Amphibian use of constructed and remnant wetlands in an urban landscape

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Abstract Urban areas are increasing in number, extent, and human population density worldwide. There is potential to mitigate negative impacts of urbanization to native pond-breeding amphibians by providing habitat in both remnant natural and constructed wetlands. This study examines amphibian use of potential breeding sites in natural and constructed ponds in a large metropolitan area to investigate habitat characteristics that are associated with successful breeding. I surveyed 62 ponds over three breeding seasons in Portland, Oregon, measuring eleven habitat characteristics that may influence their successful breeding: pond depth, nitrate level, aquatic refugia, aquatic vegetation, surrounding vegetation, pond permanence, presence of fish and of introduced bullfrogs, surrounding road density and forest cover, and whether they were constructed or remnant natural ponds. Five of the six native pond-breeding species that occur in the region were regularly found breeding in city ponds. Surrounding forest cover and amount of aquatic vegetation were highly associated with breeding, indicating that preserving and planting vegetation likely benefits urban amphibians. Non-native bullfrogs were not associated with native species richness. Surprisingly, whether a pond was natural or constructed was also only weakly associated with native species breeding, and the trend was towards higher presence for all species in constructed ponds. This indicates that novel, human-dominated areas can provide habitat for these species. Consideration of habitat characteristics associated with breeding success in urban pond management will likely benefit native amphibians in these rapidly expanding landscapes.

Keywords Frog · Salamander · Novel habitat · Human-dominated landscape · Reconciliation ecology · Urban ecology

Introduction

Urban areas are growing rapidly throughout the world, fragmenting and replacing preexisting habitats. Not all habitats are being equally overrun by urbanization: human settlements are

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often situated in flat, agriculturally productive, lowland areas where wetlands formerly existed (Mitsch and Gosselink 2007). Organisms that depend on such habitats are therefore likely to be disproportionately impacted by urbanization. However, most cities contain a variety of freshwater ponds that are potential breeding habitats for some of the species that historically inhabited the area. Potential habitats in urban areas include remnant ponds that have persisted in some form throughout the development of cities, degraded ponds that have been restored, and ponds that were newly created for aesthetic, environmental, or water management reasons, and that may or may not resemble ponds in the original landscape.

The magnitude of harm that urbanization causes to resident organisms can vary greatly depending on habitat availability and quality within cities. Although urban habitats are often substantially different from their natural counterparts, they have the potential to provide habitat for numerous species (Hobbs et al. 2009; Magle et al. 2012). It is increasingly apparent that while ecological reservation and restoration strategies are necessary, they are not sufficient for the conservation of Earth's species under current human growth and land use trends (Rosenzweig 2003; Hobbs et al. 2011). Reserves are often too small for long-term persistence and can be isolated by human development; for these reasons a hospitable matrix within human-dominated areas may greatly benefit their effectiveness (Ricketts 2001; Kupfer et al. 2006). Additionally, the focus on reserves has historically led to cities being disregarded as possible settings for conservation (Rosenzweig 2003). Documenting the importance of human-constructed habitats such as urban stormwater ponds to native biota can initiate efforts to provide or improve habitat in areas that otherwise would be overlooked.

Amphibians that depend on freshwater ponds are of particular conservation concern. Many amphibians are experiencing striking global declines (Collins and Storfer 2003; Stuart et al. 2004; Beebee and Griffiths 2005), and urbanization has been identified as greatly contributing to their downward trend (Cushman 2006; Hamer and McDonnell 2008). A recent review of urban wildlife research identified urban amphibian studies as one of the most critical gaps in the field (Magle et al. 2012). Pond-breeding amphibians are important links within and between aquatic and terrestrial food webs, and are often a major food source for fish, birds, snakes, and aquatic invertebrates (Stebbins and Cohen 1995 and references therein). Amphibians are particularly well suited to providing city residents with a personal connection with nature because they are often conspicuous and many produce calls that remind city residents that they live within a larger system.

Amphibians have been found breeding in a variety of urban water bodies including ponds and lakes in parks or private yards, stormwater facilities, and golf course ponds, thus using habitats that are substantially different from their former pristine breeding habitats (e.g. Husté et al. 2006; Colding et al. 2009; Hamer et al. 2012; Scheffers and Paszkowski 2013). Native wildlife can often adapt to novel and altered habitats if the right conditions exist, and an understanding of what factors influence amphibians in urban areas can lead to management that is better informed to mitigate the impacts of urbanization and promote persistence.

Many habitat characteristics have been shown to affect urban pond-breeding amphibians in other systems (Hamer and McDonnell 2008). The biological community of urban ponds affects native amphibians by setting the conditions for habitat structure, food, competition, and predation (Sredl and Collins 1992; Stebbins and Cohen 1995; Lawler et al. 1999). Nutrient and chemical pollution can have lethal and negative sublethal effects on pond-breeding amphibians (Rouse et al. 1999; Hatch and Blaustein 2003; Otto et al. 2007). Physical attributes such as depth and seasonality influence breeding success through effects on metabolism, activity, and survival of amphibians (Stebbins and Cohen 1995; Babbitt 2005). Landscape-level factors such as surrounding road density and forest cover have all also been shown to impact amphibian use of urban ponds by influencing upland habitat use and movement among patches (Hamer and McDonnell 2008; McCarthy and Lathrop 2011). Here I examine patterns of amphibian use of wetlands in a large urban area in the Willamette Valley of Oregon where wetlands loss has been rampant, but where constructed urban wetlands are recently becoming abundant.

In this study I aim to: (1) determine which regionally occurring amphibian species use remnant and constructed wetlands in the city of Portland, Oregon, (2) investigate habitat characteristics associated with amphibian species richness in this city, and (3) develop management recommendations to benefit amphibians in urban areas in this region. I investigated amphibian use of 62 remnant and constructed wetlands in relation to various biological, chemical, physical, and landscape features. I predicted that the city would harbor a subset of the regionally occurring species, that constructed wetlands would provide some habitat for native amphibians, but not to the extent that remnant wetlands do, and that vegetation cover would be strongly positively associated with species richness.

Methods

Study sites

This study was conducted in Portland, Oregon which is situated at the confluence of the Willamette and Columbia Rivers in the Willamette Valley ecoregion. The area was formerly dominated by interspersed wetlands and forests (Habeck 1961; Taft and Haig 2003). An estimated 87% of wetlands have been lost in this area since 1850 (Oregon Biodiversity Project 1998). The Portland area was inhabited by Upper Chinook people until the 1850s when European settlement initiated rapid urban growth (Marschner 2008). Portland is the nation's 29th largest city with ~2.3 million people in the metropolitan area (United States Census Bureau 2010). It experiences damp, mild winters and warm, dry summers. Portland has an urban growth boundary which, by law, separates areas of dense development from rural areas, reducing urban sprawl. All of the ponds in this study were within the urban growth boundary. Portland is an ideal city in which to study amphibian urban habitat use because of the formerly extensive wetlands on which it was built and the large amount and variety of ponds that have been retained, restored, or created. Additionally, this region was identified in a recent review of urban amphibian studies in North America as relatively understudied (Scheffers and Paszkowski 2012).

I surveyed 62 ponds in 18 sites within 4 watersheds. A site was defined as the contiguous area surrounding a pond before reaching impervious surfaces in all directions. Fig. 1 shows the location of the survey sites, each of which contained between one and seven ponds. The average distance between sites was 10.3km (range: 0.5-26.4km) and the average distance between ponds within a site was 137m (range: 5-668m). Although all ponds are within the urban growth boundary of the city, most ponds in Portland are distributed around the edges of the city and are generally absent from the urban core. These ponds represent a variety of sizes, uses, and management authorities. Approximately half of the ponds were remnants from areas that had historically been wetlands while the other half were constructed; the majority of the constructed ponds were excavated, unlined, and built for stormwater purposes. Ponds ranged in size from $0.25m^2$ to 3.2 hectares.

Measurement of amphibians

I surveyed ponds during peak tadpole/larvae season for three years: May-August of 2008, 2009, and 2010. I assessed the presence of amphibian species using dip-net surveys. I walked the perimeter of each pond at a depth of ~25cm, swept a handheld net every three steps for a length of ~75cm, and counted and identified all tadpoles and larvae to the species level before returning them to the water. Each pond was surveyed three times during a season. This type of

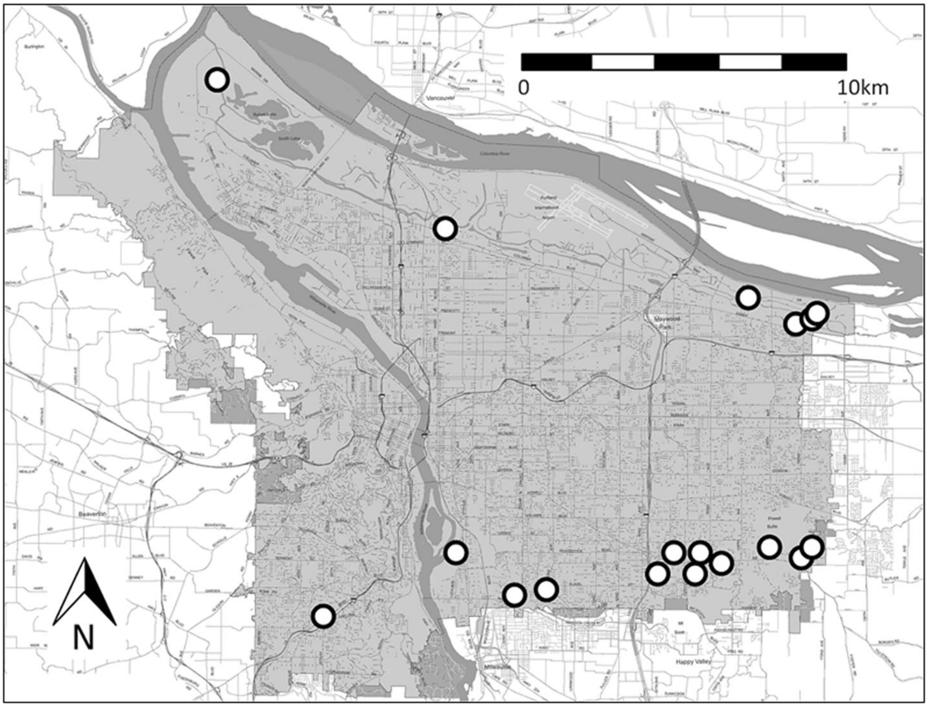

Fig. 1 Map of surveyed sites Portland, Oregon. The shaded area indicates the city's urban growth boundary. Each site contained 1–7 individual ponds

dip-net survey has been shown to be useful for determining presence/absence of amphibian species in ponds and is appropriate for use in water bodies with spatial structure and vegetation, such as many of those in this study (Shaffer et al. 1994; Kline 1998). Detection probabilities were calculated using the program PRESENCE (Hines 2006).

Selection and measurement of habitat characteristics

The habitat characteristics measured for each pond were chosen through a literature review of factors influencing pond-breeding amphibians and collaborative meetings with managers and ecologists from the various governing bodies of the sites: Metro Regional Government, private land owners, and the City of Portland's Bureau of Environmental Services, Water Bureau, and Bureau of Parks and Recreation. Selected factors were perceived by managers to have potential impacts on amphibians and were regarded as feasible to manage in the future, either for the improvement of existing ponds or for the creation of new ponds. The following factors were measured for each pond: depth, nitrate level, amount of aquatic refugia, percent cover of aquatic vegetation, surrounding vegetation cover, water permanence, fish presence, introduced American bullfrogs presence—*Rana* (*Lithobates*) *catesbeiana*, whether the pond was remnant natural or constructed, surrounding road density, and surrounding forest cover (Table 1). The majority of these factors are at the local scale because the managers indicated that information concerning this scale would be most useful to them because their management decisions and actions are generally focused at the site or pond scale.

Depth and nitrate level were measured three times per season at the deepest point of the pond up to 1.5m. Nitrate level was assessed from a 30mL water sample that was integrated

Table 1 Definitions and descriptive statistics for the habitat characteristics measured in the 62 ponds

Habitat characteristic	Mean	Range
Water depth at deepest point during wet season (average cm)	70	7- >150
Nitrate level (average mg/L with sample integrated through water column)	1.6	0-20
Aquatic refugia (average % cover of submerged material)	58	0-100
Aquatic vegetation (average % cover of all aquatic plants)	38	0-100
Surrounding vegetation (average % cover at 1m height in 10m buffer)	69	0-100
Water permanence (temporary/permanent)	NA	27/35
Formation (constructed/natural)	NA	39/23
Fish presence (absent/present)	NA	46/16
Bullfrog presence (absent/present)	NA	40/22
Road density (km of road length/km^2 in 1km radius)	15	1-43
Forest cover (% in 1km radius)	22	8-47

throughout the water column and measured with test strips from Industrial Test Systems, Inc.

The amount of aquatic refugia in a pond was visually estimated by the same observer three times per season to the nearest 20%. It was defined as the amount of submerged material, including: total aquatic vegetation (assessed as a stand-alone predictor as well), branches, and human-constructed objects. I quantified surrounding vegetative cover three times per season as the amount of a 10m buffer surrounding the pond to the nearest 20% where vegetation obstructed the bare ground from a vantage point of 1m.

I assessed fish as present in a pond if they were found during any amphibian dip-net survey or observed at any time during data collection. I determined presence of bullfrogs by conducting visual encounter surveys during the day by walking the entire edge of each pond three times per season. Juveniles and adults generally sit on the edges and dive into the water upon approach giving off a distinctive squeak. Any bullfrog tadpoles or eggs encountered during native amphibian surveys also constituted presence.

I visited each pond during the driest time of each season to observe whether or not it dried out. For ponds that are routinely drained, the managers were contacted to determine if a pond was drained that year. Each pond was scored as either temporary or permanent for each year. I contacted the managers to determine whether each pond was a natural remnant or if it was constructed. I measured road density (km of road length per km^2) and forest cover (percent) in a 1km radius of each site using satellite imagery analyses.

Data analyses

To determine which factors best explained species richness I ran mixed-effects multiple regression analyses with the habitat characteristics as fixed factors. I examined: 1) top models as determined by corrected Akaike Information Criterion (AICc; Hurvich and Tsai 1995), and 2) factor AICc weights, described below. Analyses included only a single value of each variable for each pond in each year even though several variables were measured three times in a year. The following data were averaged among the three points for a given season: depth, nitrate level, amount of aquatic refugia, percent aquatic vegetation, and surrounding vegetative cover. A data point consisted of the compiled data for each pond for each year surveyed. There were a total of 128 data points as not all 62 ponds were surveyed each year. Due to spatial and temporal autocorrelation, year and site were included in models as random factors.

All factors were tested for collinearity (Appendix A). In final models I did not include pairs of factors that had collinearity absolute values of ≥0.5. There were three pairs of factors with collinearity that exceeded this level: 1) the amount of aquatic vegetation and the amount of refugia in the pond, 2) the depth of the pond and whether it contained fish, and 3) whether the pond dried in the summer and whether it contained fish. In preliminary analyses the amount of aquatic vegetation explained more variation in amphibian richness than the amount of aquatic refugia, and depth and whether a pond dried in the summer explained more variation than the presence of fish; therefore, aquatic refugia and fish presence were not included in the remaining model analyses.

All possible multiple regression models were run with all combinations of predictor variables for a total of 512 candidate models from which I identified the top models (those for which $\Delta AIC \leq 2$; Appendix B). Models were run in R (R Core Development Team 2008) using the glmer function of the lme4 package (Bates et al. 2012). In addition to identifying top AICc models I calculated AICc weights for each factor. AICc weights are calculated by summing the delta AICc values for all models that include a given factor and then scaling them to be between 0 and 1. A weight close to zero indicates that the factor was not included in many models that had relatively high explanatory power while a weight close to 1 indicates the factor was included in many high-ranking models (Burnham and Anderson 2002). Relative AICc weights of variables were examined in addition to top models rather than hypothesis testing because the relative importance of each variable was of more interest in this study than identifying exactly which variables to include for a predictive model (Wagenmakers and Farrell 2004).

Results

Species presence

Five of the six native pond-breeding amphibian species that currently occur in the Willamette Valley were found to be breeding in the city of Portland, Oregon during these surveys: Pacific chorus frog (*Pseudacris regilla*), northern red-legged frog (*Rana aurora*), long-toed salamander (*Ambystoma macrodactylum*), northwestern salamander (*Ambystoma gracile*), and rough-skinned newt (*Taricha granulosa*). *P. regilla* and *A. macrodactylum* were the most common (present in 58% and 54% of ponds surveyed, respectively) while *T. granulosa* was relatively rare (present in 6% of ponds). *R. aurora* and *A. gracile* were intermediate, being found in 30% and 20% of surveyed ponds, respectively. The western toad (*Bufo boreas*) was not found during this survey and is currently rare or absent throughout the Willamette Valley (Pearl et al. 2005). Detection probabilities of individual species were as follows: *P. regilla*—0.65, *R. aurora*—0.42, *A. macrodactylum*—0.81, *A. gracile*—0.67, *T. granulosa*—0.50, and bullfrogs 0.85.

Habitat characteristics

Models showed that surrounding forest cover, amount of aquatic vegetation, and low nitrate levels were most associated with high species richness (Table 2 and Appendix B). The R^2 value for the top model was 0.67 for a simple regression of predicted vs. observed values.

The amount of surrounding forest cover in a 1km radius was most influential in models and was positively correlated with species richness. The percent of aquatic vegetation in a pond was also highly positively correlated with species richness. The plants species that were abundant in ponds with amphibians present were (in alphabetical order): *Alisma plantago*, *Carex obnupta*, *Eleocharis spp.*, *Juncas spp.*, *Ludwigia spp.*, *Phalaris arundinacea*,

Table 2 AICc weights of predictor variables for models of species richness. Higher AICc weight indicates that a given factor is more influential in describing species richness

Habitat characteristic	AICc weight	Direction of relationship; higher richness in ponds:
Forest cover	**0.87**	**with more surrounding forest cover**
Aquatic vegetation	**0.77**	**with more aquatic vegetation**
Nitrate level	**0.63**	**with lower nitrate levels**
Surrounding vegetation	0.21	with more surrounding vegetation
Water permanence	0.19	that dry in the summer
Formation	0.10	that were constructed rather than natural remnants
Road density	0.06	with lower surrounding road densities
Depth	0.06	that were shallower
Bullfrog presence	0.00	NA

Variables with high influence are bolded

Polygonum amphibium, *Scirpus spp.*, *Typha latifolia*, and *Veronica spp.* Nitrate level was highly influential in models and was negatively associated with richness.

The amount of surrounding vegetative cover, water permanence, whether the pond was natural or constructed, surrounding road density, and pond depth had low influence on models (Table 2). The direction of relationships is shown in Table 2. Bullfrog presence had no influence on models and was not associated with species richness. There was a trend for higher species presence in constructed vs. natural ponds that was consistent across species (Fig. 2).

Discussion

This study of pond-breeding amphibians in the large city of Portland, Oregon showed that all of the regional species except *Bufo boreas* were present in remnant natural as well as constructed ponds within the city boundary. Models of native amphibian species richness identified the relative influence of a set of habitat characteristics which can be affected by

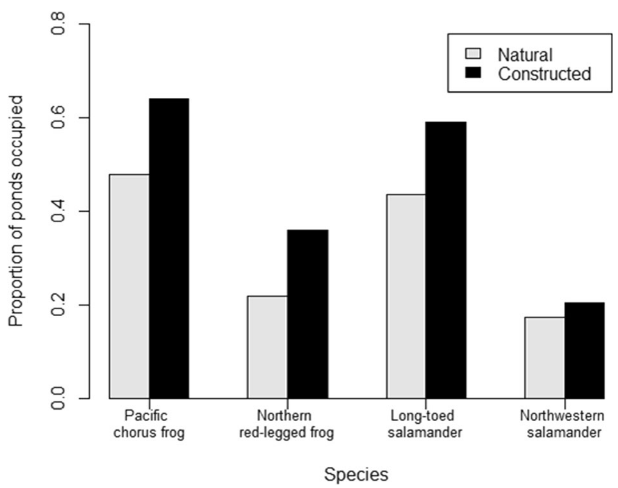

Fig. 2 Proportion of constructed and natural ponds occupied by amphibian species

management actions. Urbanization greatly alters existing landscapes, but this process often leaves some remnant habitats and creates novel habitats that have potential to support some biodiversity. Wildlife abundance and diversity can be fairly high in urban areas even though biotic communities are often relatively homogenized among cities (Chace and Walsh 2006; McKinney 2006). Even artificial features that are entirely novel for a species can have the potential to be used as habitat (Rosenzweig 2003).

Species presence

The presence of five of the six regionally occurring native pond-breeding amphibians inside the urban growth boundary of the city indicates that most of these species have been able to tolerate urbanization when appropriate habitat was provided. A seventh species, the Oregon spotted frog (*Rana pretiosa*), was at one time recorded in the region, but is presumed to be extirpated from the Willamette Valley (Nussbaum et al. 1983; Hayes 1994; Pearl et al. 2005). The cool and moist climate, relative abundance of terrestrial vegetation, and numerous streams in Portland may contribute to amphibian persistence. Similar results were found in Portland for other types of amphibians: surveys in the city detected four of the five terrestrially breeding species and the only stream-breeding species native to the region (K Holzer, unpublished data).

Urban tolerance was not limited to common species: *Rana aurora* is absent from ~70% of historical sites in the Willamette Valley (Kiesecker unpublished data referenced in Kiesecker et al. 2001) and is a Species of Concern in Oregon, yet it bred in a variety of ponds in the city. A direct comparison of species prevalence in and outside of the city is needed to better understand the effects of urbanization. Additionally, ponds are lacking from Portland's urban core, indicating that although many species are breeding within the city limits, they are generally confined to the edges.

Detection of a species during surveys does not necessarily indicate that the species will persist in the city in the long term. Urban ponds may be experiencing an extinction debt scenario where some species that are currently present are awaiting inevitable local extinction (Tilman et al. 1994, Gagne and Fahrig 2010). However, informed management could conceivably stave off this fate.

Habitat characteristics

The examination of habitat characteristics associated with urban amphibian species richness produced results that can guide management. Ponds with high native amphibian species richness tended to have high surrounding forest cover, some aquatic vegetation, and low nitrate levels. There are two main caveats for this study. First, the relationships between factors and species richness are correlational and may not be causal, although known mechanisms do exist for the influence of each factor on amphibians. Second, there are likely habitat characteristics that were not measured in this study that are influential.

The amount of forest cover surrounding a pond was the most influential factor in explaining species richness. This is consistent with other studies of urban amphibians where 14 out of 17 studies showed forest cover to be positively associated with species presence, richness, or abundance (Hamer and McDonnell 2008). This is likely because many pond-breeding amphibian species require terrestrial upland habitat in addition to aquatic breeding habitat and use vegetation corridors for movement (Semlitsch and Bodie 2003, McCarthy and Lathrop 2011). Studies examining the movement of amphibians in urban areas are rare and would improve understanding of the effect of landscape connectivity on promoting persistence in these systems. While forest cover was highly associated with richness at the landscape level, road density was not. This indicates that areas of dense urban development may be able to sustain amphibian populations if upland habitat is present.

The amount of aquatic vegetation in ponds was highly positively associated with species richness. Aquatic vegetation has been found to be favorable to amphibian populations for a variety of reasons including refuge from predators, oviposition sites, shade, periphyton substrate for grazing, and oxygen production (Sredl and Collins 1992; Stebbins and Cohen 1995; Tarr and Babbitt 2002). These findings are consistent with most urban amphibian studies: twelve out of sixteen studies found aquatic vegetation cover to be positively associated with native amphibian presence, abundance, richness, and/or diversity (Pearl et al. 2005; reviewed in Hamer and McDonnell 2008; Hamer and Organ 2008; Hamer and Parris 2011; Hamer et al. 2012).

During this study several ponds with sparse vegetation were observed to have amphibian egg masses on over 90% of plant stems. In some ponds that entirely lacked vegetation I observed egg masses on materials such as plastic fencing and barbed wire that had fallen into the water. This indicates that, for at least some sparsely vegetated ponds, adult amphibians are present and attempting to breed but may be limited by oviposition sites provided by vegetation. Therefore, planting and maintaining aquatic vegetation in urban ponds likely benefits native amphibians in this area. Further studies of specific amphibian-plant relationships with a focus on plant types and species are needed.

The only water pollutant measured during this study was nitrate (NO_3^-) which showed a high negative influence on models. It is a naturally occurring compound that is often elevated in urban and agricultural areas; at low concentrations it can stimulate primary productivity, but has been shown to have detrimental effects on amphibian larvae at high levels through direct toxicity and eutrophication (Hatch and Blaustein 2003; Rouse et al. 1999). Nutrient load in urban ponds has been shown to be negatively associated with amphibian species richness (Ensabella et al. 2003; Houlahan and Findlay 2003), although Scheffers and Paszkowski (2013) found total nitrogen to be positively associated with boreal chorus frog (*Pseudacris maculata*) occurrence. Elevated urban nitrate may originate from fertilizers, industrial effluents, waste-water treatment discharge, animal waste, and deposition from motor vehicles and industrial exhaust (Rouse et al. 1999; Camargo et al. 2005). Nitrate can be managed through regulating sources and by constructing series of runoff ponds that remove contaminants as the water moves towards downstream ponds.

It is possible that nitrate itself is responsible for the negative trend found in this study, but it is also likely that nitrate levels are correlated with other pollutants which were not measured. Ponds with high nitrate levels often receive large amounts of runoff from nearby yards, gardens, farms, and roads, which likely contains additional pollutants. These correlated factors may underlie the trend observed because some of these factors, such as water conductivity and heavy metals, have been shown to be detrimental to amphibians in urban ponds (Paul and Meyer 2001; Willson and Dorcas 2003; Simon et al. 2009). Although it is difficult to study synergistic effects of multiple pollutants, recent studies addressing this issue for aquatic organisms indicate that pollutant synergisms are likely important (e.g. Sullivan and Spence 2003; Boone 2008; Relyea 2009). Sites in Portland that were designed as a series of ponds for runoff filtration showed a trend where amphibians were often absent in the first pond but were generally present in subsequent ponds (pers. obs.). This indicates that runoff treated in these ponds may contain concentrations of pollutants high enough to limit amphibian use, but that pollutant levels may be sufficiently reduced through the filtration process.

The remaining factors measured had little influence on models of species richness even though these factors are known to be important in some circumstances. Hydroperiod, amount of surrounding vegetative cover, and depth were likely within tolerable ranges for these species in this area. Hydroperiod has been shown to be a strong predictor of urban amphibians and may have failed to emerge as influential for overall richness in this study due to differences in life histories: most of the species in this study generally do better in temporary ponds while

Ambystoma gracile benefits from permanent ponds (Rubbo and Kiesecker 2005; Shaffer 2005). The lack of influence on species richness of bullfrog presence and whether a pond was natural or constructed was more surprising.

Bullfrogs have been introduced to the west coast from the southeastern United States (Nussbaum et al. 1983), and have been shown to be detrimental to native amphibians in a number of ways including competition, predation, and disease transmission (summarized by Casper and Hendricks 2005). In theory bullfrogs can be removed, but in practice, a large amount of effort has not lead to substantial reduction in this region (pers. obs.; Adams and Pearl 2007). In this study, bullfrog presence had no influence on models of native species richness. This is particularly surprising because bullfrogs have been documented to negatively impact several native amphibians, especially *R. aurora* and their sister species the California red-legged frog, *R. draytonii* (Kiesecker and Blaustein 1998; Lawler et al. 1999; Kiesecker et al. 2001). It is plausible that bullfrogs are in fact negatively impacting amphibians in this area but are not completely excluding them. It is also possible that while bullfrogs are detrimental to native amphibians in other systems, they have less of an impact in this region. Other studies conducted in the Cascadia bioregion that either included urban areas (Pearl et al. 2005; Richter and Azous 1995; Johnson et al. 2011) or did not include urban areas (Adams et al. 1998; Adams 1999; Adams et al. 2011) failed to find evidence of bullfrogs negatively impacting native amphibians. The lessened impact of bullfrogs in this region compared to others may be due to the cooler climate: this region is at the northern edge of current bullfrog range and possibly near its physiological limits (Casper and Hendricks 2005). This indicates that money and effort currently spent on bullfrog eradication for the sake of native amphibians in this region may be better spent in other ways. However, due to changing climate, monitoring the effects of bullfrogs should continue because conditions may shift in their favor (Rahel and Olden 2008).

All amphibian species surveyed were found breeding in constructed ponds. Contrary to my hypothesis of constructed ponds sustaining lower amphibian use, there was a trend for all species to be found in a higher proportion of constructed ponds than natural ponds. Results of prior studies were mixed: Scheffers and Paszkowski (2013) found a variety of amphibians using constructed urban ponds less than natural remnant ponds while Brand and Snodgrass (2010) found the opposite. Creating new ponds could be an important part of a conservation strategy for improving amphibian populations in cities, provided the new ponds possess characteristics favored by native amphibians. The age of constructed ponds was not examined explicitly during this study due to lack of accurate information. Through time ponds may become unsuitable as they fill in with sediment and organic matter, especially those designed to collect suspended solids. Dredging can reduce this effect, but this possibility should be explored with caution because it can also be detrimental to amphibians (Aresco and Gunzburger 2004).

Management implications

These findings indicate that amphibians in urban areas use both natural and constructed ponds as long as there is appropriate vegetation and low levels of pollutants. This study supports the following recommendations for managing ponds in this region to improve their value as amphibian habitat: maintain and improve forest cover and aquatic vegetation, reduce runoff that potentially contains pollutants, construct new ponds (with appropriate characteristics), and de-prioritize bullfrog removal while continuing to monitor for changes in their effects on native amphibians. The specific influences of factors cannot necessarily be extrapolated to other species or areas. However, these findings were generally in agreement with the existing studies of habitat variables in urban ponds (Hamer and McDonnell 2008), and therefore may represent general trends beyond this study site.

Conclusion

Pond-breeding amphibians are often assumed to be particularly vulnerable in human-dominated landscapes because of their requirements for sufficient aquatic and terrestrial habitats and the movement corridors between them. This study shows that many pond-breeding amphibian species are able to breed in altered and completely constructed ponds in a large city, given suitable habitat conditions. The species in this study did not avoid novel, constructed habitats—the results indicate similar or even higher presence and richness in constructed ponds than in natural remnant ponds. Many species were surprisingly adaptable, and managers can consider urban ponds as potential amphibian breeding habitats that are not to be discounted due to structural differences from wetlands that existed there before urbanization. Studies examining which aspects are most influential for focal species in remnant and novel habitats are increasingly important conservation tools to allow for species coexistence as land continues to be converted into human-dominated landscapes.

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Appendices

	YEAR	SITE	DPTH	NITR	REF	AVEG	SVEG	DRY	NATR	FISH	BLFG	ROD	FORT
YEAR	-	0	−0.4	0	−0.3	0	0	0.2	0	0	0.1	0	0.2
SITE		-	0.3	0	0	0	0.1	−0.4	−0.2	0.4	0	0	−0.2
DPTH			-	0	−0.1	−0.2	0	−0.4	0	**0.5**	0.1	−0.1	0
NITR				-	0	−0.2	−0.2	−0.4	0	0	−0.2	0.4	−0.1
REF					-	**0.8**	0	0.3	0	0	−0.2	−0.1	−0.4
AVEG						-	0.3	0.3	0	0	−0.1	−0.2	0.2
SVEG							-	0	0	0.	0.1	−0.3	0.2
DRY								-	0	**−0.5**	0	−0.3	0.2
NATR									-	0	0	−0.1	0
FISH										-	0.2	−0.1	0
BLFG											-	−0.4	0
ROD												-	−0.1
FORT													-

Appendix A

Collinearity values for predictor variables. Variable pairs with collinearity of absolute values ≥0.5 are bolded and were assessed for the variable with more predictive power; the other variable in the pair was excluded from analyses. The predictor variable abbreviations are as follows: YEAR-year of the survey, SITE-site of the survey, DPTH-depth at the deepest point, NITR-nitrate level, REF-aquatic refugia, AVEG-aquatic vegetation, SVEG-surrounding vegetative cover, DRY-if the pond dried in the summer, NATR-if the pond was a natural remnant, FISH-presence of fish, BLFG-presence of introduced bullfrogs, ROD-road density in 1km radius, FORT-forest cover in 1km radius.

FORT	AVEG	NITR	SVEG	DRY	NATR	ROD	DPTH	BLFG	Delta AICc
1	1	−1	0	0	0	0	0	0	0
1	1	−1	1	0	0	0	0	0	0.86
1	1	−1	0	1	0	0	0	0	1.39
1	1	−1	0	0	−1	0	0	0	1.49
1	1	−1	1	0	−1	0	0	0	1.66
1	1	−1	0	0	0	1	0	0	1.80
1	1	−1	0	0	0	0	−1	0	1.83
1	1	−1	1	1	0	0	0	0	1.86

Appendix B

Top akaike information criterion models for species richness, corrected for small sample sizes (AICc). All models are shown where the difference in AICc was <2 from the top AICc model. A "0" indicates that a factor was not included in a given model, "1" indicates that it was included and positively associated with richness, and "-1" indicates that it was included and negatively associated. The predictor variable abbreviations are as follows: FORT-forest cover in 1km radius, AVEG-aquatic vegetation, NITR-nitrate level, SVEG-surrounding vegetative cover, DRY-if the pond dried in the summer, NATR-if the pond was a natural remnant, ROD-road density in 1km radius, DPTH-depth at the deepest point, BLFG-presence of introduced bullfrogs.

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