Multiscale drivers of amphibian community occupancy in urban ponds

Erin L. Sauer[1] · Jennyffer Cruz[2] · Erin Crone[1,3] · Catherine Lewis[1] · Ethan Plumier[1] · Blake Cwynar[1] · David Drake[1] ·
Bradley M. Herrick[4] · Daniel L. Preston[1,3]

Abstract

Urbanization has driven the loss of natural aquatic habitats while concurrently increasing the abundance of artificial urban ponds. Urban ponds are not typically designed for wildlife but are often colonized by species of conservation concern, including amphibians. Urban ponds may have conservation value, but it is unclear whether they are equally suitable habitat for all amphibians within a local assemblage and which factors most affect habitat quality. Here, we surveyed 96 ponds in the greater Madison, Wisconsin area from four land-use types: 1) golf course ponds, 2) urban park ponds, 3) urban stormwater ponds, and 4) ponds within mixed-use exurban regions. We assessed which local pond characteristics and landscape factors influenced occupancy of amphibian communities using a Bayesian multispecies occupancy model. We detected nine species, finding at least one species at most ponds (91.8%). Ponds within golf courses and urban parks had higher naïve species richness than other urban ponds. We grouped species based on their habitat requirements in their adult stage as (1) upland (for terrestrial adults) and (2) fully aquatic. Occupancy of upland species increased with greater forest cover and pond area, while occupancy of fully aquatic species increased with greater wetland cover, water fluorescence, and lower water turbidity. Our results suggest that species habitat preferences influence the urban ponds they occupy. Urban ponds provide important amphibian habitat for varied species assemblages. Strategic management of urban ponds could therefore provide key ecosystem services, while also facilitating the conservation of amphibians that are increasingly threatened by habitat loss.

Keywords Urbanization · Urban ecology · Amphibian conservation · Landscape · Water quality · Bayesian occupancy model · Wildlife management

Introduction

Urbanization and the expansion of suburban sprawl threaten biodiversity by increasing impervious land-cover, eliminating suitable wildlife habitat, and causing fragmentation (McKinney 2008; Miller et al. 2014). In urban environments, the replacement of porous landcover by impervious surfaces alters hydrology, increasing run-off, sedimentation, and inputs of pollutants to wetlands, lakes, and other aquatic habitats (Walsh et al. 2005; Hamer

✉ Erin L. Sauer
  erinsauer10@gmail.com

  Jennyffer Cruz
  jencruz@boisestate.edu

  Erin Crone
  erin.crone@colostate.edu

  Catherine Lewis
  cdlewis3@wisc.edu

  Ethan Plumier
  plumier@wisc.edu

  Blake Cwynar
  bcwynar@wisc.edu

  David Drake
  ddrake2@wisc.edu

  Bradley M. Herrick
  bradley.herrick@wisc.edu

  Daniel L. Preston
  dan.preston@colostate.edu

1 Department of Forest and Wildlife Ecology, University
   of Wisconsin-Madison, Madison, WI 53706, USA

2 Department of Biological Sciences, Boise State University,
   Boise, ID 83725, USA

3 Department of Fish, Wildlife and Conservation Biology,
   Colorado State University, Fort Collins, CO 80523, USA

4 University of Wisconsin-Madison Arboretum, Madison,
   WI 53711, USA

and McDonnell 2008; Miller et al. 2014). Despite the clear impacts of urbanization and sprawl on biodiversity, it is often unclear how landscape and local scale characteristics drive aquatic community structure in urban areas (Hamer and Parris 2011; Jeanmougin et al. 2014). Further, aquatic species may show differential responses to urbanization, with some taxa adapting to the urban environment and others becoming extirpated (McKinney 2006). Thus, research examining how conditions associated with urbanization and sprawl impact aquatic biodiversity is needed to inform conservation and management of urban aquatic ecosystems (Treglia et al. 2018).

Urbanization and sprawl are often accompanied by the creation of artificial ponds used to minimize polluted run-off and sediment from entering natural waterbodies and to mitigate flooding and erosion (Clevenot et al. 2018). In many cases, natural ponds and wetlands are incorporated into stormwater management systems, potentially altering their habitat quality and functioning. Urban ponds are also constructed for aesthetic and recreational purposes in parks and golf courses. Because of the various purposes these ponds serve, there is a tremendous amount of variation in how urban ponds are constructed and managed (Clevenot et al. 2018). For example, removal of aquatic and/or riparian vegetation may be an active management goal for ponds in golf courses, whereas vegetation that assimilates nutrients may be desirable in stormwater retention ponds (Winchell and Gibbs 2016; Clevenot et al. 2018). Similarly, pond morphometry and hydrology will vary based on the functions the pond is intended to provide. Many stormwater ponds have steep banks and relatively constant water levels because they are designed to maximize water residence times (Clevenot et al. 2018). This variation in management practices, alongside differences in surrounding land use in urban areas, provides wide gradients in urban pond characteristics over relatively small spatial scales.

While artificial urban ponds are not typically managed as habitat for wildlife, they are often colonized by a range of species, including taxa of conservation concern (Treglia et al. 2018). As a result, urban ponds may have significant, but frequently overlooked, conservation value (Hamer and McDonnell 2008). For example, amphibians, which are experiencing dramatic global declines, commonly use urban ponds as breeding habitat (Hamer and Parris 2011; Clevenot et al. 2018; Sievers et al. 2018), particularly in areas with low densities of suitable natural breeding wetlands (Brand and Snodgrass 2010). Amphibians face challenges from urbanization due to local, within pond changes in environmental conditions, and changes in the surrounding terrestrial landscape that affect upland habitat use for hibernation and migration to breeding sites (Birx-Raybuck

et al. 2010; Brand and Snodgrass 2010; Hamer and Parris 2011; Treglia et al. 2018).

Amphibians are useful for understanding the impacts of urbanization on aquatic ecosystems because they are generally sensitive to habitat degradation at multiple scales and because of their diverse habitat requirements (Rubbo and Kiesecker 2005; Hamer and Parris 2011; Guzy et al. 2012). Some amphibian taxa (e.g. *Anaxyrus* spp. and *Ambystoma* spp.) make long migrations between their breeding sites and overwintering sites, making them especially sensitive to losses in habitat connectivity. For example, individuals migrating to and from breeding ponds often experience heavy road mortality (Ashley and Robinson 1996; Mazerolle 2004; Elzanowski et al. 2009) and vegetation supporting juveniles can face heavy mowing activity in mid-summer, which limits food availability and increases likelihood of desiccation and predation (Hocking et al. 2008; Puglis and Boone 2012). Urban waterbodies are also prone to eutrophication and pollution by road salt, heavy metals, and other contaminants that commonly affect growth and survival of amphibians during aquatic life stages (O'Neil et al. 2012; Miller et al. 2014; Clevenot et al. 2018; Calderon et al. 2019). Furthermore, many urban ponds have a permanent hydroperiod allowing them to support fish, which can prevent colonization by amphibian species with larval stages especially vulnerable to predation (e.g. *Hylidae*) (Clevenot et al. 2018).

Our understanding of how urban land use, individual pond features, and amphibian habitat requirement correspond with amphibian success in urban ponds is limited. Our study provides a Bayesian multispecies analysis of amphibian occupancy based on these factors within a complex urban environment. We surveyed amphibian communities at 96 ponds around the city of Madison, Dane County, Wisconsin, an area where the landscape has been heavily modified for human use via urbanization, sprawl, and agriculture. Our objective was to determine which landscape and local scale pond characteristics were generally associated with amphibian occupancy and how occupancy in urban ponds is influenced by adult amphibian habitat requirements. We predicted that, generally, amphibians would occur more frequently in smaller, fish-free ponds with high connectivity (close to other waterbodies and surrounded by wetland and forest cover) and high water quality (e.g. low chloride levels and high dissolved oxygen (DO)) (Knutson et al. 1999; Burne and Griffin 2005; Porej and Hetherington 2005; Calderon et al. 2019). Further, we predicted that species with long larval stages and semi-aquatic adult stages should associate with high wetland cover and larger waterbodies (Houlahan and Findlay 2003), while species with adult stages that forage and overwinter in upland terrestrial areas should be associated with ponds surrounded by forest cover (Houlahan and Findlay 2003).

Materials and methods

Pond selection

Survey ponds were located in and around the city of Madison in Dane County, Wisconsin (US) and were selected to span a gradient of local land uses (Fig. 1). Madison has a population of ~258,000 and the urban center lies on an isthmus between two large lakes (Fig. 1). The local climate is characterized by warm, wet summers and cold winters, with ~5 months per year when precipitation falls primarily as snow. Madison ponds are frozen for several months each year and salt is applied to roads over the winter months. Most survey ponds were artificially constructed (91%), had standing water year-round (98%), were less than 10,000 m² in surface area (96%), and all received water from human-modified landscapes. We initially grouped the survey ponds into four designations that we hypothesized to be associated with distinct environmental characteristics: 1) golf course ponds (n = 31), 2) ponds within urban parks (n = 28), 3) ponds in urban residential/commercial areas (n = 14) and, 4) ponds within mixed use exurban regions in close proximity to agricultural landscapes (n = 23). These four pond types are hereafter referred to as "golf course ponds", "greenspace ponds", "urban ponds", and "exurban ponds".

Field surveys

We surveyed each pond once in May/June and a second time in July/August of 2019 during daylight hours. The seasonal timing of pond visits was intended to maximize overlap with the larval periods of local pond-breeding amphibians (Mossman et al. 1998). At every pond visit we assessed the amphibian and fish communities using a visual encounter survey around the perimeter of the pond, 8 to 10 dip net sweeps perpendicular to the shore (1 m sweeps, 600 cm² net opening, 3 mm mesh), and 3 to 5 seine drags to sample deeper pond regions (3 m drags, 1×2 m net size, 4 mm mesh). We also recorded identities of calling amphibians at every visit. While the number of dip net sweeps and seine drags did vary, the variation was minimal and not associated with any pond factors and thus unlikely to bias species detection. During each survey we recorded species identity, abundances, and life stages of all fishes and amphibians encountered. All captured vertebrates were released immediately. At each pond, we recorded floating aquatic vegetation cover (% pond area) and shoreline vegetation (% perimeter length). We also measured specific conductance, salinity (ppt), chloride (mg/L), nitrate (mg/L), and DO (%) using a YSI Pro Plus handheld meter (Yellow Springs, OH, US). Lastly, we quantified turbidity and relative phytoplankton fluorescence
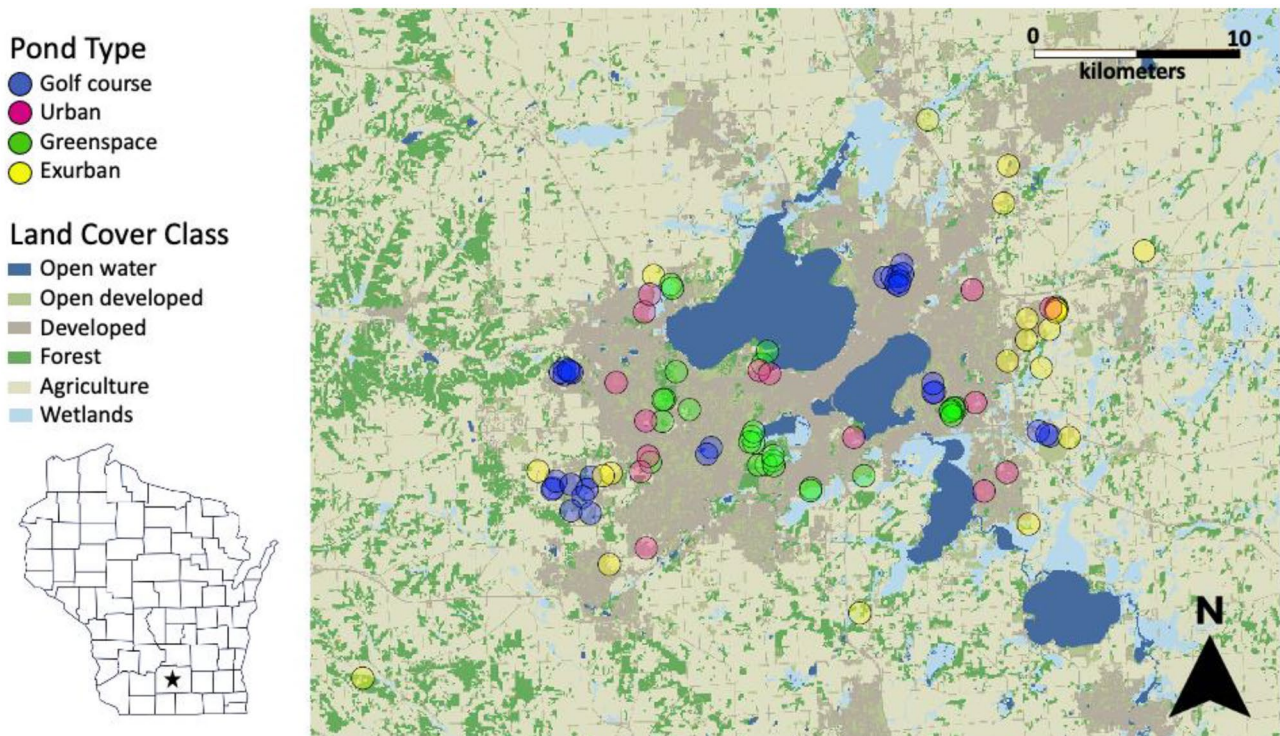

Fig. 1 Map of land cover classes in the city of Madison, Wisconsin and surrounding area. Pond locations and types are represented by points and cover class. Bottom left shows the location of the study area (represented by a star) within the state of Wisconsin (USA)

in the water column using a Turner Designs (Sunnyvale, CA, US) handheld fluorometer from water samples collected within ~ 3 m of shore at a depth of ~ 30 cm.

Remotely sensed data

We quantified pond area and land cover surrounding each pond using remotely sensed data. We digitized Google Earth aerial imagery taken in October 2018 to estimate pond area. To determine land cover effects on amphibian communities, we quantified land cover in a 200 m radius buffer surrounding each pond from the 2016 National Land Cover Database (NLCD; 30 m^2 resolution, equal-area projection, WGS 84 datum surface; Homer et al. 2015). We grouped land cover into five types based on the NLCD categories: agriculture (cultivated crops and hay/pasture cover), mowed grass (developed open space), forest (deciduous, evergreen, and mixed), wetland (woody and herbaceous), and impervious surface (low, medium, and high intensity development).

Statistical analysis

We analyzed our amphibian survey data using a multispecies occupancy model under a Bayesian framework. At each pond ($i = 1, \ldots, 96$), species were surveyed twice during their breeding season in 2019 ($j = 1,2$), using several techniques. Therefore, we aimed to account for the detection when all survey techniques were implemented, not for each technique independently. This approach helped to deal with potential overdispersion from looking at each method separately. We combined detection across methods for a given survey and focused on species ($s = 1, \ldots, 5$) that were detected in at least 5% of ponds (green frog, *Lithobates clamitans*, American bullfrog, *Lithobates catesbeianus*, American toad, *Anaxyrus americanus*, northern leopard frog, *Lithobates pipiens*, and grey/Cope's tree frog, *Hyla versicolor/chrysoscelis*). This decision prevented us from using this model to estimate richness, which we only evaluated as 'naive richness' in this manuscript. Instead, we could have included random species effects, with strong priors to regularize the estimates for these species towards the community mean. However, including these species would have made inference on their relationship with occupancy unreliable, and largely driven by the data from the other species. We instead chose to only include species with enough data so that we could be confident in how they were responding to the environment in their pond occupancy. Four other taxa were detected in three or fewer ponds, which prevented us from including them in the occupancy analyses (see Results). Observed occupancy of species, s, within pond, i, and survey j, $y_{s,i,j}$, was modelled as a Bernoulli process conditional on latent variable, $z_{s,i}$, representing true occupancy of a species at a

pond during the breeding season, and related to probability of detecting an s species at each i pond and j survey, p_{sij} as: $y_{s,i,j} | z_{s,i} \sim Bern(z_{s,i} \times p_{s,i,j})$. The detection probability was in turn related to survey date, $date_{s,i,j}$ and percentage of floating vegetation cover, $veg_{s,i,j}$, through a logit regression:

$$logit(p_{s,i,j}) = \alpha_0 + \alpha_1 \times date_{s,i,j} + \alpha_2 \times veg_{s,i,j} + \varepsilon_s$$

where α_0 represents the fixed intercept, α_1 and α_2 are fixed coefficients related to $date_{s,i,j}$ and $veg_{s,i,j}$ predictors respectively, and ε_s represents a species-level random intercept, which allowed us to account for differences in detection among species. Survey date may affect detection because amphibian species vary in their breeding phenology during the breeding season (including spring and summer; Knutson et al. 1999). Floating vegetation was included as a detection covariate because it may have decreased our ability to detect amphibians during visual and net surveys.

Coefficients were given Normally-distributed priors $\alpha_1; \alpha_2 \sim$ Normal(0,10). The intercept, α_0, was modelled as a mean response and given slightly informative Beta priors: $\alpha_0 = \log\left(\frac{\mu_{\alpha,0}}{1-\mu_{\alpha,0}}\right), \mu_{\alpha,0} \sim Beta(4,4)$, to improve convergence of the Markov Chain Monte Carlo (MCMC) algorithm we used to update posterior distributions of the model parameters. The species-level random intercept, ε_s, was assigned a Normal prior: $\varepsilon_s \sim$ Normal($0, \sigma_s^2$). The corresponding standard deviations, σ_s, were assigned half, Student-t distributions as priors: $\sigma_s \sim t(0, 2.5, 7)$ restricted to $\sigma_s > 0$, which provided some shrinkage and improved computation (Gelman et al. 2008).

The latent occupancy state of s species at i pond (where $z_{s,i} = 1$ if the species occupied the pond and $z_{s,i} = 0$, otherwise) was related to the group probability of occupancy, $\psi_{g,i}$, as a Bernoulli process, $z_{s,i} \sim Bern(\psi_{g,i})$. We grouped species into two g groups we hypothesized to respond similarly to predictors because of their shared adult habitat requirement (Knutson et al. 1999; McAllister et al. 1999; Kendell 2002; Smith and Keinath 2004; Pitt et al. 2017). The first group included species that primarily inhabit the aquatic environment throughout their entire life cycle (green frog and American bullfrog) and the second group included species that require terrestrial upland habitat outside of breeding for foraging or long migration to wintering sites (American toad, northern leopard frog, and grey/Cope's tree frog). Grouping species allowed us to compare responses of amphibian with distinct habitat requirements (i.e., upland versus aquatic). We thus modelled the probability of occupancy for g group at i pond as related to N = 8 landscape and local level predictors as:

$$logit(\psi_{g,i}) = \beta_{g,0} + \sum_{n=1}^{N} \beta_{g,N} \times X_{i,N} logit(\psi_{ci})$$

where $\beta_{g,0}$ represent the fixed intercepts for each group and $\beta_{g,N}$ are the group-level coefficients related to each of the 8 pond-level predictors, $X_{N[i]}$, including: pond area (m^2), forest cover (%), wetland cover (%), dissolved oxygen (%), nitrate concentration (mg/L), chloride concentration (mg/L), turbidity (NTU), and relative phytoplankton fluorescence. We excluded specific conductance and salinity because they were highly correlated with chloride (R > 0.8), and we excluded % impervious surface and grass cover because they were negatively correlated with % wetland cover (results of quasibinomial distributed glm: β = -4.34, SE = 0.67, p < 0.001 & β = -6.96, SE = 1.17, p < 0.001, respectively). Shoreline vegetation had low variation across ponds and, as a result, was also excluded from the model. Agriculture cover led to non-convergence, so it was also removed from the full model. However, an alternative model that included agriculture and developed land but excluded wetlands showed that agriculture cover was not associated with amphibian occupancy (Fig. S1). Finally, the simple distinction of present or absence of predatory fish did not provide enough resolution to distinguish the ponds based on amphibian species occupancy. This was apparent via non-convergence when we included fish presence in models. Further, a simple single-predictor glm (predatory fish presence or absence) showed no effect of predatory fish on overall amphibian occurrence, grouped aquatic or upland species, or naïve species richness (but see Discussion and Supplemental Table S1).

The fixed intercepts were modelled as mean occupancy probability and given slightly informative Beta priors $\beta_{g,0} = \log\left(\frac{\mu_{\beta,0}}{1-\mu_{\beta,0}}\right)$, $\mu_{\beta,0} \sim Beta(4,4)$. Fixed coefficients were given Normally-distributed priors: $\beta_{g,1,\dots 8} \sim Normal(0,10)$. All continuous covariates were standardized by subtracting their means and dividing by two standard deviations, while binary predictors were scaled to -1 when absent and 1 when present (Gelman et al. 2008).

All analyses were conducted with R 4.1.0 (R Foundation for Statistical Computing, Vienna, Austria; Team 2013). We conducted our multi-species occupancy model using the MCMC algorithm available in the program JAGs (Plummer 2003), which we called using jagsUI (version 1.5.2). We ran 3 parallel MCMC chains, thinned every 5th iteration, and ran 130,000 interactions total. We assessed model convergence using the MCMC trace plots and a Gelman-Rubin statistic of less than 1.01 (Gelman and Rubin 1992). Model goodness of fit was evaluated using a posterior predictive check using deviance residuals plotted at the species-level and Bayesian p values based on combining these deviance residuals, following Cruz et al. (2019), with values between 0.1 and 0.9 considered as good fit. The code for the multispecies occupancy model and code used to estimate deviance residuals and Bayesian p values is freely available at: https://github.com/quantitativeconservationlab/MultispeciesOccupancy.

Results

We detected amphibians at 90 of the 96 surveyed ponds; however, most ponds had relatively low richness (mean naïve richness was 2; Fig. 2). We observed nine total species (Fig. 3). The most commonly observed were: green frog (71 ponds), American toad (46 ponds), American bullfrog (45 ponds), northern leopard frog (25 ponds), and grey/Cope's tree frog (16 ponds). In contrast, boreal chorus frog (*Pseudacris maculata*, 3 ponds), eastern tiger salamander (*Ambystoma tigrinum*, 2 ponds), eastern newt (*Notophthalmus viridescens*, 1 pond), and spring peeper (*Pseudacris crucifer*, 1 pond) were rarely found.

Naïve amphibian richness varied across pond types. Exurban ponds had relatively high species richness compared to other pond types, with 52% of ponds having more than two amphibian species present. Greenspace and golf course ponds had moderate species richness (45% & 32%, respectively) and urban ponds had relatively low richness, with only 14% of ponds supporting more than two species (Fig. 2). Greenspace ponds were more likely than other pond types to be surrounded by forest (mean forest cover = 17%), golf course ponds by mowed grass (mean grass cover = 62%), exurban ponds by agriculture (mean ag cover = 43%), and urban ponds by impervious surfaces (mean impervious surface cover = 65%; Fig. S2). Greenspace and exurban ponds were more likely to be surrounded by wetlands than urban or golf course ponds (mean wetland cover = 36% & 23%, respectively; Fig. S2). Greenspace ponds were the oldest and had the highest chloride content (mean = 33 yr & 103.35 mg L^{-1}, respectively) while golf course ponds were the newest and had the lowest chloride content (mean = 28 yr & 39.68 mg L^{-1}, respectively; Fig. S3). All other variables were relatively similar across pond types (Fig. S3).

Mean pond-level detection probability varied among species: green frog (0.58; Fig. S4), American toad (0.37; Fig. S4), American bullfrog (0.41; Fig. S4), northern leopard frog (0.24; Fig. S4), and grey/Cope's tree frog (0.15; Fig. S4). Aquatic species (green frog and American bullfrog) had a higher probability of occupying surveyed ponds than upland species (American toad, northern leopard frog, and grey/Cope's tree frog), $\psi_{g=aquatic} = 0.84$, 90% CI = 0.59–0.99 & $\psi_{g=upland} = 0.72$, 90% CI = 0.42–0.96. Upland species occupancy was positively associated with % forest cover (Figs. 4 and 5), and negatively associated with pond area (m^2; Figs. 4 and 5). Aquatic species (green frog and American bullfrog) occupancy was positively associated with % wetland cover (Figs. 4 and 5) and
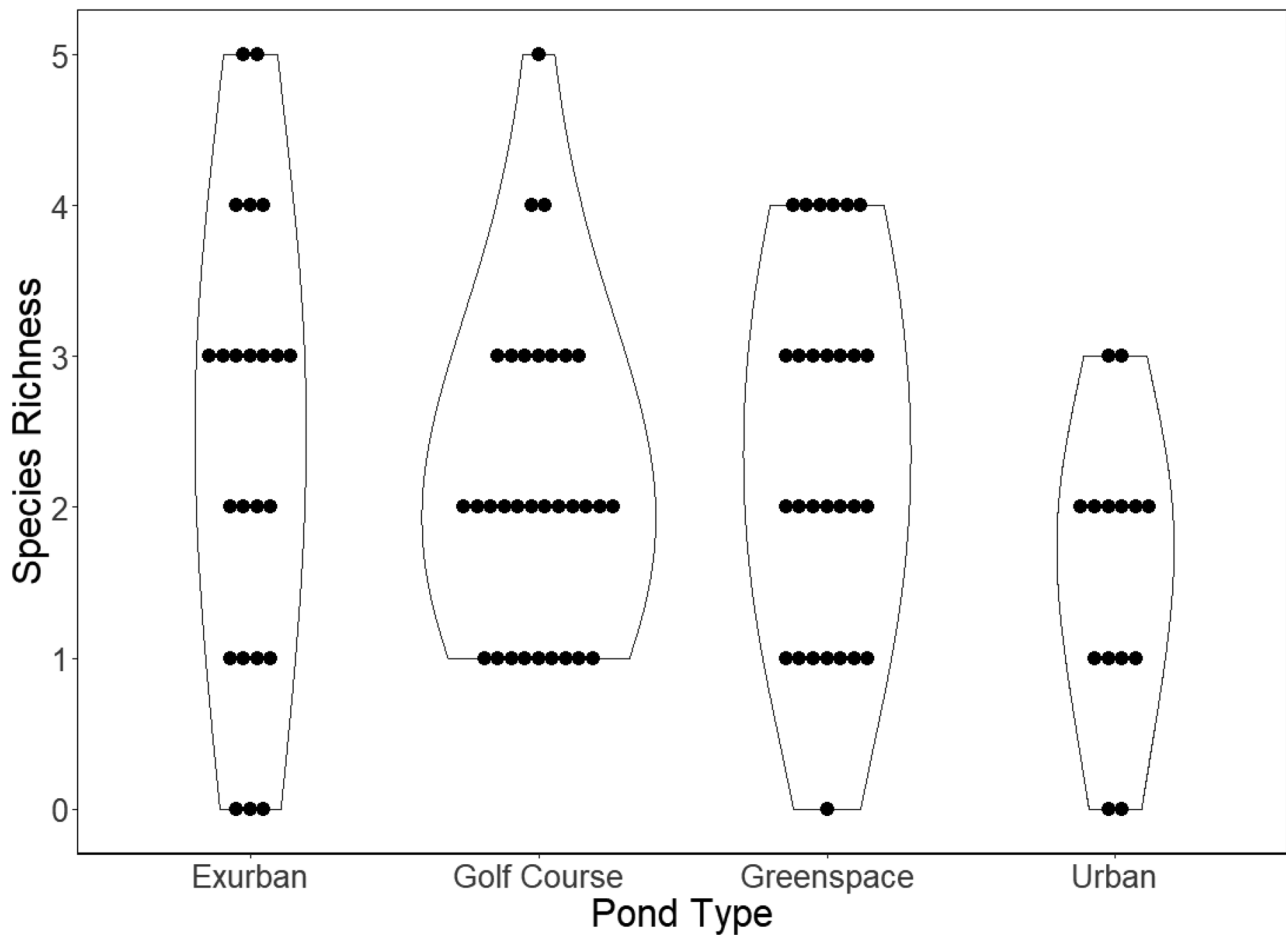
Fig. 2 Distribution of pond-level naive species richness across the four pond types in Dane County, Wisconsin, 2019. Dots indicate a single pond

fluorescence (Figs. 4 and 5), negatively associated with turbidity (Figs. 4 and 5), and not associated with other predictors (Fig. 4).

The model converged at 130,000 iterations with all parameters showing good mixing and a Gelman-Rubin statistic of < 1.01. Deviance residuals indicated good model fit

Fig. 3 Bar chart indicating the number of ponds where species were detected in Dane County, Wisconsin, 2019. The nested image shows a green frog, the most commonly detected species in our survey
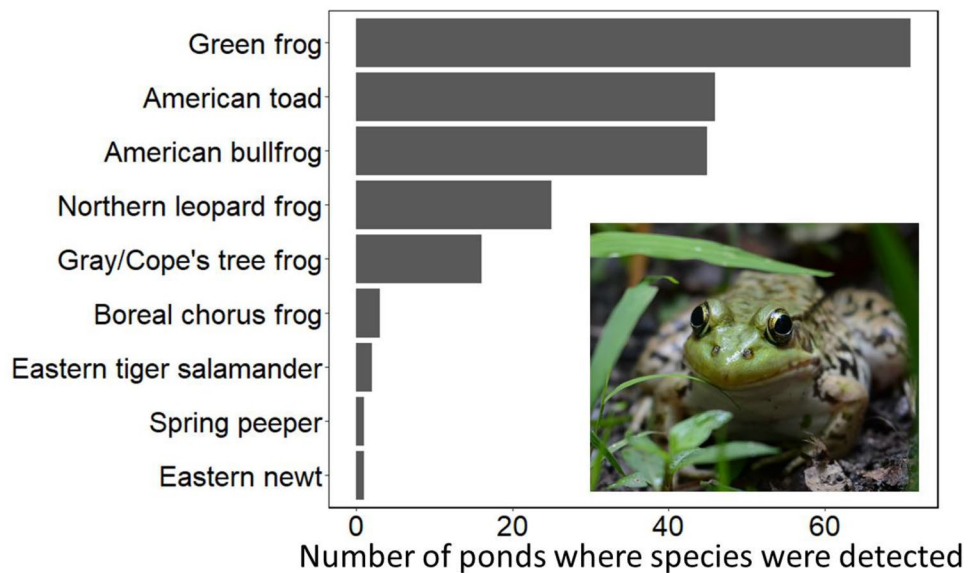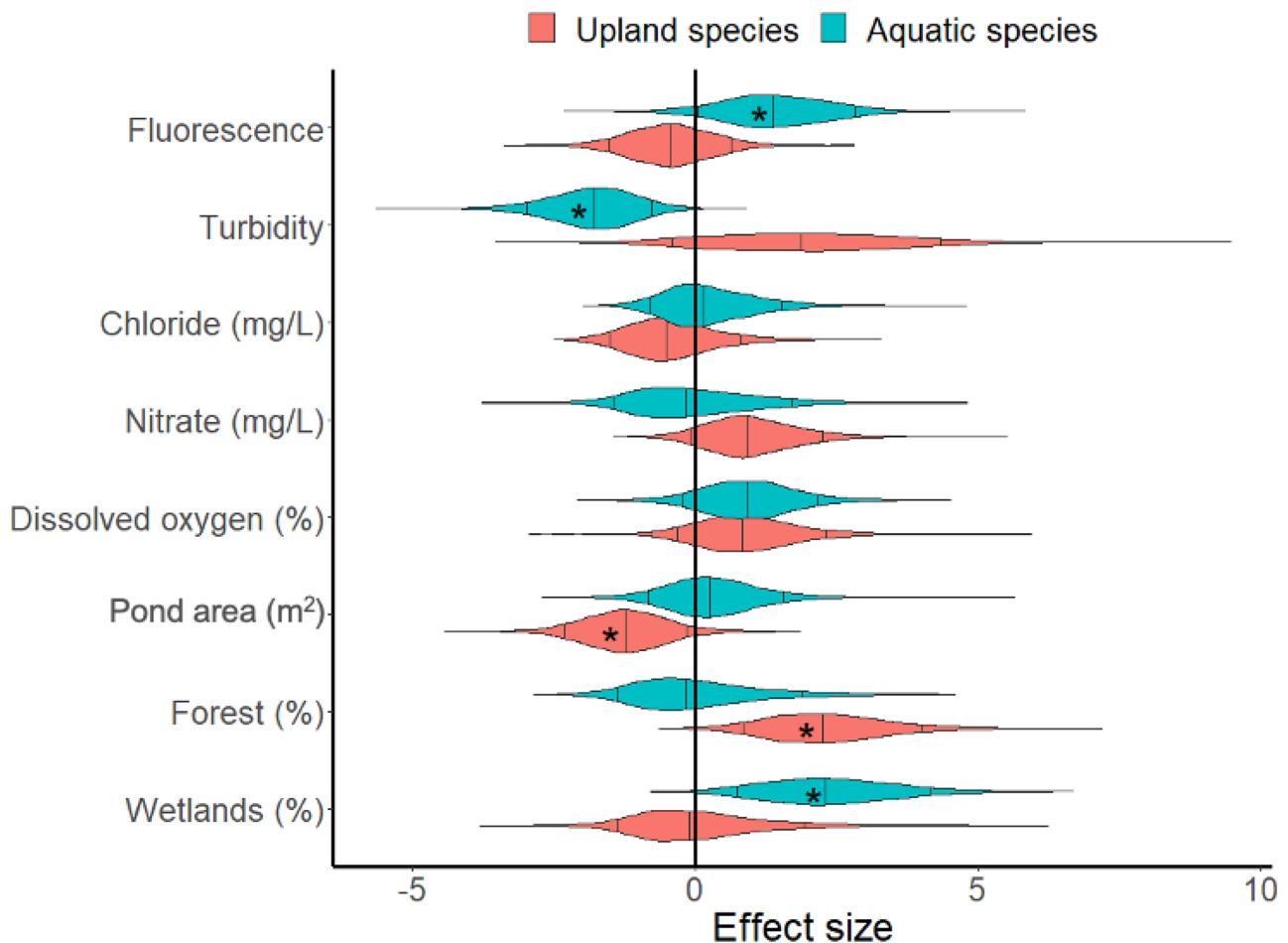
Fig. 4 Results of the amphibian multispecies occupancy model. Fixed effects are listed along the y-axis. Red and blue violins represent the effect size for the upland and aquatic groups. Upland species included American toad, northern leopard frog, and grey/Cope's tree frog. Aquatic species included green frog and American bullfrog. Center lines within each violin represent the mean effect size and error bars represent 85% credible intervals. Group effects with 85% credible intervals that do not overlap zero are marked with *

based on overlap between observed and expected occupancy for each species across the study ponds. Green frogs and American bullfrogs had the best fit, while grey/Cope's tree frogs and northern leopard frogs showed more uncertainty (Fig. S5). Overall, the model fit the data well with a Bayesian *p* value of 0.596.

Discussion

Our survey revealed that amphibians readily colonize urban and suburban ponds, but most ponds are inhabited by relatively few species. Overall, we found that differences in life histories likely drive variation in the sensitivity of amphibian species to local and landscape factors associated with urbanization. Upland species prefer smaller water bodies with forest cover while aquatic species prefer water bodies with nearby wetlands with higher phytoplankton and low

turbidity. Understanding which pond attributes influence amphibian communities across multiple scales can improve the management of urban and suburban ponds for amphibian conservation (Hamer and Parris 2011; Kruger et al. 2015; Guderyahn et al. 2016). As urbanization and sprawl continue to encroach upon undeveloped land, the need to incorporate human-modified urban and suburban aquatic habitats into conservation planning becomes more apparent.

Greenspace ponds may be comparable to the artificial exurban ponds in their ability to support amphibian communities, making them vital habitat for urban amphibian populations. Ponds in greenspaces are likely more suitable than urban ponds because of their surrounding landscapes, as local pond characteristics were mostly similar between the two pond types. For example, greenspace ponds were typically surrounded by wetland and forest cover and supported more diverse amphibian communities than urban ponds, which were dominated by impervious land cover

Fig. 5 Partial predicted relationships between amphibian group occupancy and important model predictors from a Bayesian multispecies occupancy model. Predictors include pond area (m²), % forest cover, % wetland cover, and relative turbidity. Red and blue lines and bands represent the mean effect sizes and 85% credible intervals for upland and aquatic groups. Upland species included American toad, northern leopard frog, and grey/Cope's tree frog. Aquatic species included green frog and American bullfrog
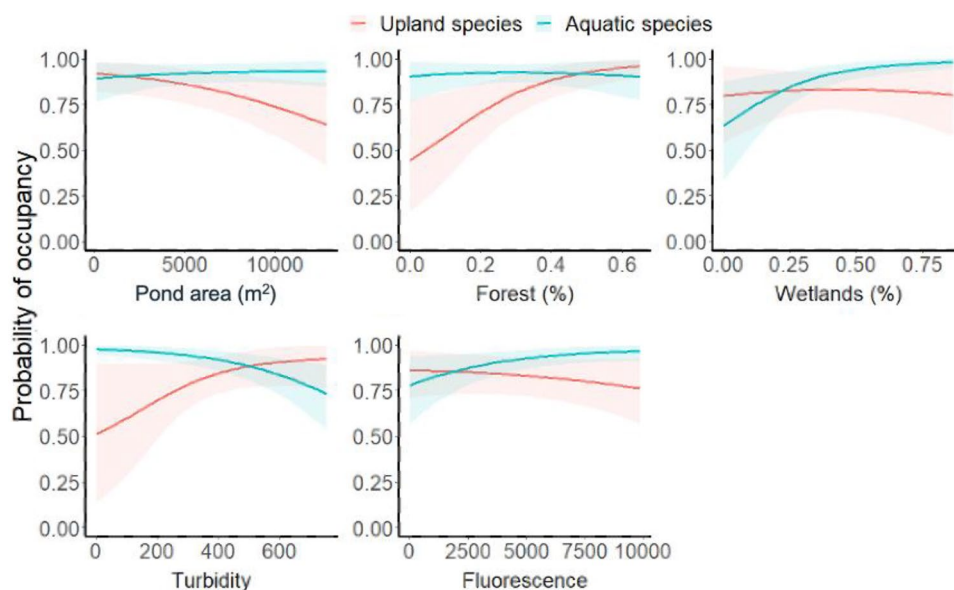
(Fig. S2). Greenspaces have been long established as important for avian, insect, and plant conservation but the use of greenspace ponds as tools in aquatic community conservation has been less thoroughly explored (Nielsen et al. 2014). This may be because many greenspace ponds are specifically developed for stormwater retention/detention and therefore not managed for conservation to the same extent as terrestrial greenspace habitats (Scheffers and Paszkowski 2012; Hassall 2014). In fact, greenspace ponds in our survey had the highest chloride levels of all pond types, likely due to high levels of runoff from roads (Fig. S3). However, at most ponds, the observed chloride levels were generally below the physiological thresholds shown to negatively impact amphibian survival or development (Collins and Russell 2009) and we did not detect a negative effect of chloride on amphibian occupancy in our model. We did find that aquatic species were negatively affected by turbidity, which may be related to sedimentation caused by stormwater runoff (Hecnar and M'Closkey 1996; Wood and Richardson 2009).

Golf course ponds supported similar naïve amphibian richness as exurban and greenspace ponds and were the only pond type to have 100% amphibian occurrence. Unlike greenspace ponds, golf course ponds have low to no stormwater input. The golf course ponds we surveyed had the lowest chloride levels of all pond types, significantly lower than greenspaces (Fig. S3). Further, individual golf courses have many ponds with little to no impervious surfaces separating them, possibly allowing for relatively high migration and dispersal opportunities compared to urban ponds. This relatively high habitat connectivity may especially benefit amphibians and other taxa that require connectivity between aquatic and terrestrial habitats (e.g. *Ambystoma* salamanders, leopard frogs, *Emydidae* turtles) (Becker et al. 2007;

Paton et al. 2008; Scheffers and Paszkowski 2012; Winchell and Gibbs 2016). Golf courses in our survey varied tremendously in their management techniques, with some mowing all the way up to the edge of the ponds and some allowing dense riparian zones to grow along the pond's edge. We also noticed differences in aquatic vegetation management among golf courses. Courses that purposely remove vegetation mechanically or via herbicide may be negatively impacting amphibians and other aquatic organisms. In fact, golf course ponds had the lowest floating vegetation cover of all four pond types (Fig. S3). The incorporation of golf course ponds into conservation plans may be as simple as allowing riparian zones to develop around the ponds. This minor landscaping change would increase the availability of wetland habitat, which was strongly associated with amphibian occupancy in our survey (Puglis and Boone 2012). Furthermore, we observed several taxa that were rare in our dataset inhabiting golf course ponds (e.g., eastern tiger salamanders). Thus, golf course ponds within the urban environment likely play useful roles as amphibian habitat.

Overall, we found that both landscape and local factors were important for amphibians in urban areas, suggesting that changes at either scale could improve conservation value of urban ponds. Among the local factors, upland species occupancy was negatively associated with pond area, consistent with our expectations (Porej and Hetherington 2005). Larger ponds are more likely to be inhabited by fish, which are known to exclude many species of amphibians via predation. While we were unable to include fish presence in our occupancy model, predation of larval amphibians by fish is likely impacting occupancy of some species in ponds. Using a simplified analysis, we found that grey tree frogs were detected less often in ponds with predatory

fish (see Supplemental Table S1 for details). The presence of predatory fish may be difficult to manage as many urban retention ponds are deep in order to hold large volumes of stormwater, and some are intermittently connected to larger water bodies, making them prone to colonization by fish (Porej and Hetherington 2005; Clevenot et al. 2018). We detected predatory fish in ~ 45% of the ponds we surveyed. Preventing human-aided fish introductions and evaluating potential for fish removal efforts are likely to greatly benefit pond-breeding amphibians. Within the local amphibian assemblage, the treefrogs and salamanders are generally highly susceptible to fish predation, while American bullfrogs, green frogs, and toads are better adapted to co-occur with fish (Kats et al. 1988; Porej and Hetherington 2005). As a result, fish introductions into artificial urban ponds are likely to favor the latter set of taxa.

While we detected amphibians at the vast majority of ponds, some species were far more commonly observed than others, suggesting that specific traits likely facilitate persistence while environmental filters prevent other species from colonizing or persisting. For example, green frogs were by far the most widespread species, occurring at 74% of ponds while American toads and American bullfrogs were detected at 48% and 47% of ponds, respectively. All three of these species regularly breed in permanent waterbodies and are generally unpalatable to predatory fish (Kats et al. 1988). These three species are also generally tolerant to stormwater pollutants unlike some of the more uncommon taxa we observed (Collins and Russell 2009; Gallagher et al. 2014; Matlaga et al. 2014; Green et al. 2019). Despite being well adapted to the urban environment, we found that green frogs and American bullfrogs are more common at ponds surrounded by wetlands and negatively impacted by impervious surface cover (Fig. S1). Upland species however, all which overwinter in terrestrial habitats, were associated with forest cover, reflecting taxon-specific differences in surrounding habitat needs.

Most species were detected at less than a third of ponds, including Northern leopard frogs, grey tree frogs, boreal chorus frogs, Eastern tiger salamanders, spring peepers, and Eastern newts. For many of these species, roads and habitat fragmentation may be major barriers preventing them from establishing in urban ponds (Ashley and Robinson 1996; Becker et al. 2007). In fact, all of these species use upland habitats for hibernation and/or foraging (Knutson et al. 1999). Further, Eastern newt efts, grey tree frogs, boreal chorus frogs, and spring peepers hibernate in forests, which are very limited in urban areas (Knutson et al. 1999; Becker et al. 2007). Some of these species (i.e. chorus frogs, spring peepers, and grey tree frogs) primarily breed in ephemeral ponds and may be far more abundant in ephemeral urban water bodies than in the largely permanent ponds that were the focus of our surveys (Knutson et al. 1999). Additionally, we did not conduct nocturnal call surveys, nor did we conduct call surveys in the spring, which may have limited our ability to detect nocturnal calling species, such as spring peepers and grey tree frogs, and early spring breeders including spring peepers and boreal chorus frogs.

While altering the characteristics of urban ponds to meet conservation needs may be challenging, conservation plans can take advantage of the existing variation in urban ponds and focus on management that can be easily adapted. For example, the terrestrial landscapes surrounding greenspace and golf course ponds are often more complex than urban retention ponds located along highways or in housing developments and may already be suitable for amphibian populations. However, greenspace ponds with high levels of stormwater input may negatively impact amphibian populations by acting as ecological traps (Sievers et al. 2018). In this scenario, adult amphibians preferentially colonize highly polluted greenspace ponds over ponds with higher water quality because they are attracted to the relatively high-quality landscape cues resulting in very low to no breeding success (due to predatory fish, pollutants, or hydroperiod; Sievers et al. 2018). Less suitable greenspace ponds may be improved by reducing inputs of stormwater pollutants via green infrastructure that increase water absorption on surfaces that would typically be impervious (e.g. bioretention, porous pavement, green roofs, etc.; Chen et al. 2019). Similarly, golf courses often use large amounts of fertilizer which may promote eutrophic conditions that lead to mass larval mortality (Baris et al. 2010; Clevenot et al. 2018). While amphibians do colonize urban ponds, environmental filters likely prevent many species from persisting and increasing species diversity. Understanding which environmental factors prevent species from persisting and diversifying in urban habitats and managing these limiting factors will be key in managing urban habitats for wildlife.

Declarations

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