likelihood of their mortality. To control the expansion of unfavorable habitat for *R. aurora*, mapping should integrate the effects of the local landscape on the dispersal and occurrence of *R. aurora*. Also, friction and cost-distance mapping could help conservation planning by identifying a connected network of functioning and accessible aquatic and upland habitats throughout the landscape before development projects are started. As Beninde et al. (2015) emphasized, biodiversity in cities requires space, and *R. aurora* is a prime example of a species with extensive space requirements. A network approach could help conservation strategies move away from the fixed width buffer model, which results in a more fragmented landscape, and toward a landscape with contiguous forests and wetlands that could benefit multiple migratory species (Baldwin et al. 2006). This

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would allow a jurisdiction to set aside land and make efforts to purchase development rights or use other methods to preserve upland habitats at high enough percentages and distances from the breeding ponds to support *R. aurora*. Such an approach is greatly preferable to restoration efforts that favor exclusively large steep-sided and deep wetlands, which lack large emergent vegetation zones, and are placed in areas of high development with high road densities, or areas with permanent hydroperiods that support fish and bullfrog predators. These projects are a more costly, not typically ecologically successful, and commonly call for wetland relocation resulting in the extirpation of local populations.

This study suggests that the area of undeveloped terrestrial habitat juxtaposed with breeding ponds may represent a fundamental control on amphibian population size for some species. The patterns observed for *R. aurora* support the need for more research on how to manage across varied forested PNW landscapes. This research also suggests that urban development policies should begin to consider and plan for maintaining high-quality habitat on the landscape scale. Importantly, this study reinforces the idea that landscape issues such as habitat complementation deserve exploration among other lentic-breeding amphibians that seasonally require both aquatic and terrestrial habitats.

Abbreviations
AREA: Wetland area; BULL: Bullfrog occurrence; CON: Connectivity as reported by COHESION in FRAGSTATS v4.0; CTA: Classification tree analysis; EMG: Area of emergent vegetation; ESS: Effect strength for sensitivity; FISH: Fish occurrence; FRP: Forested perimeter; GIS: Geographic information systems; GPS: Global positioning system; LOO: Leave-one-out analysis; ODA: Optimal discriminant analysis; PCF: Percent forest; PNW: Pacific Northwest of the United States; *R. aurora*: *Rana aurora*, northern red-legged frog; WDFW: Washington Department of Fish and Wildlife

Availability of data and materials
The dataset supporting the conclusions of this article is included within the article.

Authors' contributions
LG designed the study; collected, analyzed, and interpreted the data; and wrote and revised the manuscript. MH generated the idea, designed the study, interpreted the data, and wrote and revised the manuscript. KV designed the study, interpreted the data, and revised the manuscript. PY analyzed and interpreted the data. All authors participated in its design and coordination and helped to draft the manuscript. All authors read and approved the final manuscript.

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