Habitat value of cities and rice paddies for amphibians in rapidly urbanizing Vietnam

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Abstract

The lowlands of Southeast Asia are rich in biodiversity and many are being drastically altered through rapid urbanization. There are few remaining pristine ecosystems to support amphibian species that depend on these lowlands, and human-dominated landscapes contain an increasing proportion of potential habitats. We studied amphibian communities and associated habitat characteristics of water bodies in three land-use types (urban, suburban, and rice paddy) in each of three large metropolitan areas (Hanoi, Da Nang, and Ho Chi Minh City). Each of the 12 amphibian species documented was found in all three land-use types. Although all species were present in urban habitats, their occurrence, alpha diversity, and abundance were lower there compared with suburban areas or rice paddies. Individual species showed differential responses to habitat characteristics, and species richness was positively associated with presence of aquatic vegetation, presence of shallow areas, amount of surrounding vegetated uplands, and banks constructed of soil rather than concrete or rock. Urbanization tended to decrease all of these associated features. During the 10 months of this study, at least 14% of the surveyed urban and suburban water bodies were altered in ways that greatly or entirely reduced amphibian breeding. However, simple habitat enhancements could be beneficial; half of the species we found bred in concrete fountains that included potted ornamental plants and that were located in manicured parks in the center of Ho Chi Minh City. Although continued urbanization threatens native amphibians, cities are able to support many species where key habitat features are present.

Key words: anuran, novel habitat, Asia, tropics, aquatic

Introduction

Urbanization threatens many species globally and the potential threat is elevated in regions where high biodiversity is paired with rapid urban growth rates (McDonald et al. 2008; Seto et al. 2012). Studies of urban biodiversity have largely focused on terrestrial species in Europe, North America, and Australia (Magle et al. 2012; McDonnell 2015). This study investigates aquatic habitat use by amphibians in human-dominated landscapes in Southeast Asia. By comparing results to studies from other urban-influenced ecosystems, we aim to broaden the growing field of urban ecology and to uncover patterns that can inform the design and management of urban areas throughout the world to support diverse aquatic communities.

The lowlands of Southeast Asia contain many water bodies that represent potential habitats for aquatic species, but few are
removed from the influence of human activities. The rice paddies, urban lakes, fish ponds, and ornamental fountains in these human-dominated landscapes thus represent a large amount of the potential habitat for the aquatic species that depend on lowland habitats, and understanding species’ use of these altered landscapes can be an important tool for conservation (Rosenzweig 2003; Sodhi et al. 2010).

Aquatic freshwater organisms are often disproportionately affected by urban growth because the productive lowland habitats they depend on are also desirable for human settlement (Huston 1993; Mitsch and Gosselink 2007; Kontgis et al. 2014). In particular, amphibians are experiencing drastic global declines, and urbanization has been identified as one of the leading stressors (Stuart et al. 2004; Cushman 2006). Recent studies have shown that urban areas have the potential to either exclude amphibians or to allow their persistence, depending on design and management (reviewed in Hamer and McDonnell 2008; Scheffers and Paszkowski 2012). The freshwater habitats used by amphibians do not always resemble habitat that was present before urbanization, and amphibians have been shown to use various human-constructed water bodies when certain habitat or landscape features were present (Simon et al. 2008; Hamer et al. 2011; Holzer 2014). Identification of key features that allow population persistence can advance understanding of amphibian ecology and aid management efforts to promote their persistence.

Many studies of urban wildlife habitat compare cites to relatively pristine reference sites, but the reality is that urbanization often influences areas that are already dominated by human activities (McClurey 2010; Shochat et al. 2010). Agriculture is particularly common surrounding cities because humans often build settlements in flat, productive areas with access to fresh water, and which are also attractive for growing food (Huston 1993; Mitsch and Gosselink 2007). Rice paddies are often the most abundant wetland type in many tropical and subtropical countries (Aselmann and Crutzen 1989) and have been shown to support amphibians in some systems (e.g. Machado and Malchik 2010; Naito et al. 2013), but their potential as amphibian habitat has rarely been explored. Urbanization of rice paddy areas in Japan have been shown to reduce amphibian populations (Tsujii et al. 2011). Wildlife use of suburbs between the urban centers and rural expanses has also been given little attention although human population growth in these areas is increasingly common in Southeast Asia and elsewhere (Webster 2002; Simon 2008; Magle et al. 2012).

Urban areas throughout the world are growing rapidly from both human population expansion and migration from the countryside, and this is especially true in Southeast Asia; the human population of the largest metropolitan area in Vietnam grew by over 40% from 1990 to 2012, and the urban land area grew almost 400% in that same period (Kontgis et al. 2014). This growth is leading to both intensification of in-filling of urban centers and sprawling growth at the edges (Webster 2002). Although the current changes are rapid, many of Southeast Asia’s large cities have had continuous human settlement for hundreds of years; for instance, Hanoi, Vietnam recently celebrated its 1000th anniversary as a provincial capital. The biological communities that currently occur in cities have thus had centuries to adjust to these altered environments, allowing a unique opportunity for studying urban ecosystems. Their continued persistence relies on contemporary urban growth practices continuing to provide suitable habitat.

Where wildlife is able to persist in cities, understanding patterns of use in relation to habitat characteristics can allow for informed management decisions to maintain and improve coexistence with humans (Rosenzweig 2003). Amphibians are affected by a variety of local and landscape-level factors in urban areas (Hamer and McDonnell 2008). Physical attributes, such as water body size, slope of edge, and presence of shallows, can affect ability of amphibians to gain resources, maintain beneficial metabolic rates, and move in and out of water bodies (Stebbins and Cohen 1995; Babbitt 2005). Biological aspects of water bodies, such as water-pervious banks and aquatic vegetation, can benefit amphibians by providing oviposition structure, substrate for periphyton growth for grazing larvae, support for calling males, and refuge from predators (Stebbins and Cohen 1995; Tarr and Babbitt 2002; Hamer and McDonnell 2008; Holzer and Lawler 2015). Landscape-level factors, such as the amount of accessible and vegetated upland habitat, can influence persistence by providing non-breeding habitat and connection to other breeding populations (Hamer and McDonnell 2008; Seary and Shaffer 2011; McCarthy and Lathrop 2011).

In this study we examined patterns of amphibian diversity in large, long-standing urban centers, rapidly-expanding suburbs, and surrounding agricultural areas throughout Vietnam. Our goals were to determine how amphibian species richness, diversity, occupancy, and abundance differed among these land-use types, and to investigate which habitat features were most associated with amphibian use of water bodies in these human-dominated landscapes.

We predicted that in urban areas we would find fewer species of amphibians than in surrounding areas due to habitat fragmentation and alteration (Cushman 2006; Gardner et al. 2007; Hamer and McDonnell 2008). We also predicted increased abundance of a subset of species in urban habitats because of reduced interspecific competition and because we predicted available habitats to be relatively homogenous in urban areas and thus beneficial for those species that prefer those particular habitats (McKinney 2006; McClurey 2010; Shochat et al. 2010). We predicted that the habitat features most strongly associated with amphibian richness would be aquatic vegetation and surrounding vegetated uplands because of the numerous benefits already described, plus strong associations with these factors in other urban systems (Hamer and McDonnell 2008). We also predicted that individual species would have differential associations to habitat characteristics due to differences in the individual habitat needs of each species. By examining patterns of distribution and key features associated with amphibian presence in and around large, old cities, we can inform the process of designing and maintaining urban areas that are both livable for people and rich in biodiversity.

**Methods**

**Study sites**

Vietnam is a narrow country spanning 16 degrees of latitude, with marked climatic differences from north to south, and with major cities occurring in the lowlands. To capture the breadth of diversity of Vietnamese lowland climates we surveyed three of the largest cities in Vietnam: Hanoi in the north, Da Nang on the central coast, and Ho Chi Minh City (formerly Saigon) in the south. Hanoi (~7 million people) is 600 km north of Da Nang (~1 million people), which is 600 km north of Ho Chi Minh City (~8 million people). Hanoi exhibits a humid subtropical climate with hot, humid summers and relatively cool, dry winters; Da Nang has a tropical monsoon climate with warm, dry summers and warm, wet winters; Ho Chi Minh City exhibits a tropical savanna climate with hot, rainy summers and warm, dry winters.
All rice paddies surveyed were within 50 km of the urban core. As far apart as feasible to obtain 20 sites that were few roads; we therefore selected rice paddy sampling locations. The dominant types of lowland land use: dense urban cores (hereafter: urban), expanding boundary areas with mixed land-cover types (hereafter: suburban), and active rice cultivation fields (hereafter: rice paddies). The urban and suburban areas of a city along with the surrounding rice paddies will hereafter be referred to as a metropolitan area. We used the proportion of water-impervious surface in a 500 m radius of a site to distinguish between urban and suburban land-use types: those with >80% of land covered by impervious surfaces were considered urban (mean = 95%, range: 80–99%) while those with ≤70% were considered suburban (mean = 48%, range: 4–70%). Water-impervious surfaces included vegetation and bare soil while water impervious surfaces included concrete, stone, brick, and asphalt. We selected 20 representative water bodies for each of the three land-use types in each of the three regions for a total of 180 water bodies (Fig. 1). Because there were >20 water bodies of each land-use type in each metropolitan area, we used a stratified random sampling design to select study sites among these water bodies in order to maintain the relative distribution of water bodies with soil vs. constructed banks and presence/absence of aquatic vegetation for that metropolitan area. To do this we first visited each known water body in the study areas to classify habitat characteristics; we then used these characteristics to select a random subsample within bank types and vegetation presence/absence, at which we conducted amphibian surveys. All urban and suburban water bodies were separated from each other by at least one paved road >3 m wide. Rice paddies were often relatively contiguous across the landscape with few roads; we therefore selected rice paddy sampling locations as far apart as feasible to obtain 20 sites that were >1 km apart. All rice paddies surveyed were within 50 km of the urban core.

**Habitat characteristics**

We characterized five local habitat features and one landscape feature for each water body: size, presence of aquatic vegetation, type of bank, slope of bank, presence of shallows, and amount of surrounding vegetated upland habitat. Other habitat characteristics, such as water chemistry and fish presence, likely influence amphibian communities, but we were unable to measure them because we were not permitted to enter a large portion of the water bodies that lay in restricted areas such as airports, construction zones, and military sites. We were only permitted to observe from the edge of the water at such sites. To identify possible impacts of development in this rapidly changing landscape, we returned to each water body within 6 months of the amphibian surveys and noted if any of the habitat characteristics had been altered.

The size of water bodies was estimated in the field and verified with satellite images; because the sizes varied throughout seasons, we classified water bodies into five log-scaled size categories: <100 m², 100–999 m², 1000–9999 m², 10,000–99,999 m², or ≥ 100,000 m². We assessed rooted aquatic vegetation as being present or absent. We classified the bank type as either soil or as water-impervious, and described the slope of the bank as being either vertical (>85°) or sloped (≤85°). We visually estimated the presence of shallows in water bodies as at least 10 m² being <20 cm deep. We chose this size based on preliminary observations of where we observed tadpoles basking, and the measure included artificial shallows that were created by crumbling walls or debris. We used satellite images to quantify surrounding upland habitat by measuring the amount of water-impervious surface before encountering a water-impervious surface in all directions. This measure was log-transformed to meet normality assumptions.

**Amphibian surveys**

We used call surveys to determine anuran presence at each site. We focused on anurans because males of all frog species known to the lowlands of Vietnam produce identifiable calls, there are no known salamanders in these areas, and caecilians are rare and difficult to detect. We conducted call surveys on rainy nights in 2011–2 during the anuran breeding season for each metropolitan area: September–November 2011 for Da Nang, March–May 2012 for Hanoi, and May–June 2012 for Ho Chi Minh City.

We surveyed each water body three times at least one week apart. A survey consisted of standing quietly at the edge of the water body for 5 min and noting the presence and relative
abundance of all frog species calling. We noted abundance of each species as low (1–2 individuals), medium (3–8 individuals), or high (>8 individuals) by counting the number of distinguishable calls. For each species, the maximum abundance observed during the three surveys was used as the sample from that site. We conducted all surveys between half an hour after sunset and 1:00 am (Weir and Mossman 2005). Because of the spatial arrangement of rice paddies, it was infeasible to sample them in a random order. However, we did not sample adjacent sites on the same night and we reversed the order in which we visited paddies after each survey. To reduce observer bias, K.A.H. and R.P.B. were present for all surveys and reached consensus for the presence and abundance of species at each site during each survey (Lotz and Allen 2007). We calculated detection probabilities of each species using the program PRESENCE (Mackenzie et al. 2002).

Statistical analyses

We employed generalized linear models (GLMs, Guisan et al. 2002) to determine if amphibian occupancy and alpha, beta, and gamma diversity were associated with metropolitan area or land-use type. For this analysis we considered nine data points: one for each land-use type in each metropolitan region each with 20 sub-samples. We used the gamma family with inverse link for these models and conducted likelihood ratio tests to determine if predictor variables significantly improved the models. We determined significance level for multiple comparisons within each hypothesis family via the sequential Holm–Bonferroni correction, where the most significant result is compared against \( s/n \) (where \( n \) = the number of comparisons), then the next significant compared with \( s/(n-1) \), and so on until a non-significant result is encountered (Holm 1979). We used a significance level of \( z = 0.05 \). For significant variables we ran Tukey’s Honestly Significant Differences tests (Tukey’s HSD) to determine which categories within the variables differed.

To determine if habitat factors differed by region or land-use type, we examined another set of GLMs. For these models we considered each of the 180 sites as a data point. We used the gamma family with inverse link for size and amount of surrounding upland habitat, and the binomial family with the logit link for presence of aquatic vegetation, material of side construction (coded as zero for constructed, one for natural), presence of shallows, and slope (zero for slope \( <85^\circ \), one for slope \( >85^\circ \)). We conducted likelihood ratio tests to determine if predictor variables significantly improved the models. We used sequential Holm–Bonferroni corrections for significance at \( z = 0.05 \). For significant variables we ran Tukey’s HSDs to determine which levels of the variables differed.

To determine which habitat characteristics were associated with amphibian richness and presence of individual species, we conducted model selection of generalized linear mixed models (GLMMs, Bolker et al. 2009) on the 180 site-scale data points. Our response variables were species richness, for which we used the Poisson family with the log link, and presence/absence of individual species, for which we used the binomial family with the logit link. In order to produce models with reasonable explanatory power, we only assessed individual species presence/absence for species that were detected at 30–75% of sites. Our fixed factors were the six measured habitat characteristics, and our random factors were metropolitan area and land-use type. Our candidate model sets included all possible additive combinations of the fixed factors and always included both of the random factors. We examined predictor variables for intercorrelation, and for any pairs of variables with correlation \( r > 0.4 \) we only included the most biologically relevant variable in a model. We used AICc values to evaluate the best models (Yamashita and Kamimura 2007). We checked for overdispersion by comparing the residual deviance to the residual degrees of freedom. For overdispersed models where the response variable was not zero-inflated we included observation number as a random factor to reduce model bias (Harrison 2014). We examined possible spatial autocorrelation of amphibian richness models with spline correlograms by plotting the correlation of residuals of the top model against the spatial separation of sites based on latitude and longitude (Fortin and Dale 2005). We chose this method of examining spatial autocorrelation because there were many more sites in our landscapes than we measured in our surveys, and therefore we did not have accurate information to determine the distance to nearest site.

To examine similarities in community composition among metropolitan areas and land-use types, we ran non-metric multi-dimensional scaling analyses (NMDS) for nine data points: one for each land-use type in each metropolitan area. For this analysis we evaluated two dimensions and used the distance matrix of the relative abundance of each species. The stress of NMDS analyses (the square root of the ratio of the squared differences between a monotonic transformation of the calculated dissimilarities and the plotted distances and the sum of the plotted distances squared) gives a measure of ability of the plot to represent the variation in the observed distances.

All analyses were conducted in R Version 3.0.1 with the lme4, MASS, multcomp, and ncf packages (R Core Development Team 2008).

Results

Amphibian communities

We detected 12 species of amphibians (Table 1); all 12 species were found in each of the three land-use types (urban, suburban, and rice paddy). A given metropolitan area contained seven to nine species. All of these species are native to the region and belong to eight genera and five families (Table 1).

There was a wide range of detection probabilities among species from 0.17 in Kalula pulchra to 0.99 in Hylarana guentheri (Table 1). The detection probabilities indicate that we likely detected at least 90% of the occurrences for the majority of the 12 species, but we may have missed up to half of the occurrences of three rarer species. Because of the very low detection probability of K. pulchra, which we only observed on nights with monsoon rain, we removed occurrences of this species from the calculation of species richness for GLMM analyses. Although we considered the common treefrog (Polypedates leucomystax) as one species, it is now recognized as a species complex, and individuals surveyed likely consisted of two species Polypedates megacephalus and Polypedates mutus (Kuraishi et al. 2013).

Total species richness (gamma diversity) did not differ among land-use types, but Hanoi had lower overall richness than Da Nang or Ho Chi Minh City (Table 2, Fig. 2). Average species richness per site (alpha diversity) was lower in urban areas than in suburban areas or rice paddies (Table 2, Fig. 2). Species turnover (beta diversity) was higher in urban areas than in suburban areas or rice paddies (Table 2, Fig. 2). Neither alpha nor beta diversity differed among metropolitan regions (Table 2, Fig. 2).

The occupancy of water bodies (at least one calling amphibian present) was lower in urban areas than in the other two land-use types, and did not differ among metropolitan areas...
Across all metropolitan areas, we detected at least one calling amphibian in all surveyed rice paddies, in 91% of suburban water bodies, and in 62% of urban water bodies. Abundance of each species peaked either in rice paddies (eight species, Table 1) or in suburban water bodies (four species). No species was most abundant in urban areas. The species that were most abundant in rice paddies were from the families Bufonidae (one species), Dicroglossidae (five species), and Ranidae (two species). The species that were most abundant in suburban areas were from the families Microhylidae (three species) and Rhacophoridae (one species). Focusing on the species that were more abundant in suburban areas, all of the egg masses and tadpoles of the Microhylidae we observed were found in small, intermittent water bodies (supplementary material: S1). The Rhacophoridae species (P. leucomystax) laid egg foams on the vertical sides of concrete fountains or on sturdy stems of vegetation (S2), and were also often detected calling in large-stemmed plants at the edges of rice paddies and their associated ditches.

Community composition clustered both by metropolitan region and by land-use type (Fig. 3; NMDS stress = 0.061). Our stress value of 0.061 for two dimensions is generally interpreted as a fair or good representation of the variation. Community composition was explained by both region ($F_{2,4} = 4.01, P < 0.001$) and land-use type ($F_{2,4} = 3.60, P < 0.001$). Species identity was often associated with region while relative occupancy of species was influenced more by land-use type (Table 1, Fig. 2).

**Habitat characteristics**

Rice paddies were larger than suburban or urban water bodies (Table 2). Rice paddies had more surrounding upland vegetation than suburban water bodies, which had more than urban water bodies (Table 2). All other habitat characteristics (slope, edge material, presence of shallows, and presence of aquatic vegetation) did not differ between rice paddies and suburban water bodies, but were different for urban water bodies compared with the other two land-use types where urban water bodies had steeper sides, fewer shallows, fewer natural banks, and less aquatic vegetation than suburban water bodies or rice paddies (Table 2). None of the habitat characteristics differed among metropolitan areas (Table 2). Habitat characteristics changed for several urban and suburban water bodies between the commencement of amphibian surveys and up to 6 months after the surveys. Of the 120 urban and suburban study water bodies, at least three had soil banks that were converted to constructed banks, at least seven were drained, and at least seven more were filled in and built over (S6).

**Table 1:** Location and most common land-use types for frog species recorded during surveys

| Family          | Species (descriptor, description date) | Detection probability | Presence* | Land-use type where species was most abundant (# of sites of that land use where species was present out of 60 possible) |
|-----------------|----------------------------------------|-----------------------|-----------|-----------------------------------------------------------------|
| Bufonidae       | Duttaphrynus melanostictus (Schneider, 1799) | 0.75                  |           | Rice paddy (26)                                                 |
| Microhylidae    | Kaloula pulchra (Gray, 1831)           | 0.17                  |           | Suburban (13)                                                   |
|                 | Microhyla butleri (Boulenger 1900)     | 0.90                  |           | Suburban (7)                                                    |
|                 | Microhyla fassipes (Boulenger, 1884)   | 0.86                  |           | Suburban (28)                                                  |
| Dicroglossidae  | Fejervarya limnocharis (Gravenhorst, 1829) | 0.90                  |           | Rice paddy (58)                                                 |
|                 | Hoplobatrachus rugulosus (Wiegmann, 1834) | 0.47                  |           | Rice paddy (27)                                                 |
|                 | Occidozyga lima (Gravenhorst, 1829)    | 0.98                  |           | Rice paddy (44)                                                 |
|                 | Occidozyga martensii (Peter, 1867)     | 0.98                  |           | Rice paddy (21)                                                 |
|                 | Occidozyga viitata (Andersson, 1942)   | 0.98                  |           | Rice paddy (20)                                                 |
| Ranidae         | Hylarana guentheri (Boulenger, 1882)   | 0.99                  |           | Rice paddy (31)                                                 |
|                 | Hylarana taipehensis (Van Denburgh, 1909) | 0.64                  |           | Rice paddy (9)                                                  |
| Rhacophoridae   | Polypedates leucomystax complex (Gravenhorst, 1829) | 0.92                  |           | Suburban (46)                                                   |

*Location of species detection: grey boxes indicate presence while white boxes represent absence. Rows are metropolitan areas, from top to bottom: H-Hanoi, D-Da Nang, C-Ho Chi Minh City; columns are land-use types, from left to right: U-urban, S-Suburban, R-rice paddies.
The size of 1 ha was chosen as a point for upland habitat because it represents the comparison point for upland habitat as it is the exception in that they were also associated with aquatic vegetation, and with shallow areas. Paddy frogs were associated with water bodies with aquatic vegetation, and with shallow areas. Toads were associated with water bodies with shallow areas, without vertical sides, with aquatic vegetation, and with shallow areas. Paddy frogs were associated with water bodies with shallow areas, without vertical sides, with aquatic vegetation, and with shallow areas. Guenther’s frogs were associated with water bodies with aquatic vegetation and natural banks. Treefrogs were associated with water bodies with aquatic vegetation, natural banks, and were the exception in that they were also associated with

| Test | Statistic | P-value and significance level |
|------|-----------|--------------------------------|
| GLM: Bank type | Metropolitan area | $X^2 = 1.40$ | $P = 0.4965$ |
| Land-use type | $X^2 = 86.93$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = -6.28$ | $P_{adj} < 0.0001$*** |
| Urban–rice | $z = 4.86$ | $P_{adj} < 0.0001$*** |
| Suburban–rice | $z = 2.06$ | $P_{adj} = 0.0909$ |
| GLM: Bank slope | Metropolitan area | $X^2 = 1.52$ | $P = 0.4683$ |
| Land-use type | $X^2 = 55.97$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = 4.61$ | $P_{adj} < 0.0001$*** |
| Urban–rice | $z = 3.80$ | $P_{adj} = 0.0004$*** |
| Suburban–rice | $z = 0.31$ | $P_{adj} = 0.9450$ |

Amphibian species richness was best explained by the preservation of aquatic vegetation, presence of shallows, the amount of surrounding vegetated upland habitat, and natural banks (S3). The top two models had similar AICc values; all other models had delta AICc $> 1.75$. The top model included presence of aquatic vegetation, amount of surrounding habitat, and presence of shallows ($r^2 = 0.45$); the second-best model contained all of these factors as well as natural banks ($r^2 = 0.44$). The size of water bodies and slope of the sides did not substantially explain species richness. No factors were intercorrelated with each pair having a correlation of $r < 0.4$. Richness was on average about five times higher in water bodies with aquatic vegetation than in those without, four times as high in those with shallows as those without, three times higher in those with $> 1$ ha of surrounding vegetated upland habitat than those with less, and three times higher in those with natural banks than those with constructed banks (Table 3). The size of 1 ha was chosen as a comparison point for upland habitat because it represents the major inflection point in the data. We did not find evidence of spatial autocorrelation among sites (S4) and the response variable was not zero inflated. We included individual observation number as a random factor in richness models because the models were overdispersed (Harrison 2014).

We evaluated habitat characteristic associations for the four species which were present in sufficient proportion of survey sites: Duttaphrynus melanostictus (toads), Fejervarya limnocharis (paddy frogs), H. guentheri (Guenther’s frogs), and P. leucomystax (treefrogs). Habitat associations were generally in the same direction as in species richness models, although the relative strength of association varied greatly among species (S3). Toads were associated with water bodies without vertical sides, with aquatic vegetation, and with shallow areas. Paddy frogs were associated with water bodies with shallow areas, without vertical sides, with natural banks, and with aquatic vegetation. Guenther’s frogs were associated with water bodies with aquatic vegetation and natural banks. Treefrogs were associated with water bodies with aquatic vegetation, natural banks, and were the exception in that they were also associated with

Table 2: Statistical results for amphibian communities and habitat features across land-use types and metropolitan areas. We present likelihood ratio tests on generalized linear models (GLM). For significant factors we present Tukey’s honestly significant difference tests (HSD). For HSD statistics, the $P_{adj}$ is directly compared to $x$. For GLM likelihood ratio tests, $z$ is compared to $P/n$ for the most significant result, to $P/(n-1)$ for the next most significant result, and so on until a non-significant result is encountered where $n$ is the number of tests being compared (4 for amphibian community diversity and 6 for habitat characteristics). Asterisks indicate significance levels for the following: * for $x = 0.05$, ** for $x = 0.01$, *** for $x = 0.001$.

| Test | Statistic | P-value and significance level |
|------|-----------|--------------------------------|
| GLM: Gamma diversity | Metropolitan area | $X^2 = 11.88$ | $P = 0.0026$* |
| Land-use type | $X^2 = 3.95$ | $P = 0.1387$ |
| HSD: | Hanoi–Da Nang | $z = 3.05$ | $P_{adj} = 0.0070$** |
| Hanoi–Ho Chi Minh City | $z = -2.76$ | $P_{adj} = 0.0155$* |
| Da Nang–Ho Chi Minh City | $z = 0.29$ | $P_{adj} = 0.9545$ |
| GLM: Beta diversity | Metropolitan area | $X^2 = 0.63$ | $P = 0.7281$ |
| Land-use type | $X^2 = 21.67$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = 3.09$ | $P_{adj} = 0.0049$** |
| Urban–rice | $z = 3.72$ | $P_{adj} < 0.0001$*** |
| Suburban–rice | $z = 1.00$ | $P_{adj} = 0.5665$ |
| GLM: Occupancy | Metropolitan area | $X^2 = 3.84$ | $P = 0.1466$ |
| Land-use type | $X^2 = 36.02$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = -3.96$ | $P_{adj} < 0.0001$*** |
| Urban–rice | $z = -5.13$ | $P_{adj} < 0.0001$*** |
| Suburban–rice | $z = -1.60$ | $P_{adj} = 0.2387$ |
| GLM: Upland vegetation | Metropolitan area | $X^2 = 1.10$ | $P = 0.5763$ |
| Land-use type | $X^2 = 65.88$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = 5.48$ | $P_{adj} < 0.0001$*** |
| Urban–rice | $z = 8.07$ | $P_{adj} < 0.0001$*** |
| Suburban–rice | $z = 6.16$ | $P_{adj} < 0.0001$*** |
| GLM: Shallows | Metropolitan area | $X^2 = 1.27$ | $P = 0.5290$ |
| Land-use type | $X^2 = 57.98$ | $P < 0.0001$*** |
| HSD: | Urban–suburban | $z = -4.91$ | $P_{adj} < 0.0001$*** |
| Urban–rice | $z = -4.08$ | $P_{adj} < 0.0001$*** |
| Suburban–rice | $z = -0.40$ | $P_{adj} = 0.9145$ |
The most surprising result was that all 12 species of amphibians detected were present in all three land-use types: rice paddies, growing suburban areas, and dense urban cores. We had expected that some species would be absent from urban areas (reduced gamma diversity) because of habitat degradation and fragmentation. Our result is unlikely to be a fleeting artifact of extinction debt (sensu Tilman et al. 1994) because two of the three cities are large (~7 million people) and hundreds to thousands of years old, and rice cultivation has dominated the surrounding landscape for hundreds to thousands of years (Hanks 1972). However, extinction debt in the urban core cannot be entirely ruled out because suburban areas are expanding dramatically, possibly isolating urban cores from surrounding rice paddies which may be providing important source populations. Nevertheless, the presence of a variety of amphibian species across these landscapes is likely related to land-use practices that make the areas relatively hospitable for some amphibian species.

It is likely that amphibian species richness and diversity were much higher when natural areas were common, but unfortunately, we could not provide a comparison of these human-dominated landscapes to pristine lowland landscapes near these cities because of the rarity of the latter. Contemporary studies of relatively pristine areas in other lowland areas in Southeast Asia as well as historical surveys in this region have indicated that 16–42 amphibian species may have formerly been present (Nguyen et al. 2009; Das and Dijk 2013). All 12 species detected during this study are considered to be relatively tolerant of human disturbance (Nguyen et al. 2009).

Urban growth in Southeast Asia has often retained or incorporated a variety of water bodies (Mitsch and Gosselink 2007). This is different than general practices in the global West of filling wetlands during urban growth and occasionally constructing other wetlands in some form later (Mitsch and Gosselink 2007). All three cities in this study contained over 100 water bodies including urban lakes surrounded by cafes, large vegetated wet fields to capture storm water, ornamental fountains in urban parks, large ponds for fish rearing, and spiritual pools in temples. Amphibians were found in each of these water body types when appropriate habitat characteristics were present. This form of growth that incorporates water bodies likely increases amphibian presence.

Discussion

Our results show that many lowland amphibian species in Vietnam can persist in water bodies in a variety of human land uses when certain local habitat and landscape features are present, such as aquatic vegetation, shallow, vegetated uplands, and soil banks. We found that at least one amphibian in the majority of water bodies in each land-use type (100% of rice paddies, 91% of suburban, and 62% of urban water bodies), demonstrating that these landscapes showed good potential for continued coexistence of these species with human activity.

Our results are consistent with other urban amphibian studies in showing that urban ecosystems often provided habitat for many amphibian species when certain local and landscape habitat factors are present (Hamer and McDonnell 2008; Scheffers and Paszkowski 2012). Similar to other studies, our results highlighted the importance of vegetation (both in and surrounding the water bodies) to amphibian communities in human-dominated ecosystems (Hamer and McDonnell 2008; Holzer 2014). In line with other studies, we did not find any individual amphibian species to be more abundant in urban areas than in the surrounding habitats (Hamer and McDonnell 2008). Our study shows that the urban amphibian populations of Southeast Asia likely follow the general patterns that have been found for amphibians in cities in Europe, North America, and Australia; however, we found that the cities of Southeast Asia may provide more opportunities for aquatic amphibian breeding as there were a large number of water bodies that were incorporated into urban growth.

Land use

The most surprising result was that all 12 species of amphibians detected were present in all three land-use types: rice paddies, small water bodies and vertical sides. The top model for toads had poor explanatory power ($r^2 = 0.07$), while the top model for the other species had moderate explanatory power (paddy frog: $r^2 = 0.38$, Guenther’s frog: $r^2 = 0.57$, treefrog: $r^2 = 0.35$).

Table 3: Habitat characteristics measured for water bodies in urban and suburban areas and their associations with amphibian richness

| Habitat characteristic | Description | Distribution$^a$ | Direction$^b$ | Effect size$^c$ |
|------------------------|-------------|------------------|--------------|----------------|
| Aquatic vegetation     | Rooted vegetation in the water body | Present: 151 Absent: 29 | + | 4.9 |
| Shallows               | At least 10 m² is > 20 cm in depth | Present: 159 Absent: 21 | + | 4.5 |
| Natural banks          | Sides of water body are natural (dirt substrate) vs. constructed (stone, brick, or concrete) | Natural: 135 Constructed: 45 | + | 2.9 |
| Surrounding vegetated upland habitat | Amount of pervious surface until an impervious surface is reached in all directions (hectares)$^d$ | Mean: 29.5 Median: 5.0 Range: 0–319 | + | 2.8 (at 1 ha cutoff) |
| Slope of edge          | Edge slope | $\leq 85^\circ$:156 $>85^\circ$:24 | ns | NA |
| Size                   | Average size during breeding season$^d$ | Mean: 61 945 m² Median: 5395 m³ Range: 0.6–120 785 m² | ns | NA |

$^a$For categorical features the number of water bodies (out of the total 180) in each category are listed. For continuous features, the mean, median, and range values are given.

$^b$The direction of association is for generalized linear mixed models where “ns” indicates non-significance.

$^c$The effect size is given as proportional change in species richness.

$^d$For urban and suburban water bodies only. Rice paddies were so large, connected, and far from impervious surfaces that exact numbers are difficult to calculate.
Rice paddies supported the greatest overall abundance of the taxa we found. Throughout the world, rice paddies are able to support diverse native aquatic wildlife communities under some management regimes, especially those without extreme hydrologic fluctuations and those with low or no pesticide use (Lawler 2001). Because rice paddies can mimic seasonal wetlands, their habitat value for preserving local species assemblages may be higher in areas that have been converted from seasonal wetlands than from other land cover, such as forest (Lawler 2001). Many Vietnamese lowland rice paddies replaced former seasonal wetlands and do not experience rapid fluctuations in hydrology, which likely benefits the native amphibians. Most amphibians were more abundant in rice paddies than in urban centers. This could be due to a species–area relationship (Gleason 1922) because rice paddy habitat and adjacent uplands are larger and more contiguous. While it is encouraging that several taxa are abundant in rice paddies, it is unclear whether these habitats are functioning optimally to support these and other aquatic taxa. Pesticides have been shown to cause numerous negative effects on amphibians throughout the world (reviewed in Mann et al. 2009; Bruhl et al. 2011), and specifically in rice paddies (Liu et al. 2011; Egea-Serrano et al. 2012). Pesticide use in rice paddies in Vietnam rose rapidly in the early 1990s, and although use has been drastically reduced through recent campaigns, it is currently practiced to some extent by the majority of rice farmers (Huan et al. 1999; Nguyen et al. 1999; Berg and Tam 2012). Therefore, current pesticide use is likely causing negative effects on amphibians in this system.

Not all species were most abundant in rice paddies: species of Microhylidae and Rhacophoridae were more abundant in suburban water bodies. For Microhylidae species this may be explained by preferences for small, intermittent water bodies which are rare in the large, semi-permanent rice fields. The pattern for the Rhacophoridae species (P. leucomystax) is likely related to oviposition above the water surface and the ability to utilize vertical surfaces by climbing with its sticky toe pads. P. leucomystax deposits large egg foams on vegetation or structures above the water (Yorke 1983). The stems of rice plants are likely not sturdy enough to support these egg foams, but fountain walls and ornamental plants are often used (S2). Our observations of this species in the edges and ditches of rice paddies indicate that it was using vegetation other than rice plants for oviposition. We observed adult P. leucomystax crawling on vertical structures throughout the city, including ascending buildings to breed in water bodies on upper levels (S5). We conclude that some amphibian species are better suited to water bodies in suburban landscapes that provide diverse habitat structures, rather than to the relatively homogeneous rice paddies.

Species turnover among sites (beta diversity) was higher in urban areas than in other land-use types, and fewer species on average were found at a given site (alpha diversity) in urban areas (one or two species per water body) than in suburban areas or rice paddies (three or four species per water body). A species–area relationship in breeding habitat is unlikely to explain the higher site richness in suburban vs. urban water bodies because there was no detectable difference in water body size; however, upland habitat surrounding water bodies was larger in suburban than urban sites (Table 2). Similarly, surrounding upland habitat contributed to explaining species richness while water body size was a poor predictor. The increased species turnover and reduced site richness in urban areas are likely related to landscape isolation by roads and buildings (Hamer and McDonnell 2008; Hale et al. 2012; Van Buskirk 2012).

Because of the dense infrastructure and age of the urban centers of two of the cities, it was surprising to find several kinds of amphibians persisting at sites in the urban core. Local populations have either persisted for decades or centuries as urbanization increased around them, or some individuals have been able to traverse the built landscapes of downtown Hanoi and Ho Chi Minh City. We observed frequent flooding of streets in all three cities which may have facilitated movement; individuals may also be released by people or inadvertently transported around cities in products such as produce or landscaping materials. We were not able to directly assess the relative importance of dispersal in this study, but ability of individuals to move through the landscape is likely important to site occupancy in urban settings. Studies examining movement or population genetics of amphibians among sites in urban areas are needed to better understand the role of fragmentation in species richness, composition, and abundances.

Although all species detected were found in urban cores, none were most abundant there, which is in contrast to patterns for birds and mammals (McKinney 2002; McCleery 2010; Shochat et al. 2010). We predicted higher abundance of some species due to reduced interspecific competition and favorable homogeneous habitats for a subset of species. However, any reduction in competition did not seem to increase abundance of any species, and habitat characteristics were not homogeneous as we saw the greatest differences in habitat characteristics among urban sites. Occupancy was also lower in urban areas than in the other two land-use types. Abundances for each species peaked in either rice paddies or suburban areas, and two species—Hoplobatrachus rugulosus and Hylarana taipehensis—are very rare in urban water bodies. Mechanisms that
exclude the possibility that some taxa bred outside of the sampling window for each region and hence, were not detected.

To sum overall patterns of landscape use, these urban amphibian communities of Vietnam diverged from general patterns for urban wildlife (mostly from studies of birds and mammals in Europe, North America, and Australia): they did not have reduced species richness, increased abundances of those species present, or homogenous communities (McKinney 2006; Aitkenhead-Peterson and Volder 2010). Our patterns of comparable richness with surrounding agricultural areas, low abundances in urban areas, and dissimilarity among cities are similar to those found by Herrmann et al. (2012) in parasitoid wasp species in cities throughout California, USA. Like amphibians, parasitoid wasps are relatively low-vigilant taxa that generally do not consume human-associated food. Additional studies of urban wildlife in under-studied systems could further elucidate natural history mechanisms that underlie how different taxonomic groups respond to urbanization.

**Habitat characteristics**

Both local and landscape-scale factors contributed to explaining amphibian distributions. Habitat characteristics that were positively related to amphibian richness—aquatic vegetation, shallow areas, surrounding upland habitat, and soil banks—were more common in rice paddies than in urban water bodies with suburban areas being intermediate (Table 2). However, many urban water bodies possessed these characteristics, and many of those supported native amphibians. Suburban water bodies were often more similar to rice paddies than to urban water bodies, even though they were often interspersed with more dense urban areas (Fig. 1 and Table 2). This suggests the importance of local habitat features over broad landscape characteristics.

Aquatic vegetation was associated with higher species richness, which is consistent with other studies of urban amphibians (Hamer and McDonnell 2008; Holzer 2014; Holzer and Lawler 2015). Even potted ornamental plants seemed to provide substantial benefits. For example, Tao Dan Park in the center of Ho Chi Minh City’s urban core contained several small, vertically-sided, concrete fountains that were accessible for thorough observation; those without any aquatic vegetation had zero or one species calling while those with potted lilies contained up to six species calling and in them we directly observed amplexing adults and egg masses, tadpoles, and metamorphs (Fig. 4a and b).

Amphibian richness was associated with water bodies that provided some shallow areas, likely because tadpoles benefit from the ability to bask (Stebbins and Cohen 1995). Some urban and suburban water bodies in Vietnam are deep and steep-sided such that there are no shallow areas, and these rarely supported amphibians. Even artificial shallows provided by plant pots, broken walls, or garbage were used by tadpoles for basking.

The amount of vegetated upland area surrounding a water body was positively associated with amphibian richness. We expected this because many species only come to water bodies to breed, and spend the majority of their adult lives in the surrounding terrestrial environment. This result is consistent with many other urban amphibian studies (Hamer and McDonnell 2008). What was surprising was that a prominent threshold occurred at only 1 ha of surrounding vegetated upland habitat, and that many parks and stormwater sites around this size contained several species. Although more upland habitat is...
generally better, it is encouraging that setting aside a relatively small amount of vegetated uplands may have a large benefit to amphibian communities.

Banks made of soil (rather than water-impervious material) were positively related to amphibians, which has been found in other systems (Fujioka and Lane 1997; Cornelis and Hermy 2004; Hou et al. 2010; Chang et al. 2011; Naito et al. 2012). There is a general construction trend in Southeast Asia of converting the banks of water bodies from soil to impervious surfaces, likely because of the perception that it promotes clean and modern city landscapes (Fig. 4c and d). When this occurred during our surveys we noticed a decline in amphibians in the affected water bodies. Ideally, this practice would be reversed. This observation could warrant a conservation-awareness campaign to city managers and the public, who may not be aware of the cost to wildlife of such conversions. Similarly, introduction of predatory fish may be detrimental to amphibian communities. Damage to amphibian communities could be lessened if rooted aquatic vegetation is provided, even if it is in the form of potted plants. Although these plants are not “natural,” they likely still benefit amphibians through providing substrate for oviposition and periphyton growth, increasing oxygen in the water, and/or providing refuge from predators (Stebbins and Cohen 1995). These features may also benefit other aquatic taxa, like dragonflies and damselflies which were abundant in many urban parks that contained vegetated water bodies (KH and RB personal observations).

Individual species showed differential responses to habitat features, and associations were generally in the same direction as for overall richness. All four individual species evaluated were positively associated with the presence of aquatic vegetation, which further supports the understanding that aquatic vegetation is important for amphibians in human-dominated landscapes. The slope of the edge was the strongest predictor for toad presence, which may be because this species has limited climbing and jumping ability compared with other anurans and steep sides may provide a movement barrier (Naito et al. 2012). The top model was a poor predictor of toad presence, which may be due to the chorusing habitats of this species which may produce congregations at only a subset of suitable sites (Stebbins and Cohen 1995). Large toad choruses were sometimes present in one water body when a seemingly very similar adjacent water body had no chorus (KH and RB personal observations). Treefrogs were unusual in that they were positively associated with vertical slopes (S3). This is likely because these edges provided substrate for attachment of their egg foams when sturdy emergent vegetation was not present (S3).

During the 10 months of our study, at least 14% of our urban and suburban survey sites were drastically altered in some way that likely greatly reduced or entirely eliminated amphibian breeding activity with at least 6% entirely filled in with buildings or roads built on top of them (Fig. 4c and 4d, S6). This rapid rate of alteration demonstrates that current habitat value of urban and suburban water bodies may quickly decrease depending on local planning and management.

To benefit amphibians in the vast and rapidly expanding urban areas of Southeast Asia, we recommend promoting the presence of aquatic vegetation, ensuring presence of shallows, allowing soil banks, and maintaining vegetated upland areas where possible.

**Conclusion**

Urban and agricultural areas should not be discounted from providing potential habitat for wildlife; with proper management they can help sustain some taxa that are losing habitat in more pristine areas (Rosenzweig 2003; McDonnell 2015). Our results indicate that landscapes of intense human use, including cities and rice paddies, can provide habitat for many amphibian species. However, the specific planning and management of these landscapes can have large impacts on habitat quality and use.

The lowlands of Vietnam are dominated by rice paddies and rapidly growing cities, and have likely lost many species that were not able to cope with these land-use changes. However, at least 12 amphibian species continue to breed in rice paddies, suburbs, and dense urban cores of the country’s largest cities. We identified several aspects of how amphibians use these human-dominated areas that can guide conservation and management for their continued coexistence.

Land management practices, such as maintaining diverse rice paddy ecosystems at urban margins and incorporating water bodies into urban growth, have likely contributed to amphibian use of these areas. Encouraging city planning that incorporates water bodies with aquatic vegetation, shallow areas, vegetated upland habitats, and soil banks could allow continued persistence of many species of native amphibians, and likely other aquatic taxa, in urban areas. However, some worrying trends—such as widespread pesticide use, rapid urban growth and infill that removes water bodies and green spaces, and conversion of soil to water-impervious banks—will decrease the suitability of these habitats for amphibians. Continuing to research the drivers of biodiversity in cities and rice paddies will allow planners and managers to develop policies and practices that promote human-wildlife coexistence in areas of intense human use.

**Data availability statement**

Data from this study will be available on Dryad.

**Supplementary data**

Supplementary data S1-S6, are available at JUECOL online.

**Conflict of interest statement.** None declared.

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