Landscape Ecol (2007) 22:205–215
DOI 10.1007/s10980-006-9012-3

RESEARCH ARTICLE

Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada

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Received: 1 November 2005 / Accepted: 30 April 2006 / Published online: 5 August 2006

Abstract Land cover change, predominantly habitat conversion to agricultural use and urbanization, has recently been recognized as the primary cause of biodiversity loss in terrestrial ecosystems. We evaluated the relative effects of urban and agricultural landscapes on anuran species richness and the abundance of six anuran species found at breeding ponds in and around the cities of Ottawa, Ontario and Gatineau, Quebec. We performed six call surveys at 29 permanent focal ponds surrounded by one of three landscape contexts: primarily urban, primarily agricultural, and primarily forested. We also measured three local pond variables to control for the effects of local habitat quality in our analyses. We found that anuran species richness was significantly lower in breeding ponds in urban landscapes compared to forested and agricultural landscapes, which exhibited no significant difference in species richness. The abundances of individual anuran species were also consistently lower in urban landscapes for all species except one, which exhibited no response to landscape type. Three species had their highest abundances in ponds in forested landscapes, whereas two species had their highest abundances in ponds in agricultural landscapes. We conclude that ponds embedded in urban landscapes support lower biodiversity than ponds in agricultural settings. We suggest that landscapes composed of a mosaic of forest and open habitats surrounding wetlands would hold the highest biodiversity of these species.

Keywords Land use · Urbanization · Agriculture · Forest cover · Amphibian conservation · Species richness · Abundance

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Introduction

Land cover change during the past 50 years is now recognized as the primary driver of biodiversity loss in terrestrial ecosystems (Millennium Ecosystem Assessment 2005). Worldwide, the dominant land cover change has been conversion of natural land cover to agricultural use, resulting in croplands and pastures now covering 40% of the Earth's land surface (Foley et al. 2005). In addition to this habitat loss, fertilizer and pesticide use on agricultural lands have been shown to affect biodiversity and the functioning of ecosystems (Benton et al. 2003).

Intensifying human land use is generally accompanied by urbanization, or the conversion of rural land use to urban land use (DeFries et al. 2004). In Canada, the total urbanized area almost doubled between 1971 and 1996 (Canadian Biodiversity Information Network 2004) and grew by nearly 50% between 1982 and 1997 in the United States (Platt 2004). Although urban areas only represent a small portion of the Earth's land surface (2%) (Grimm et al. 2000), the effects associated with urbanization are widespread. In the United States, urbanization has been cited as a major cause of more than half of threatened or endangered species declines (Czech et al. 2000). Much of the remaining natural habitat in the United States is likely affected by urbanization, either in the form of imminent suburban development or as adjacent ex-urban development, increasingly occurring on the boundaries of many important conservation sites and large reserves (Knight and Landres 1998). Direct and indirect effects of urbanization include habitat loss and fragmentation, disturbed and compacted soils, changes in disturbance regimes, introduction of exotic species, and increases in feral pets (Bradley 1995).

In light of the above trends and considering that one third of amphibian species are now thought to be globally threatened (Stuart et al. 2004), it is not surprising that researchers have begun studying the effects of urban and agricultural land use on amphibian species richness and abundance. In general, agricultural and urban land covers have been shown to negatively affect amphibian species richness (Richter and Azous 1995; Bonin et al. 1997; Knutson et al. 1999; Lehtinen et al. 1999; Atauri and de Lucio 2001). Only Knutson et al. (1999) have addressed the question of which land use, agriculture or urbanization, has the greater impact on amphibian species richness. Their results are difficult to interpret because they found a positive effect of agriculture on amphibian species richness, which is inconsistent with the other literature to date.

Patterns of amphibian occurrence and abundance in urban and agricultural areas have been less straightforward. The proportion of urban land cover in the surrounding landscape has been shown to have a negative effect on total or guild amphibian abundance (Mensing et al. 1998; Knutson et al. 1999). More recently, Riley et al. (2005) reported both positive and negative patterns of amphibian occurrence in natural and urban streams. With respect to agriculture, studies have reported negative effects on total amphibian abundance (Mensing et al. 1998), and both positive and negative effects on the occurrence and abundance of individual species and guilds (Knutson et al. 1999; Joly et al. 2001; Trenham et al. 2003; Gray et al. 2004; Weyrauch and Grubb 2004). So far only Johnson et al. (2002) and Gibbs et al. (2005) have investigated the occurrence of individual anuran species with respect to both urbanization and agriculture. However, no study has, as yet, directly compared the impact of these land uses on the abundance of individual amphibian species.

We evaluated the relative effects of urban and agricultural landscapes, as compared to landscapes dominated by forested habitat, on anuran species richness and the abundance of individual anuran species found at breeding ponds. Based on findings by previous authors (Knutson et al. 1999; Houlahan and Findlay 2003), we expected species richness to be lower in ponds situated in agricultural and urban landscapes compared to forested landscapes, with ponds in urban landscapes having the fewest anuran species. We also expected the responses of individual species to landscape type to vary according to their terrestrial habitat requirements. Species that prefer open terrestrial habitat should be most abundant in ponds in agricultural landscapes whereas those that rely on forest habitat should be more abundant in ponds in forested landscapes. However, we predicted that all anuran species would consistently exhibit the lowest abundance in ponds in urban landscapes.

Methods

Landscapes

We selected 29 landscapes in the National Capital Region (NCR), Canada (45°42′ N–75°71′ W; Fig. 1). Landscapes were situated in and surrounding the cities of Ottawa, Ontario and

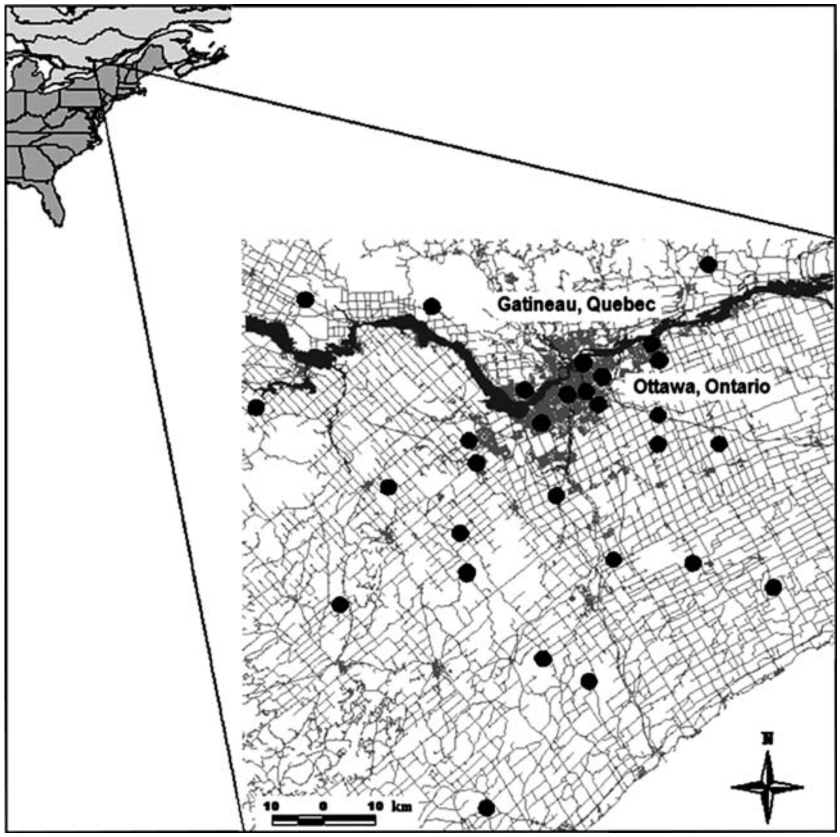


Fig. 1 The National Capital Region, Canada. Landscapes are black circles. Ponds sampled for anurans are at the centre of each landscape

Gatineau, Quebec over a total area of 12,200 km^2. We defined landscapes as the area within a 1.5 km radius of permanent focal ponds. Landscapes were non-overlapping. The scale used here reflects both the life history characteristics of the organisms under study and the hypotheses being tested. Dam (2005) tabulated the mean dispersal distances reported in the literature for several of the species included in this study. The largest values for each species ranged from 40 m for the gray treefrog (*Hyla versicolor*) to 2414 m for the northern leopard frog (*Rana pipens*). In addition, landscape variables have been shown to affect amphibian abundance and species richness at distances as great as 1.5 km (Carr and Fahrig 2001) and 3 km (Houlahan and Findlay 2003), respectively. We chose a 1.5 km radius to correspond to these movement and effect distances, and to maximize the number of available sites, considering the other criteria used for site selection in this study (see below).

We chose landscapes to represent one of three types: urban (>50% urban land cover; 10 landscapes), agricultural (>70% open land cover; 10 landscapes), and forested (>50% forested land cover; 9 landscapes). Although some amphibian species have been found to exhibit a threshold response to urbanization at lower proportions of the landscape [8% (Riley et al. 2005), 20% (Wilson and Dorcas 2003)], our goal was to investigate the maximum effects of urbanization and agriculture, by defining landscape types using the maximum possible proportion of each land cover, as determined by the distribution of each land cover in the NCR with respect to potential pond sites. We identified potential sites using 1:50,000 topographic maps (produced by the Centre for Topographic Information, Natural Resources Canada) and chose focal ponds based on the surrounding landscape composition, distance to the next surveyed pond (≥3 km), permanence, accessibility and landowner permission.

We determined urban land cover amounts by digitizing the most recent aerial photos available (1:15,000, City of Ottawa, 2002). We included residential, commercial and industrial land uses in the urban land cover class. We derived forested and open land cover amounts from 1:50,000 National Topographic Database (NTDB) digital maps (Edition 3.1, produced by the Centre for Topographic Information, Natural Resources Canada). Less than a 2% difference has been reported between forested land cover amounts digitized from the 2002 aerial photos above and the NTDB maps (Dam 2005). The forested land cover class included all types of forested habitat (deciduous, coniferous, and mixed). The agricultural land cover class included all land cover types that did not fall within the forested land cover class, nor could be classified as wetland or open water. The majority of open land cover in the NCR is used for agricultural purposes. We used ArcView 3.2 × (Environmental Systems Research Institute 1999) for all manipulations.

To further characterize the land cover composition and configuration of each landscape type, we measured the proportions of wetland and open water cover, the number of wetlands, road density (derived from the National Road Network, Edition 1.1, produced by Natural Resources Canada), the mean forest patch area, forest patch cohesion and the distances to the nearest forest patch, wetland and open water. We calculated all variables with ArcView 3.2 × except for forest patch cohesion, which we calculated with FRAGSTATS 3.0 (McGarigal et al. 2002). To assess whether the three landscape types (urban, agricultural, and forested) differed significantly in their land cover composition and configuration, we analyzed each variable with a Kruskal–Wallis one-way analysis of variance followed by a Tamhane's T2 post-hoc pairwise comparison test.

Anuran surveys

We performed six call surveys at the 29 focal ponds between April and June 2004 to assess anuran species richness and abundance. One pond was only surveyed 4 times due to lack of access at the end of the season. The ten species that occur in the NCR were included in this study: western chorus frog (*Pseudacris triseriata*), wood frog (*R. sylvatica*), spring peeper (*P. crucifer*), northern leopard frog, pickerel frog (*R. palustris*), American toad (*Bufo americanus*), gray treefrog, green frog (*R. clamitans*), mink frog (*R. septentrionalis*), and bullfrog (*R. catesbeiana*). Surveys occurred approximately every week and a half on warm humid evenings with little or no wind, between a half-hour after sunset and midnight. After waiting for one minute to allow frogs to become accustomed to their presence, trained volunteer observers listened at the pond edge for 5 min and assessed the abundance of calling anurans using the following index: (0) no individuals calling; (1) individual(s) can be counted, calls are not overlapping; (2) calls of <15 individuals can be distinguished, but there is some overlapping; and (3) ≥ 15 individuals are calling (as in Pope et al. 2000). For each survey, we randomly assigned observers to survey routes. Routes were driven forward, backward and from a middle starting point to vary survey times at the ponds.

Local habitat variables

To control for the effects of local habitat (pond) quality on anuran species richness and abundance in ponds within urban, agricultural and forested landscapes, we performed a vegetation and water quality survey of the focal ponds in June and July 2004. Local habitat quality in June and July is not perfectly representative of habitat quality for species that breed earlier in the season (April and May). However, we did not conduct local habitat surveys during April and May because at that time we needed to focus our efforts on performing the maximum number of call surveys possible. We chose three variables as the most likely determinants of anuran habitat at each pond: the length of the perimeter of the pond, the percent cover of emergent vegetation, and pH. The first two variables have been identified as important in explaining patterns of amphibian species richness in southwestern Ontario ponds (Hecnar and M'Closkey 1998) and pH has been shown to affect northern leopard frog abundance in eastern Ontario (Pope et al. 2000).

We measured the perimeter of each pond by walking around the pond with a Global Positioning System unit, accurate to 10 m. We estimated the percent cover of emergent vegetation along 2 m line transects perpendicular to the pond edge. Measurements were taken at regular intervals along the shoreline so that 6–8 values were collected at each pond, regardless of pond size. We then averaged these values to produce an overall estimate of the percent cover of emergent vegetation within 2 m of the shore for each pond. When access to the pond edge was not possible, we made a visual estimate of the total percent cover of emergent vegetation within 2 m of the shore. We measured water pH 1 m from shore at a depth of 5 cm with a Fisher Scientific accumet portable AP62 pH meter. We took four equally spaced measurements at each pond and calculated their average using the hydrogen ion concentrations.

Analysis

We performed an analysis of co-variance (ANCOVA) to determine the relative effects of surrounding landscape type (urban, agricultural, and forested) on anuran species richness in the ponds. The dependent variable was the number of species detected at each focal pond during the evening call surveys. The predictor variables included landscape type and the three local habitat variables described above: pond perimeter, the percent cover of emergent vegetation, and mean pH. We used Tukey's honestly significant difference test to identify which landscape types had significantly different numbers of species. We examined residual plots for homogeneity of variance and normality. We performed all analyses with SPSS 12.0 (SPSS 2003).

Of the ten species investigated, six were widespread enough to be included in further analyses: wood frog, spring peeper, northern leopard frog, American toad, gray treefrog, and green frog. For each species, we summed the abundance indices from all call surveys for each pond to provide an estimate of abundance that reflected high calling intensity as well as consistent calling (as in Pope et al. 2000). To test the validity of CALLSUM as a measure of abundance, we performed a Pearson correlation between CALLSUM and the summed number of green frogs seen at a subset of 20 ponds that were also surveyed during daytime visual encounter surveys (as in Carr and Fahrig 2001). CALLSUM and green frog abundance were significantly correlated (r=0.45, P=0.044). Using CALLSUM as the dependent variable, we performed ANCOVAs for each species as above. When General Linear Model assumptions were not met, the dependent variable was square-root transformed to account for increasing variance typical of count data. In the case of the wood frog and the northern leopard frog, the residuals were not normally distributed and we were unable to find an appropriate transformation; therefore, Poisson regressions were performed for these species using S-PLUS 6.0 (Insightful 2001). In addition, we used Tamhane's T2 post-hoc pairwise comparison tests to detect differences in abundance of wood frogs and northern leopard frogs between pairs of landscape types.

Results

Landscape composition and configuration

Not surprisingly, road density was significantly higher in urban landscapes than agricultural or forested landscapes, which did not differ (Table 1). The proportions of wetland and open water, the number of wetlands, and the distances to the nearest wetland and open water were not significantly different among landscape types. Not surprisingly, forest patches were significantly larger, less isolated, and more connected in forested landscapes than the other two landscape types. Significant differences occurred in mean forest patch area between all landscape types. The distance to the nearest forest patch was significantly different between agricultural and forested landscapes only. Finally, forest patch cohesion was significantly different between forested and agricultural landscapes and between forested and urban landscapes (Table 1).

Anuran species richness

Landscape type and the three local habitat variables together explained over half of the variance

Table 1 Land cover composition and configuration of urban, agricultural and forested landscapes in the National Capital Region, Canada

Variable	Landscape type		
	Urban	Agricultural	Forested
ROAD	0.011 (±0.002)[a]	0.0017 (±0.0004)[b]	0.0016 (±0.0006)[b]
WET	0.01 (±0.02)[a]	0.06 (±0.06)[a]	0.35 (±0.31)[a]
WATER	0.004 (±0.006)[a]	0.007 (±0.006)[a]	0.01 (±0.02)[a]
WET_NO	3.00 (±2.83)[a]	2.67 (±1.53)[a]	2.17 (±2.04)[a]
PATCH	0.042 (±0.004)[a]	0.13 (±0.04)[b]	1.66 (±1.04)[c]
DISTFOR	146.52 (±184.71)[a, b]	121.88 (±78.02)[a]	9.87 (±29.62)[b]
COHESION	97.69 (±0.92)[a]	98.31 (±0.68)[a]	99.87 (±0.09)[b]
DISTWET	879.07 (±757.28)[a]	515.98 (±10.06)[a]	467.45 (±574.14)[a]
DISTWATER	195.32 (±262.67)[a]	398.65 (±690.48)[a]	574.70 (±343.52)[a]

[a]ROAD = road density (m/m^2), WET = proportion of wetland cover, WATER = proportion of open water cover, WET_NO = number of wetlands, PATCH = forest patch area (km^2), DISTFOR = distance to the nearest forest patch (m), COHESION = forest patch cohesion, DISTWET = distance to the nearest wetland (m), DISTWATER = distance to the nearest open water (m)

[b]Values are mean (±standard deviation). Lowercase letters indicate significant differences between landscape types

in anuran species richness observed in the study area (Table 2).

Landscape type had a significant effect on species richness, resulting from significantly fewer species in urban landscapes (mean = 2.10±1.14 (95% CI) species) than agricultural (mean = 5.10±0.92 (95% CI) species) and forested (mean = 5.56±1.28 (95% CI) species) landscapes (Fig. 2). Species richness was also found to be significantly greater in large ponds (Table 2).

Wood frog

We recorded the wood frog at 13 of the 29 ponds surveyed (45%). Wood frog abundance was found to be significantly different among landscape types ($\chi^2_{2,\ 20}$=22.84, P=0.00001) with a significantly greater abundance of wood frogs in ponds in forested landscapes (mean = 2.33±1.27 (95% CI) individuals) than in ponds in agricultural (mean = 0.60±0.50 (95% CI) individuals) or urban landscapes (0 individuals) (Fig. 3a). No local variables were found to be significant predictors of wood frog abundance.

Spring peeper

The spring peeper was the second most common anuran recorded during this study (79% occurrence, 23 ponds). The model including landscape type and the three local habitat variables explained 65% of the variance in spring peeper abundance in the study area. Landscape type significantly affected spring peeper abundance ($F_{2,\ 20}$=19.28, P=0.00002). Spring peepers were significantly more abundant in ponds surrounded by forested landscapes [mean = 6.89±1.78 (95% CI) individuals] followed by ponds surrounded by agricultural landscapes [mean = 3.90±1.28 (95% CI) individuals] and were least abundant in ponds surrounded

Table 2 Analysis of co-variance of the effects of landscape type and three local habitat variables on anuran species richness in ponds surrounded by primarily urban, agricultural, and forested landscapes in the National Capital Region, Canada. Adjusted R^2 = 0.58

Variable	Type III SS	df	MS	F	P
Pond perimeter	16.37	1	16.37	8.46	0.009
Percent cover of emergent vegetation	0.48	1	0.48	0.25	0.625
pH	0.0008	1	0.0008	0.0004	0.984
Landscape type	67.22	2	33.61	17.37	0.000
Error	38.69	20	1.93		

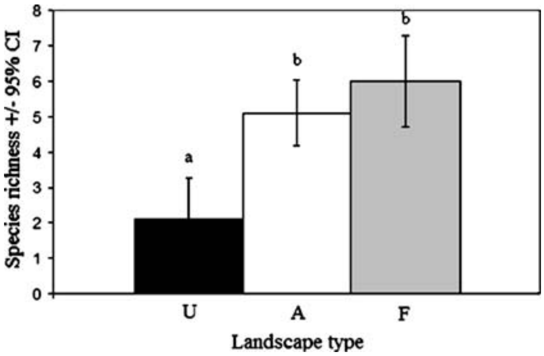


Fig. 2 The mean number of anuran species (±95% confidence interval) recorded in ponds surrounded by primarily urban (U), agricultural (A), and forested (F) landscapes in the National Capital Region, Canada. Lowercase letters indicate significant differences between pairs of landscapes

by urban landscapes [mean = 0.90±0.92 (95% CI) individuals] (Fig. 3b). No local variables were found to be significant predictors of spring peeper abundance.

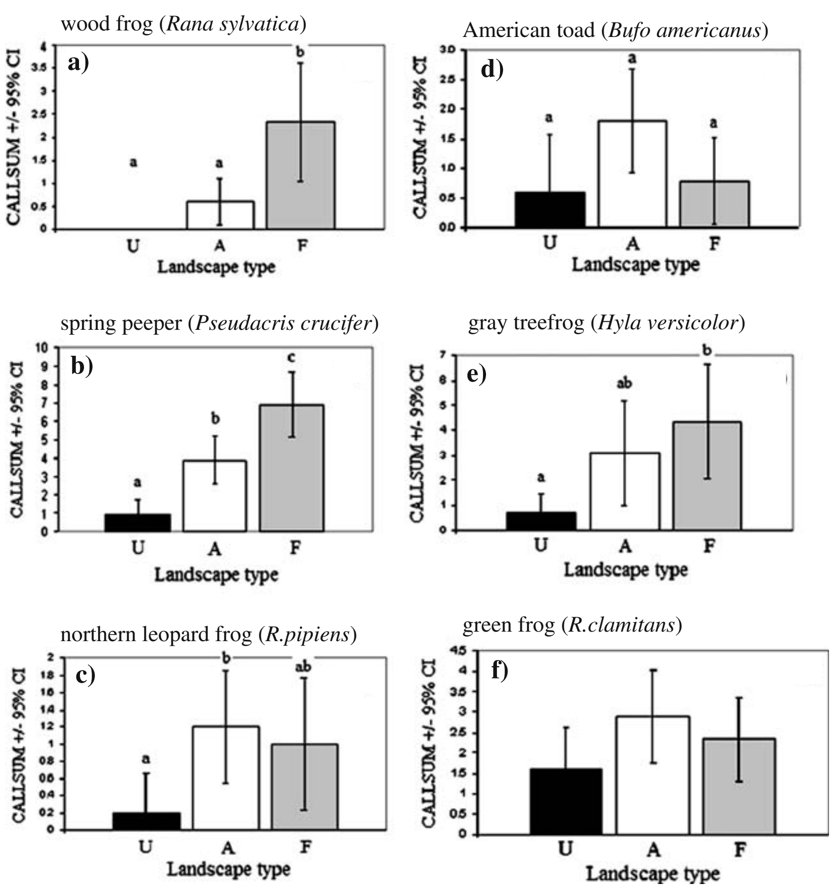
Northern leopard frog

We recorded the northern leopard frog at approximately half the ponds surveyed (52%, 15 ponds). Northern leopard frog abundance was significantly different among landscape types ($\chi^2_{2, 20}$=11.96, P=0.002), with significantly more leopard frogs in agricultural landscapes [mean = 1.20±0.66 (95% CI) individuals] than urban landscapes [mean = 0.20±0.45 (95% CI) individuals] (Fig. 3c). Ponds in forested landscapes had an intermediate number of northern leopard frogs [mean = 1.00±0.77 (95% CI) individuals]. Northern leopard frogs were also more abundant in large ponds ($\chi^2_{1, 20}$=7.82, P=0.005).

American toad

The American toad occurred at 52% of sites (15 ponds). The model including landscape type and the three local habitat variables explained 53% of

Fig. 3 Mean abundance (±95% confidence interval) of six anuran species in ponds surrounded by primarily urban (U), agricultural (A), and forested (F) landscapes in the National Capital Region, Canada. Values are the mean of summed abundance indices from all call surveys performed at each pond (see text). Lowercase letters indicate significant differences between pairs of landscapes



the variance in American toad abundance in the study area. Landscape type had a significant overall effect on American toad abundance ($F_{2,20}$=13.51, P=0.0002), with more American toads in agricultural landscapes [mean = 1.80±0.88 (95% CI) individuals] than forested [mean = 0.78±0.74 (95% CI) individuals] and urban [mean = 0.60±0.97 (95% CI) individuals] landscapes (Fig. 3d). However, Tukey's honestly significant difference test revealed no significant differences in American toad abundance between pairs of landscape types. American toads were also more abundant in large ponds ($F_{1, 20}$=11.71, P=0.003) with low percent cover of emergent vegetation ($F_{1, 20}$=13.27, P=0.002).

Gray treefrog

The gray treefrog was a common inhabitant of the ponds we selected for this study (72% occurrence, 21 ponds). The model including landscape type and the four local habitat variables explained 39% of the variance in gray treefrog abundance in the study area. Landscape type had a significant effect on gray treefrog abundance $F_{2, 20}$=9.86, P=0.001), with significantly fewer gray treefrogs in urban landscapes [mean = 0.70±0.76 (95% CI) individuals] than forested landscapes [mean = 4.33±2.30 (95% CI) individuals] (Fig. 3e). Ponds in agricultural landscapes had an intermediate number of gray treefrogs [mean = 3.10±2.09 (95% CI) individuals]. Gray treefrogs were also more abundant in large ponds ($F_{1, 20}$=4.73, P=0.042).

Green frog

The green frog was the most common anuran recorded during this study (86% occurrence, 25 ponds). The model including landscape type and the three local habitat variables explained very little of the variance in green frog abundance in the study area (adjusted R^2 = 0.00). None of the predictor variables included in the model significantly affected green frog abundance. Green frogs had similar abundances in urban landscapes [mean = 1.60±1.02 (95% CI) individuals], agricultural landscapes [mean = 2.90±1.14 (95% CI) individuals] and forested landscapes [mean = 2.33±1.01 (95% CI) individuals] (Fig. 3f).

Discussion

Contrary to our expectations, we found no significant difference between anuran species richness in ponds in agricultural and forested landscapes. However, as expected, ponds in urban landscapes did have the fewest anuran species. It appears that breeding ponds surrounded primarily by urban land use sustain a less diverse anuran community than those surrounded by primarily agricultural land use. Urban land use can affect amphibian persistence in breeding ponds through inputs of pesticides and road salt, which may influence the development and survival of tadpoles and froglets (Relyea 2005; Sanzo and Hecnar 2006), as well as through changes in water flow regimes (Richter and Azous 1995). Urban land use is also associated with increased human recreational use and increased predation by domestic animals (Woods et al. 2003). Amphibian communities in urban breeding ponds may also experience a higher probability of local extinction due to higher mortality from road traffic (Fahrig et al. 1995; Carr and Fahrig 2001), and lower movement success in landscapes characterized by a high proportion of roads and other impervious surfaces (Lehtinen et al. 1999; deMaynadier and Hunter 2000). The ecological impacts of some forms of agricultural land use are less numerous and include pesticide and fertilizer inputs, soil compaction, and possibly underground disturbance to amphibians hibernating in and around breeding ponds (Knutson et al. 1999). In addition, two of the five species exhibiting a response to landscape type, the northern leopard frog and the American toad, were shown to prefer ponds in agricultural rather than forested landscapes, leading to similar species richness in ponds surrounded by these two landscape types.

Urbanization also creates discrete habitat patches within a matrix of residential, commercial and industrial development resulting in the fragmentation of natural habitat (Wilcox and Murphy 1985). In this study, urban landscapes were found to have the highest road densities as well as the smallest, most isolated and least connected forest patches. In addition to the effect of habitat loss, the spatial arrangement of remnant habitat in human-dominated landscapes may affect the persistence of species that depend on successful movement between patches, such as pond-breeding amphibians. Forest proximity and wetland isolation, two common measures of the spatial arrangement of remnant habitat, have been shown to be strong predictors of amphibian species richness and occurrence in both urban and agricultural areas (Laan and Verboom 1990; Kolozsvary and Swihart 1999; Lehtinen et al. 1999; Guerry and Hunter 2002; Ficetola and De Bernardi 2004). Thus, the spatial arrangement of forest patches may have contributed to the observed patterns of anuran species richness and abundance in this study. In particular, the high degree of forest fragmentation measured in urban landscapes likely resulted in the species-poor anuran communities encountered in ponds surrounded by this landscape type.

For those species that exhibited a response to landscape type, the preferred landscape type varied according to the terrestrial habitat requirements of the species in question. The majority of anuran species rely on both aquatic and terrestrial habitats for their survival. Breeding takes place in wetlands, ponds and streams. After breeding, the adults move into forest or open habitat to forage and hibernate. Species that are known to use forest habitat, such as the wood frog, spring peeper, and gray treefrog, were more abundant in ponds in forested landscapes whereas species that are either habitat generalists, such as the American toad, or use open habitat, such as the northern leopard frog, were more abundant in ponds in agricultural landscapes. Some species, however, remain at the breeding site year-round, feeding on aquatic prey and hibernating buried beneath the bottom mud of ponds. This is the case of the green frog, which showed no response to landscape type. In addition, regardless of whether a species was more abundant in ponds in agricultural or forested landscapes, all species investigated, except the green frog, were least abundant in ponds in urban landscapes.

Although landscape type explained the majority of observed variation in anuran species richness and abundance, local variables, specifically pond perimeter, contributed significantly to the pattern of species richness and the abundance of 3 of the 6 species investigated. However, when we examined plots of pond perimeter against anuran species richness and abundance, we discovered the effect to be largely due to two very large ponds. These ponds had perimeters of 1238.90 and 838.32 m, respectively, compared to the mean perimeter of the remainder of the ponds [mean = 240.78±54.27 (95% CI) m]. When we removed these ponds from our analyses, pond perimeter was no longer significant. Ficetola and De Bernardi (2004) report no relationship between amphibian species richness and wetland size, which they attribute to the limitation of the species–area relationship applied to wetlands. They surmise that other wetland features may more directly influence the species richness of wetlands.

The American toad exhibited a negative relationship with the percent cover of emergent vegetation. This is in contrast to results presented by other authors who report a positive association between most frog species, including the American toad, and this variable (Heinen 1993; Hecnar and M'Closkey 1998; Weyrauch and Grubb 2004). American toads were more abundant in ponds in agricultural landscapes, which were generally used as water reservoirs for livestock. These ponds often had very steep slopes and were deeper than those in forested and urban landscapes, leading to lower vegetative cover on average. It may be that the negative relationship between American toad abundance and the percent cover of emergent vegetation reported here is reflective of the higher abundance of toads in ponds in agricultural landscapes, which happen to have low percent cover of emergent vegetation.

Ponds embedded in urban landscapes were shown to support lower anuran biodiversity than ponds in agricultural settings. Other taxa have demonstrated a similar pattern. Forest fragments surrounded by urban landscapes have lower Neotropical migrant bird abundance and species richness than forest fragments surrounded by landscapes dominated by agriculture (Dunford 2001). Fewer fish species are found in urban areas as compared to forested and agricultural areas (Phelps 2001). Finally, introduced plant species richness is higher in forest fragments surrounded by urban landscapes than in forest fragments surrounded by agricultural and forested landscapes, which do not differ (Duguay 2004). We are not, however, suggesting that all remaining forest habitat can be converted to agricultural use without affecting anuran biodiversity. Rather, ponds in agricultural and forested landscapes had similar richness but supported different species. The similar richness but differing community composition of ponds in forested and agricultural landscapes highlights the importance of considering biodiversity not only in terms of species richness but also with respect to the abundance of individual species. This is especially true if individual species exhibit different habitat requirements, as is the case for amphibians. Thus, we suggest that landscapes composed of a mosaic of forest and open habitats surrounding wetlands would likely hold the highest anuran biodiversity.

Acknowledgements First and foremost, we thank the volunteers and landowners who made the fieldwork for this study possible. We also thank the members of the Geomatics and Landscape Ecology Research Laboratory for their support. Natural Science and Engineering Research Council of Canada grants supported S.A.G. and L.F. This research is dedicated to Lionel.

References

Atauri JA, de Lucio JV (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landsc Ecol 16:147–159

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182–188

Bonin J, Desgranges J-L, Rodrigue J, Ouellet M (1997) Anuran species richness in agricultural landscapes of Quebec: foreseeing long-term results of road call surveys. In: Green DM (ed) Amphibians in decline: Canadian studies of a global problem. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA, pp 141–149

Bradley G (1995) Urban forest landscapes: integrating multidisciplinary perspectives. In: Bradley G (ed) Urban forest landscapes: integrating multidisciplinary perspectives. University of Washington Press, Seattle, Washington, USA, pp 3–11

Canadian Biodiversity Information Network (2004) Urban biodiversity. Environment Canada, Ottawa, Ontario. Available from http://www.cbin.ec.gc.ca/primers/urban.cfm (accessed August 2005)

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conserv Biol 15:1071–1078

Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. Bioscience 50:593–601

Dam A (2005) Landscape structure affects different eastern Ontario anuran species at different spatial scales. MSc Thesis, Carleton University, Ottawa, Ontario, Canada, pp 69

DeFries RS, Foley JA, Asner GP (2004) Land-use choices: balancing human needs and ecosystem function. Front Ecol Environ 2:249–257

deMaynadier PG, Hunter ML Jr (2000) Road effects on amphibian movements in a forested landscape. Natl Areas J 20:56–65

Duguay S (2004) Effect of landscape context on the plant species richness of forest fragments. MSc Thesis, Carleton University, Ottawa, Ontario, Canada, pp 53

Dunford W (2001) Effects of agricultural and urban land uses on birds breeding in forest fragments near Ottawa, Ontario. Carleton University, Ottawa, Ontario, Canada, pp 91

Environmental Systems Research Institute (1999) ArcView (3)2x. Redlands, California, USA

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73:177–182

Ficetola GF, De Bernardi F (2004) Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. Biol Conserv 119:219–230

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574

Gibbs JP, Whiteleather KK, Schueler FW (2005) Changes in frog and toad populations over 30 years in New York State. Ecol Appl 15:1148–1157

Gray MJ, Smith LM, Brenes R (2004) Effects of agricultural cultivation on demographics of Southern High Plains amphibians. Conserv Biol 18:1368–1377

Grimm NB, Grove JM, Pickett STA, Redman CL (2000) Integrated approaches to long-term studies of urban ecological systems. Bioscience 50:571–584

Guerry AD, Hunter ML Jr (2002) Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conserv Biol 16:745–754

Hecnar SJ, M'Closkey RT (1998) Species richness patterns of amphibians in southwestern Ontario ponds. J Biogeogr 25:763–772

Heinen JT (1993) Substrate choice and predation risk in newly metamorphosed American toads Bufo americanus: an experimental analysis. Am Midl Nat 130:184–192

Houlahan JE, Findlay CS (2003) The effects of adjacent land use on wetland amphibian species richness and community composition. Can J Fish Aquat Sci 60:1078–1094

Insightful (2001) S-PLUS 6.0. Seattle, Washington, USA

Johnson CM, Johnson LB, Richards C, Beasley V (2002) Predicting the occurrence of amphibians: an assessment of multiple-scale models. In: Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds) Predicting species occurrences: issues of accuracy and scale. Island Press, Washington DC, USA, pp 157–170

Joly P, Miaud C, Lehmann A, Grolet O (2001) Habitat matrix effects on pond occupancy in newts. Conserv Biol 15:239–248

Knight RL, Landres PB (1998) Stewardship across boundaries. Island Press, Washington, DC, USA

Knutson MG, Sauer JR, Olsen DA, Mossman MJ, Hemesath LM, Lannoo MJ (1999) Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conserv Biol 13:1437–1446

Kolozsvary MB, Swihart RK (1999) Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. Can J Zool 77:1288–1299

Laan R, Verboom B (1990) Effects of pool size and isolation on amphibian communities. Biol Conserv 54:251–262

Lehtinen RM, Galatowitsch SM, Tester JR (1999) Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19:1–12

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html

Mensing DM, Galatowitsch SM, Tester JR (1998) Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. J Environ Manage 53:349–377

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC, USA, pp 86

Phelps A-M (2001) Investigating the fish community of the Rideau River, Ontario, with respect to historical changes and current land-use practices. MSc Thesis, University of Ottawa, Ottawa, Ontario, Canada, pp 176

Platt RH (2004) Toward ecological cities: adapting to the 21st century metropolis. Environment 46:11–27

Pope SE, Fahrig L, Merriam NG (2000) Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498–2508

Relyea RA (2005) The lethal impact of Roundup on aquatic and terrestrial amphibians. Ecol Appl 15:1118–1124

Richter KO, Azous AL (1995) Amphibian occurrence and wetland characteristics in the Puget Sound Basin. Wetlands 15:305–312

Riley SPD, Busteed GT, Kats LB, Vandergon TL, Lee LFS, Dagit RG, Kerby JL, Fisher RN, Sauvajot RM (2005) Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. Conserv Biol 19:1894–1907

Sanzo D, Hecnar SJ (2006) Effects of road de-icing salt (NaCl) on larval wood frogs (*Rana sylvatica*). Environ Pollut 140:247–256

SPSS (2003) SPSS 12.0 for Windows. Chicago, Illinois, USA

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786

Trenham PC, Koenig WD, Mossman MJ, Stark SL, Jagger LA (2003) Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecol Appl 13:1522–1532

Weyrauch SL, Grubb TC Jr (2004) Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: an information-theoretic approach. Biol Conserv 115:443–450

Wilcox BA, Murphy DD (1985) Conservation strategy: the effects of fragmentation on extinction. Am Nat 125:879–887

Wilson JD, Dorcas ME (2003) Effects of habitat disturbance on stream salamanders: implications for buffer zones and watershed management. Conserv Biol 17:763–771

Woods M, McDonald RA, Harris S (2003) Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Rev 33:174–188