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# More amphibians than expected in highway stormwater ponds

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ABSTRACT

Some structures developed for particular technical anthropogenic uses are colonized by biodiversity, but their potential roles have not been seriously considered. Here, we examined whether and how highway stormwater retention ponds are colonized by amphibians and are used as reproduction sites in human-dominated landscapes.

We addressed their role as habitats for amphibians by sampling amphibians in highway ponds ($n = 58$) and in surrounding non-highway ponds ($n = 45$) and comparing the species richness and the amphibian abundance using occupancy models that take detectability into account.

As expected, highway ponds differed in abiotic conditions from surrounding ponds. Surprisingly, we found seven different amphibian species with breeding populations, including one emblematic rare species (*Triturus cristatus*), in these artificial ponds. Further, the proportion of the highway ponds where amphibians were detected was about similar to that of surrounding ponds. Note, however, that the amphibian abundances were lower in highway ponds.

Surprisingly, our results suggest that highway ponds may contribute in altered landscapes to the biodiversity of the pond network at a regional scale. Because the adoption of biodiversity-friendly management measures for these artificial ponds could promote biodiversity in such landscapes, we highlight the most important factors driving amphibian distribution in these ponds. Due to the importance of these issues, we stress the need for complementary studies to continue to precisely examine the potential roles of these ponds as habitats for amphibians and then to propose, if useful, technical pond design and management recommendations relevant for common biodiversity.



## 1. Introduction

The conservation of biodiversity cannot be achieved only by focusing on biodiversity hotspots and/or rare and protected species. Indeed, in major industrial countries, protected natural areas represent only a small area (13%: MEA, 2005). It is necessary to continue the efforts of designating protected areas (COP-CBD, 2011), but a complementary emergent view highlights the need to consider biodiversity in the usually human-dominated landscape matrix, to favor in situ conservation and enhance connectivity among natural areas (Edwards and Abivardi, 1998; Rosenzweig, 2003). Thus, although some elements of urban infrastructure, e.g., roads and urban parks, have a strong negative impact on biodiversity (Trombulak and Frissell, 2000; Forman et al., 2003; McKinney, 2006), they could shelter a certain (at least "common") biodiversity and might play roles as refuges (Le Viol et al., 2009; Brand and Snodgrass, 2010.) and corridors in altered landscapes in addition to their primary technical function for which they were built.

This approach applied to aquatic ecosystems would be interesting (MEA, 2005), as these habitats have drastically regressed due to fast anthropogenic changes in land use during recent decades (Gibbs, 2000; Zacharias and Zamparas, 2011): for example by 40% to 90% over the last century in a number of northern European countries (Hull, 1997). This is particularly true for ponds (EPCN, 2007), which are among the most species-rich aquatic habitats at the regional scale (Davies et al., 2008). In the UK, pond numbers declined for example from approximately 800,000 in the nineteenth century to 200,000 by the 1980s (see for details Jeffries, 2012), and the number of ponds has gone up by 11% between 1998 and 2007 (EPCN, 2007). The anthropogenically created and natural ponds have strongly decreased while, simultaneously, other types of ponds have been created in response to new uses: recreational (golf courses, green parks, fishing), safety (firefighting water supply) and pollution retention. Among those, stormwater ponds along highways are, for example, required by legislation to retain stormwater runoff and pollutants deposited on roads by traffic (heavy metals, sediments, nutrients, petroleum

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hydrocarbons, salts, pesticides: see Davis et al., 2001; Karouna-Renier and Sparling, 2001), with the aim of reducing the impact of automobile traffic on other water bodies (Scher and Thièry, 2005).

As for other types of man-made ponds (see Beja and Alcazar, 2003; Knutson et al., 2004; Canals et al., 2011 for livestock water ponds, Wood et al., 2001 for industrial ponds; Brand and Snodgrass, 2010; Hsu et al., 2011 for urban ponds), these urban stormwater ponds have been suggested to potentially serve as corridors and refuges because these spatial structures may provide alternative stable habitats where species can complete their life cycles when their habitats are degraded. These potential roles of corridors and refuges should depend on the surrounding landscape; in semi-natural ecosystems generally supporting high species diversity, urban stormwater retention ponds may have negative effects on biodiversity due to their high level of pollution and may even act as sinks (or traps) for some species (McCarthy and Lathrop, 2011). In contrast, in strongly altered landscapes, where wildlife habitats are critical for the conservation of biological diversity and ecological processes, they may play a more positive role for biodiversity because they form large networks often connected by ditches.

Urban stormwater ponds support wildlife (Karouna-Renier and Sparling, 2001; Scher and Thièry, 2005; Le Viol et al., 2009), notably amphibians (Scher and Thièry, 2005; Snodgrass et al., 2008; Simon et al., 2009). However, their suitability for reproduction and their ability to serve as adequate habitats in maintaining populations at the landscape scale are still poorly documented (Scher and Thièry, 2005; Barrett et al., 2010; Brand and Snodgrass, 2010; Birx-Raybuck et al., 2010). Brand and Snodgrass (2010) recently reported that anthropogenic stormwater ponds may be the most productive amphibian breeding habitats remaining in some regions where natural wetland densities are low and wetland destruction has been extensive. The importance of these urban stormwater ponds likely depends on their technical function and management.

Surprisingly, few studies have concerned highway ponds (Scher and Thièry, 2005; Le Viol et al., 2009) despite their density (e.g., one pond every 2 km along highways in France, often connected by ditches) and their potential negative and positive effects on amphibians, a particularly threatened taxonomic group (IUCN, 2011). The relationship between highway ponds and amphibians is worth studying because these stormwater ponds are in proximity to roads that have strong negative impact on amphibians (Forman et al., 2003). The roads act as barriers to dispersal, and animals are subjected to pollutants and direct mortality (Trombulak and Frissell, 2000; Hels and Buchwald, 2001; Sriyaraj and Shutes, 2001; Eigenbrod et al., 2009; Fahrig and Rytwinski, 2009). Their negative impact is suggested among the causes (habitat destruction resulting from urbanization and the increase in intensive arable farming, environmental contamination, road mortality, climate change) (Blaustein and Kiesecker, 2002; Stuart et al., 2004; Johnson et al., 2007) of the strong worldwide decline of amphibians (for details about the decline, see Wake and Vredenburg, 2008).

Additional studies are thus strongly needed to address the potential role of highway ponds as habitats for amphibians in human-dominated landscapes where natural habitats are absent (Scher and Thièry, 2005). We still do not know the frequency of occurrence or the abundance of amphibians in comparison to other types of ponds, nor whether they use this stormwater pond system for reproduction. We need also to assess the relative roles of biotic and abiotic factors that act on amphibians at the pond and landscape levels. One might expect that highway ponds would differ in amphibian species composition and abundance from ponds located in the surrounding landscape, depending on their location and technical function in relation to the retention of polluted water.

We first assessed differences in biotic and abiotic conditions between highways and surrounding ponds (i.e., non-highway stormwater ponds: farmland, woodland ponds usually more "semi-natural" which are located in the crossed landscape), considering: (i) landscape variables such as woodland, farmland and built-up areas; (ii) local variables such as the chemical properties of the water; and (iii) biotic elements such as the presence of fish or vegetation. We then examined whether the occupancy, the richness and the abundance of the more abundant amphibian species detected (adult and larval) in highway ponds differed from surrounding ponds using standardized sampling methods. Because amphibian detection may vary in space and time, we used models (Royle, 2004) to correct larval and adult abundance data based on detection probabilities of individual species. We then tried to distinguish the relative effects of local landscape composition and within-pond parameters on amphibian species abundance.

## 2. Methods

### 2.1. Study sites

We carried out this study along a 100-km section of highway A11 (48°N, 1°E), built in 1972 in France. The study area was characterized by a temperate climate, and the highway successively passed through landscapes dominated by urban, woodland and agricultural land covers. The traffic levels were among the highest in France, with an average of 88,000 vehicles per day (Cofiroute, unpublished data).

### 2.2. Site selection and sampling of amphibian populations

#### 2.2.1. Site selection

We surveyed 58 highway ponds within 50 m of the roadway edge along the studied section, on both sides of the highway. Using geomorphic maps, aerial photographs and field surveys, we identified in the landscapes crossed by the highway 45 additional "surrounding" ponds according to the following criteria: surrounding ponds were within 15 km of the highway but at least 150 m away from any road, with water in March, and easily accessible. Therefore, none of the selected surrounding ponds received road runoff, while all selected highway ponds were built to collect and retain highway water runoff. Nevertheless, the surrounding ponds should not be considered "natural", "unaltered" ponds, or "ideal" ponds for biodiversity but rather as ponds representative of those located in landscapes crossed by the studied highway (i.e., landscapes dominated by urban, woodland and agricultural land). All these surrounding ponds were most likely anthropogenic (71% for hunting, 10% for farm use), although 19% did not actually have a specific use. Note that these ponds (highway and surrounding) were not connected to the hydrographic network.

#### 2.2.2. Sampling of amphibian populations

Pond-breeding amphibians gather at ponds and wetlands to mate and deposit their eggs, which hatch and develop in the aquatic environment until they metamorphose into terrestrial or semi-aquatic juveniles. In 2006, amphibian populations were sampled twice, in early spring and early summer. Note that each pond was only visited once per each season. Further visits would have been preferable, but due to security reasons, access to highway ponds was strongly limited. In early spring (March 23 to April 4), we especially looked for breeding newts (*Lissotriton* (previously *Triturus*) *helveticus*, *L. vulgaris*, *Ichthyosaura* (*Triturus*) *alpestris* and *Triturus cristatus*) and for frog (*Rana temporaria* and *Rana dalmatina*) and toad (*Bufo bufo*) egg masses. In early summer (June 15 to July 15), we focused on sampling toad and frog larvae (*Pelophylax* (*Rana*) *esculentus* complex). All ponds were sampled during the early spring visit, and only 29 highway ponds and 20 surrounding ponds were visited in early summer due to technical reasons (security, available effort, pond drying). We carefully choose the dates of sampling in order to sample alternatively surrounding ponds and highway ponds and to avoid temporal correlation with the pond type particularly in early spring period, i.e. during the laying period ($P = 0.72$). For early summer period, more highway ponds tended to be sampled earlier than surrounding ponds ($P = 0.02$): we then take into account the effect of sampling date in modeling. It was a typical year in terms of weather: The average maximal and minimal temperatures in 2006 (calculated on the average of January, February and March daily data) were slightly colder than those calculated over the prior 30-year period (2006/1976–2005: $T_{max}$: 8.18 °C/9.74 °C; $T_{min}$: 2.32 °C/2.48 °C), and rainfall was slightly greater (2006/1976–2005: 1.96 mm/1.53 mm). We adapted sampling to account for potential heterogeneity in species detectability (Schmidt, 2004). Amphibians were sampled at ten sites per pond; sampling sites were evenly distributed around the pond. The first sampling site was always located to the north. For small ponds (perimeter <50 m), only five sites were sampled. At each site, we made one 3-m sweep of 30 s in the littoral zone (0.5–1 m from the shore) using a D-frame net, for a total sampling of 1 $m^2$. We identified according to morphological criteria all species captured in the field (ACEMAV et al., 2003; Miaud and Muratet, 2004) and counted all captured individuals (larvae and adults). All amphibians were released within 10 min of capture to minimize risk of mortality. Given this time constraint, we did not discriminate between larvae of *L. helveticus* and *L. vulgaris*. However, as *L. vulgaris* is rare in our dataset, these larvae were most likely *L. helveticus*. In addition, we counted all egg masses of *R. temporaria* and egg masses of *R. dalmatina* per pond at the end of the spawning season.

### 2.3. Landscape and pond characteristics

At the landscape scale, we used a geographic information system and the CORINE Land Cover mapping database (European Environmental Agency) to calculate surface areas of artificial (urban, road, railway), farmland and woodland habitats within a 500-m radius around each pond. This buffer size corresponded to a compromise between the CORINE land cover polygon size (>25 ha) and the known influence of land uses on pond biodiversity at small scales (Semlitsch and Bodie, 2003; Simon et al., 2009). For each pond, we measured pond perimeter (m), depth (cm), the presence/absence of macrophytes at the 10 amphibian sampling points and water chemistry at three points evenly distributed around the pond, 50 cm from the bank. We recorded in situ conductivity and salinity and collected water samples to estimate $PO_4$, $NO_2$ and $NO_3$ concentrations and pH. We calculated the frequency of macrophytes and water quality parameters at the pond level as the average value of each variable measured at the point level. In addition, we categorized the pond permanence status as temporary or permanent (observations in summer), classified the pond bottom type as with or without leaf litter and recorded the presence/absence of fish based on field observations and unpublished data (Cofiroute and Natural Park of la haute vallée de Chevreuse). Note that all selected highway ponds had the same regular design (slope of the bank approximately 30°) because they were built to collect and retain highway water runoff.

### 2.4. Statistical analysis

Except when specified, we used the R software program for statistical analyses.

#### 2.4.1. Ecological differences between highway ponds and surrounding ponds

To assess environmental differences between highway and surrounding ponds, we performed Fisher's exact tests on contingency tables (non-continuous variables: fish, pond bottom type, permanence status) and Kruskal–Wallis tests (continuous variables: artificial, farmland and woodland areas; macrophyte vegetation; chemical characteristics; perimeter; depth). We then calculated correlations among the environmental variables using Fisher's exact tests, Kruskal–Wallis tests and Pearson's correlation tests (for continuous variables).

#### 2.4.2. Amphibian richness

Amphibian richness could potentially vary with pond characteristics (e.g., water quality, depth, perimeter, permanence status, macrophyte frequency, fish presence, pond type) and with variables at the landscape scale (woodland areas, agricultural areas, urbanized areas). Because of the correlations among covariates (Appendix A), we selected a set of variables according to their ecological significance and correlation. At the local scale we chose macrophyte frequency, fish presence, and pond type, and at the landscape scale we chose woodland areas (because this variable could fit with species requirements during the terrestrial phase of the life cycle) and agricultural areas (because agricultural practices influence the chemical characteristics of the water, such as discharge of nitrogen and phosphorous). We tested the relationships between amphibian richness and these explanatory variables using a generalized linear model (GLM), with a Poisson error distribution (Crawley, 2009). We performed goodness-of-fit tests using the package vcd under R environment (R Development Core Team, 2012) to check that the Poisson distribution is relevant. We built model that contained all variables of interest. The analyses of variance were performed using type-II error (package car): tests were thus calculated according to the principle of marginality, testing each term after all others. *P*-Values were corrected for over-dispersion according to Faraway approaches (Faraway, 2006). These tests were performed on naïve richness and on estimated richness which takes into account the detection probability of species (see Boulinier et al., 1998, R package vegan).

#### 2.4.3. Relationships between species abundance and pond characteristics

We compared the abundances of individual species (after adjusting for detection probabilities) between the two pond types. Abundance measures, due to their greater degree of sensitivity, are expected to provide better information than the occupancy rate alone (but see Joseph et al., 2006). Although often used in amphibian surveys, counts may provide uncorrected estimations of abundance because detection of individuals and species in the field is imperfect and may vary between habitats (Dodd and Dorazio, 2004; Schmidt, 2004; Schmidt and Pellet, 2005). To limit biases due to differences in detectability, we used models developed by Royle (2004), which make it possible to estimate population densities corrected by detection, based on spatially replicated sampling counts within a pond (see Appendix B in Supporting Information for details of the statistical framework).

We then compared amphibian species abundance between surrounding and highway ponds and assessed the relationships between abundance and environmental variables using R package unmarked. We restricted our abundance analyses to the most

**Table 1**
Abiotic characteristics of highway stormwater and surrounding ponds (summary of mean values and standard errors (SE) for quantitative variables, and proportion rate for qualitative variables).

| Variables tested | Highway pond (SE) | Surrounding pond (SE) | $\chi^2$ value | $P$[a,b] |
|---|---|---|---|---|
| *Landscape variables* | | | | |
| Artificial area ($m^2$)[b] | 14,142 (4,194) | 118 (83) | 16.6 | <0.01 |
| Woodland area ($m^2$)[b] | 191,941 (25,192) | 415,209 (42,257) | 15.1 | <0.01 |
| Agricultural area ($m^2$)[b] | 458,718 (33,990) | 291,288 (45,528) | 7.1 | 0.01 |
| *Pond variables* | | | | |
| pH[b] | 7.96 (0.14) | 6.84 (0.19) | 20.7 | <0.01 |
| Salinity (mg NaCl/L)[b] | 0.44 (0.40) | 0.11 (0.01) | 55.3 | <0.01 |
| Conductivity (mS/cm)[b] | 0.95 (0.07) | 0.22 (0.02) | 62.2 | <0.01 |
| $NO_2$ (mg/L)[b] | 0.06 (0.02) | 0.02 (0.01) | 2.9 | 0.08 |
| $NO_3$ (mg/L)[b] | 3.95 (0.83) | 2.38 (0.76) | 7.3 | 0.01 |
| $PO_4$ (mg/L)[b] | 0.47 (0.09) | 0.87 (0.17) | 4.5 | 0.03 |
| Pond perimeter (m)[b] | 137 (10) | 146 (17) | 54 | 0.22 |
| Depth (cm)[b] | 58 (3) | 46 (3) | 5.35 | 0.02 |
| Permanence status[c,d] | 72% | 58% | | 0.23 |
| Fish[c,e] | 18% | 12% | | 0.43 |
| Fish in permanent pond[c,e] | 25% | 25% | | 1.00 |
| Vegetation[c,e] | 56% | 54% | | 0.85 |
| Pond bottom type[c,f] | 28% | 61% | | <0.01 |

[a] Values are based on Kruskal–Wallis tests for quantitative variables and Fisher's exact tests for qualitative variables.
[b] Continuous variable.
[c] Qualitative variable.
[d] Rate of permanent ponds vs. temporary ponds.
[e] Presence rate.
[f] Rate of ponds with russet litter vs. without russet litter.

abundant species, *L. helveticus* (adults and larvae; see above regarding *L. helveticus*/*L. vulgaris*) and *P. esculentus* (larvae). In the latter case, we performed analyses on data matched in decimal classes given the data distribution. Then, using Royle's procedure (2004), we ran the whole set of possible nested models, assuming the following.

(i) Detection of individuals could vary with macrophyte frequency, fish presence, date – for early summer dataset – and pond type (surrounding ponds vs. highway ponds). Macrophytes may serve as refuges for amphibians and could reduce the detection of species as well as that of fish that prey on amphibians. Detection may also vary with pond type due to differences in pond structure because highway ponds had more regular banks.
(ii) Abundance could vary with those four above-mentioned variables (macrophyte frequency, fish presence, date – for early summer dataset – and pond type) and with landscape variables, so we chose the same selected explanatory variables as previously described (woodland and agricultural areas). Few models were eliminated from the selection because they did not reach algorithm convergence (see Appendix B for details of these models). Models were ranked using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). Models with the lowest AIC and AIC differences of less than 2 had a substantial level of empirical support (Burnham and Anderson, 2002).

For the species stages for which data were too scarce to perform abundance estimations, we performed occupancy modeling (MacKenzie et al., 2002; Royle and Nichols, 2003) using the package unmarked.

Note that we checked that Poisson distribution is relevant using a goodness-of-fit test of our best models using bootstrap procedure. We performed model averaging for the models with closed AIC values using the package AICcmodavg (Mazerolle, 2006). Because egg masses of *R. temporaria* and of *R. dalmatina* are easy to detect and could be used as a proxy for breeding-female population size (Veysey et al., 2011), we counted these egg masses at the pond scale. We tested the effect of pond type on the pond occupancy using GLM (binomial error distribution), and the relationships between their abundance and the same explanatory variables (pond type, woodland and agricultural areas, fish presence and macrophyte frequency) using GLM and the same approach used for richness analysis.

## 3. Results

### 3.1. Landscape and pond characteristics

Landscape and pond abiotic characteristics differed between highway and surrounding ponds (Table 1). There was more artificial and agricultural land cover and less woodland land cover around highway ponds than around surrounding ponds. Salinity, pH, conductivity, nitrogen ($NO_2$), nitrate ($NO_3$) and phosphate ($PO_4$) concentrations were also higher in highway ponds. In contrast, we found no difference in the permanence status, in the presence or absence of fish or the frequency of macrophytes between the two pond types. As expected, agricultural surface area was positively correlated with $NO_3$, $NO_2$, conductivity, salinity and pH (Appendix A) whereas woodland surface area was not.

### 3.2. Amphibian richness

Eight amphibian species were identified in the surrounding ponds. Of these species, seven were also found in highway ponds (Table 2). Surprisingly, we did not detect any significant difference in amphibian richness (naïve and estimated) between surrounding ponds and highway ponds (Table 3 and Appendix C). Richness was only influenced positively by the proportion of woodland area, not by agricultural area, macrophyte frequency or fish presence.

The proportion of highway ponds (71%) inhabited (overall species) was similar to that of surrounding ponds (80%), and the (naïve) occupancy rate did not significantly differ from that of surrounding ponds for two-thirds of the cases examined (overall stages or species) (Table 2). However, for four of the six cases, *L. helveticus* adult, *T. cristatus* larvae, *R. temporaria* and *R. dalmatina*

**Table 2**
Proportion of ponds inhabited for each amphibian species among pond types assessed by egg mass count and dip netting (naïve data).

| Species | Stage | Highway ponds | | Surrounding ponds | | P |
|---|---|---|---|---|---|---|
| | | Number | Percentage | Number | Percentage | |
| *Lissotriton vulgaris*[a] | Adult | 5 | 8% | 2 | 4% | 0.55 |
| *Lissotriton helveticus*[a] | Adult | 8 | 14% | 19 | 42% | <0.001 |
| *Lissotriton helveticus/vulgaris*[b] | Larvae | 14 | 50% | 12 | 60% | 0.57 |
| *Ichthyosaura alpestris*[a] | Adult | 1 | 2% | 0 | 0% | 0.69 |
| *Ichthyosaura alpestris*[b] | Larvae | 1 | 3% | 2 | 10% | 0.55 |
| *Triturus cristatus*[a] | Adult | 1 | 2% | 0 | 0% | 0.69 |
| *Triturus cristatus*[b] | Larvae | 1 | 3% | 5 | 25% | 0.03[d] |
| *Salamandra salamandra*[a] | Adult | 0 | 0% | 2 | 4% | 0.18 |
| *Bufo bufo*[a] | Adult | 5 | 8% | 7 | 16% | 0.36 |
| *Bufo bufo*[a] | Larvae | 3 | 9% | 1 | 5% | 0.08 |
| *Bufo bufo*[a] | Frogspawn | 0 | 0% | 3 | 7% | 1.00 |
| *Rana dalmatina*[a] | Frogspawn | 7 | 12% | 11 | 24% | <0.001 |
| *Rana temporaria*[a] | Frogspawn | 14 | 24% | 21 | 47% | <0.001 |
| *Rana temporaria*[a] | Adult | 0 | 0% | 3 | 7% | 0.08 |
| *Pelophylax esculentus*[a] | Adult | 8 | 14% | 0 | 0% | <0.001 |
| *Pelophylax esculentus*[b] | Adult | 14 | 50% | 1 | 5% | <0.001 |
| *Pelophylax esculentus*[b] | Larvae | 13 | 47% | 10 | 50% | 1.00 |

[a] Sampling done in early spring in 58 highway ponds and 45 surrounding ponds.
[b] Sampling done in early summer in 29 highway and 20 surrounding ponds.

egg masses for which significant differences occurred, the naïve occupancy rate was higher in surrounding than in highway ponds (Table 2). Note however that accounting for the detectability of species (occupancy modeling), we did not detect difference in the occupancy rate of the common newt adults (*L. vulgaris* adult), of the great crested new larvae (*T. cristatus* larvae) of the palmate newt adults and larvae (*L. helveticus* adult, *L. helveticus/vulgaris* larvae), and of green frog tapdoles (*P. esculentus* larvae). For the other species, the low occupancy of ponds suggests that more data are needed.

### 3.3. Relationships between species abundance and pond characteristics

#### 3.3.1. Egg masses of Rana temporaria and Rana dalmatina

The abundance of *R. temporaria's* egg masses was significantly greater in surrounding ponds than in highway ponds (Table 4), while the abundance of *R. dalmatina's* eggs masses did not differ significantly between the two pond types. We found positive effects of woodland area, agricultural area on egg mass abundance of the two species, but no significant effect of fish presence and macrophyte frequency (Table 4).

#### 3.3.2. Palmate newt larvae and adults (L. helveticus)

The abundance of adult and larvae palmate newts was also higher in surrounding ponds than in highway ponds (Table 5, *adult*: $\beta = +1.23 \pm 0.37$ SE, $P < 0.001$; larvae: $\beta = +0.28 \pm 0.27$ SE, $P < 0.001$), with 2.96 vs. 0.21 larvae in early summer and 0.94 vs. 0.27 adults in early spring respectively, per sampled site within pond (per approximately 1 $m^2$), accounting for detection probabilities (Fig. 1). Palmate newt abundance was also affected by agricultural (negatively, adult: $\beta = -1.62 \pm 0.52$ SE, $P = 0.002$; larvae: $\beta = -1.74 \pm 0.31$ SE, $P < 0.001$) and woodland area (positively, for adult: $\beta = +4.32 \pm 1.68$ SE, $P = 0.01$; but surprisingly negatively for larvae: $\beta = -4.30 \pm 0.36$ SE, $P < 0.001$), and by the sampling date in the summer period for larvae ($\beta = -0.09 \pm 0.01$ SE, $P < 0.001$).

Local environmental variables also affected the detectability of palmate newt larvae but not of adult. The detectability of larvae (Table 5 and Appendix D) was lower in surrounding ponds than in highway ponds ($\beta = -1.24 \pm 0.20$ SE, $P < 0.001$), lower when fish were present ($\beta = -4.27 \pm 8.16$ SE, $P < 0.001$), and slightly higher when sampling was done later in the summer season ($\beta = 0.05 \pm 0.01$ SE, $P < 0.001$). Interestingly, we noted a strong effect of fish presence on the detection of palmate newt larvae, but no effect of macrophytes.

#### 3.3.3. Green frog complex tadpoles (P. esculentus larvae)

Green frog tadpoles were less abundant in surrounding ponds than in highway ponds ($\beta = -0.46 \pm 0.17$ SE, $P < 0.001$). The abundance of green frog tadpoles was positively affected by woodland area ($\beta = +3.42 \pm 0.68$ SE, $P < 0.001$) and macrophyte frequency ($\beta = +1.24 \pm 0.17$ SE, $P < 0.001$), negatively by fish

**Table 3**
Effects of environmental variables on naïve richness.

| Variable | Estimate | *F* value | *P* value |
|---|---|---|---|
| Surrounding ponds vs. highway ponds | $\beta = +0.29 \pm 0.21$ | $F_{1,97} = 1.34$ | 0.25 |
| Proportion of woodland area | $\beta = +0.22 \pm 0.06$ | $F_{1,97} = 15.9$ | <0.001 |
| Proportion of agricultural area | $\beta = -0.05 \pm 0.05$ | $F_{1,97} = 1.09$ | 0.30 |
| Macrophyte frequency | $\beta = +0.00 \pm 0.19$ | $F_{1,97} = 0.00$ | 0.99 |
| Presence of fish | $\beta = -0.08 \pm 0.30$ | $F_{1,97} = 0.07$ | 0.78 |

**Table 4**
Effects of environmental variables on abundance of *Rana temporaria* and *Rana dalmatina* egg masses.

| Variable | Estimate | *F* value | *P* value |
|---|---|---|---|
| *R. temporaria egg masses* | | | |
| Surrounding ponds vs. highway ponds | $\beta = +1.36 \pm 0.12$ | $F_{1,97} = 12.63$ | <0.001 |
| Proportion of woodland area | $\beta = +4.35 \pm 0.48$ | $F_{1,97} = 13.82$ | <0.001 |
| Proportion of agricultural area | $\beta = +2.46 \pm 0.31$ | $F_{1,97} = 7.03$ | <0.001 |
| Macrophyte frequency | $\beta = +0.47 \pm 0.11$ | $F_{1,97} = 1.53$ | 0.22 |
| Presence of fish | $\beta = -0.06 \pm 0.17$ | $F_{1,97} = 0.01$ | 0.92 |
| *R. dalmatina egg masses* | | | |
| Surrounding ponds vs. highway ponds | $\beta = +0.68 \pm 0.24$ | $F_{1,97} = 1.26$ | 0.26 |
| Proportion of woodland area | $\beta = +28.75 \pm 5.76$ | $F_{1,97} = 14.22$ | <0.001 |
| Proportion of agricultural area | $\beta = +1.48 \pm 0.48$ | $F_{1,97} = 1.47$ | 0.23 |
| Macrophyte frequency | $\beta = +0.50 \pm 0.21$ | $F_{1,97} = 0.84$ | 0.36 |
| Presence of fish | $\beta = +0.62 \pm 0.29$ | $F_{1,97} = 0.61$ | 0.43 |

**Table 5**
Selected AIC (Akaike's Information Criterion) models for palmate newts (larvae and adults) and green frog tadpoles, accounting for detection probability using a point-count model.

| Model[a] | ΔAIC | w | np |
|---|---|---|---|
| *Palmate newt larvae (L. helveticus/vulgaris)* | | | |
| p (hvsp, fish, veg, date), n (hvsp, wood., agri., veg, fish, date) | 0.00 | 1 | 12 |
| *Palmate newt adults (L. helveticus)* | | | |
| p (hvsp, fish), n (hvsp, wood., agri.) | 0 | 0.43 | 7 |
| p (hvsp, fish, veg), n (hvsp, wood., agri., veg) | 0.14 | 0.40 | 9 |
| *Green frog tadpoles (P. esculentus)* | | | |
| p (hvsp, fish, veg. date), n (hvsp, wood., agri., veg., fish) | 0.00 | 1 | 11 |

[a] Models are supported by biological hypotheses and ranked according to ΔAIC. Factors affecting abundance (n) and detection (p) probabilities included the pond type, "highway stormwater versus surrounding ponds" (hvsp), the proportion of woodland areas (wood), the proportion of agricultural areas (agri), the presence/absence of fish (fish), the frequency of macrophyte vegetation (veg) and the date of sampling (date). The relative differences in AICc values are given compared to the top-ranked model (Δ), AICc weights (w) and the number of parameters (np) in the various models (see Appendix B for model selection procedure) were given.

($\beta = -2.75 \pm 0.47$ SE, $P < 0.001$) and not significantly by agricultural area ($\beta = -0.35 \pm 0.24$ SE, $P = 0.15$). The detection probability of tadpoles was significantly higher in surrounding ponds ($\beta = 1.71 \pm 0.21$ SE, $P < 0.001$) than in highway ponds, and negatively affected by the date in the summer period ($\beta = -0.033 \pm 0.006$ SE, $P < 0.001$).

## 4. Discussion

Surprisingly, we found that highway ponds harbored nearly as many amphibian species and a similar richness and occupancy rate as surrounding ponds. However, as expected, the majority of species were less abundant in highway than in surrounding ponds, the reverse only being true for *P. esculentus*.

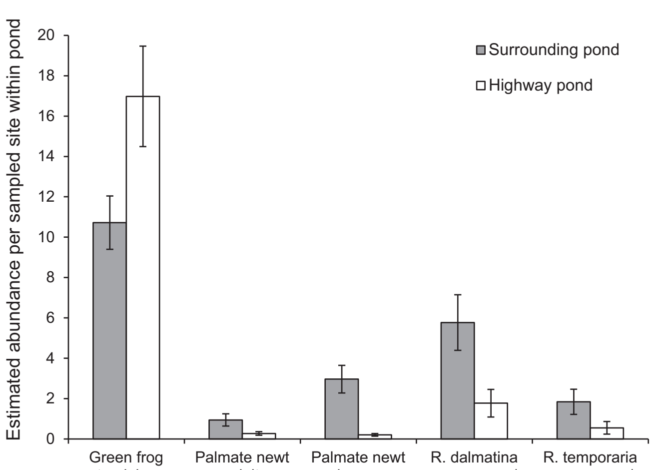


**Fig. 1.** Abundance, adjusted to local and landscape variables and corrected by detection probability, estimated per sampled site within pond (per 1 $m^2$) in highway and surrounding ponds for tadpoles of the green frog complex (*Pelophylax esculentus*) and palmate newt adults and larvae (*Lissotriton helveticus*, *Lissotriton helveticus/vulgaris*), and abundance per pond (*) of *Rana temporaria* and of *Rana dalmatina* egg masses.

### 4.1. Abiotic differences between highway and surrounding ponds

Highway ponds differed from surrounding ponds with respect to abiotic characteristics, likely due to their function and the proximity of the carriageway. As expected, they were located in more human-dominated landscapes due to the proximity of road networks and urbanization, which implies a high percentage of impervious cover increasing the pollution rate in ponds. The highway ponds were also located in landscapes with more agricultural areas than surrounding ponds, most likely due to the low number of other pond types in such intensive agricultural landscapes. Thus, the higher nutrient (nitrate and phosphate) concentration found in highway ponds is most likely explained by these landscape characteristics and by traffic, as motor vehicles are known to be a major source of nitrogen oxides (Cape et al., 2004). Similarly, we found a higher salinity in highway ponds, which was likely due to road management, as salt (NaCl) is a common deicing agent and high concentrations of chlorides are characteristics of motorway ponds (Scher and Thièry, 2005; Van Meter et al., 2011). In contrast, surrounding ponds were located in more wooded landscapes than highway ponds, which may explain the higher frequency of leaflitter (russet) and, consequently, the more acidic pH. Overall, these results are in accordance with previous studies on chemical and physical characteristics of urban stormwater runoff in comparison to ponds located in less disturbed habitats (Karouna-Renier and Sparling, 2001; Rubbo and Kiesecker, 2005). Interestingly, surrounding and highway pond samples did not differ according to the other factors described, such as fish occurrence (here, perch: *Lepomis gibbosus*; carp: *Cyprinus carpio*) macrophyte frequency, pond perimeter or permanence status. All of these factors can strongly influence the structure of amphibian communities (Semlitsch, 2002).

### 4.2. Different amphibian populations between highway and surroundings ponds

Surprisingly, even if highway ponds were not on par with surrounding ponds, especially when accounting for species abundance, we did not find the strong differences that might be expected between the two pond types regarding amphibian population. The presence of amphibians was similar between the two pond types, with, for example, more than 70% of highway ponds sheltering amphibians, compared to 80% of surrounding ponds. Seven out of the eight species detected in surrounding ponds were also found in highway ponds (the exception was the salamander), and evidence of reproduction was found for six species. Further, no difference was detected in species richness (naïve and estimated). Note, however, that some results have to be taken with caution because some species were too rare in our dataset to draw conclusions about the relative role of highway ponds compared to other pond types for reproduction (*Salamandra salamandra*, *I. alpestris*, Table 2).

Local environmental variables significantly affected the detectability of amphibian larvae. For example the presence of fish strongly affected the detectability of palmate newt larvae (not of adults). This result may be linked to the development of behavioral adaptations in the presence of predators that render them less susceptible to be captured (Teplitsky et al., 2003). This differential effect according to newt stages may be explained by their vulnerability to be caught by fish and thus by newt size. Fish presence is indeed known to have a strong effect on the abundance of amphibians and has been suggested as a major structuring factor of amphibian assemblages (Hecnar and M'Closkey, 1996). The less regular structure of surrounding pond banks as opposed to highway pond banks may also explain the differences in green frog tadpoles and palmate newt larvae detectability between the two pond types. Finally we found an effect of the sampling date (during the early summer period) which affected positively the detectability of palmate newt larvae and negatively the detectability of green frog tapdoles. We thus strongly stress the need to carefully account for this effect when studying amphibian community. We believed that these effects (fish, date) should not have affected our results on species richness thanks to our sampling design: the absence of correlation between the pond type and the presence of fish, and in general between the pond type and the main local described variables (Table 1), the absence of correlation between the sampling date and the pond type in early spring period when all species were detected, and the absence of date effect on the estimated occupancy rate of species.

The occupancy rates of species did not significantly differ in the majority of cases examined (Table 2 and see before). In this respect, our results are comparable to those found by Brand and Snodgrass (2010) in a study on North American amphibians that breed in natural and artificial ponds. However as expected, when differences were found (for the more frequently found groups), species tended to occur more frequently in surrounding ponds than in highway ponds e.g., adults of *L. helveticus*, larvae of *T. cristatus*, and frogspawns of *R. temporaria* and *R. dalmatina*. For the latter four species, these results seem partly consistent with their habitat preferences (ACEMAV et al., 2003). The reverse was only true for the adults of *P. esculentus*, a species known for its ubiquity (Morand and Joly, 1995), its capacity to colonize eutrophic ponds (Scher and Thièry, 2005), and its high abundance in road stormwater ponds (Scher and Thièry, 2005). Note that the densities estimated in our study are consistent with the literature (for newt larvae and green frog tadpoles, see Van Buskirk, 2005).

Abundance analyses for the most common species (*R. dalmatina*, *R. temporaria*, *L. helveticus*, *P. esculentus*) confirmed the trends in the occurrence data for palmate newt adults and egg masses of *R. dalmatina* and of *R. temporaria*, which were more abundant in surrounding than in highway ponds. They also made it possible to detect differences not found in the occurrence rates for larvae of *L. helveticus/vulgaris* and tadpoles of *P. esculentus*, i.e., in two of the four cases examined.

The abundance of palmate newts was influenced by surrounding environmental factors likely because they overwinter in the surroundings. Note that this positive effect of woodland areas on palmate newt adults was also found on the abundance of *R. temporaria* and *R. dalmatina* egg masses and on the abundance of *P. esculentus* tadpoles. For that matter, some authors have suggested that the lower occurrence of some amphibian species, including newts, salamanders and frogs, in urban wetlands may be associated with the loss of forested terrestrial habitats in the areas surrounding the sites because these species have life-history stages that require forested habitats adjacent to breeding sites (Guerry and Hunter, 2002; Rubbo and Kiesecker, 2005; Van Buskirk, 2005; Babbitt et al., 2006,). Thus, amphibian abundance was also strongly negatively affected by the amount of agricultural area surrounding the ponds, in accordance with other studies (Beja and Alcazar, 2003), which was possibly due to the lower abundance of overwintering sites in highly intensive agricultural landscapes as well as to the higher level of fertilizers (*L. helveticu*). The higher levels of pollutants and salinity reported in highway ponds (Karouna-Renier and Sparling, 2001; this study) may explain the difference in the distribution of species abundance between the two pond types because their negative effects (nutrients: Johnson et al., 2007; pesticides and herbicides: Sparling et al., 2001; heavy metals: Snodgrass et al., 2008 but also salt: Karraker et al., 2007, 2010; Brand et al., 2010; Harless et al., 2011) are suggested to be important factors influencing amphibian community composition (Snodgrass et al., 2008). For example, the higher concentrations of nutrients (nitrogen oxides and phosphates) occurring in ponds in agricultural landscapes (Table 1, see also Bishop et al., 2000; Garcıa-Munoz et al., 2010), as they receive runoff from surrounding land where fertilizers and pesticides are applied, might impair amphibian fitness (Marco et al., 1999; Brand et al., 2010). The aquatic eutrophication also promotes pathogenic infection in amphibians (Johnson et al., 2007). A higher nutrient concentration may also result in a greater development of vegetation, which may indirectly explain the positive effect of macrophyte frequency on the abundance of *P. esculentus*, considered more tolerant to aquatic eutrophication than the other species.

It is therefore highly probable that these various factors (landscape and local) act together (Ficetola and De Berardi, 2004; Van Buskirk, 2005) in a context-dependent fashion to influence amphibian assemblage structure in these artificial ponds.

### 4.3. Overall assessment on the amphibian community

Man-made ponds with recent technical function were suggested to have a conservation value – depending obviously on regional settings and design criteria (Herzon and Helenius, 2008; Brand and Snodgrass, 2010). Our results, based on count data and taking detectability into account, showed that the highway stormwater retention ponds constructed with the aim of retaining pollutants are not equivalent to the other pond types ("natural"/farmland). They cannot of course replace the compensatory measures that consist in creating or restoring ponds for the conservation of threatened species.

Highway pond networks do not increase regional biodiversity in terms of species presence and are less important for amphibian reproduction than "semi-natural" ponds. However, they form large networks (e.g., one pond every 2 km along highways in France) and most likely contribute to the connectivity between remote ponds within a context of intensive agricultural landscapes where natural and farmland ponds have disappeared. They thus may contribute to maintaining populations in such landscapes. Note that we have focused on highway ponds with natural substrates, not with artificial laminated (plastic) bottoms, for which the results would be expected to be very different (e.g., a possible trap effect).

### 4.4. Interest for biodiversity-friendly management of stormwater retention ponds

Despite the restricted number of species, the single-year study and the restricted range of the study, our findings have important implications: In the context of strong biodiversity decrease, we think that road engineers should consider highway water bodies not only for their function of retaining pollutants but also for their potential roles in biodiversity, both negative and potentially positive in human-dominated landscapes. One key issue is to prevent these ponds from becoming traps due to their design and management regimes (McCarthy and Lathrop, 2011; see also Zhen-xing et al., 2010).

Among the environmental conditions that influenced the amphibian occupancy and abundance in ponds, some can be taken into account in construction choices and in management decisions. During construction, the preservation of woods within highway edges should be a priority, as they are necessary for the life cycle of many amphibian species. Revegetation should take into account this aspect. Because the slope of a pond influences aquatic vegetation, which in turn impacts amphibian abundance and accessibility (Chang et al., 2011), at least one part of each pond bank should have a gentle slope. Management decisions could also favor amphibian abundance through the extensive management of macrophytes and of fish occupancy, which strongly affects the occupancy and abundance of amphibians (Hecnar and M'Closkey, 1996; Hamer and Parris, 2011). Due to the runoff regulation function of these highway ponds, draining frequency can be easily controlled. Permanently ponded stormwater basins in southern New Jersey, USA, function as traps for some frog species and as source habitats for potentially problematic invasive species, such as *Rana catesbeiana* (McCarthy and Lathrop, 2011). As the permanence status of ponds strongly affects fish presence, which negatively affects amphibian occupancy and abundance (Van Buskirk, 2005; this study), dryness in late summer should be encouraged to suppress the fish populations (such as the exotic species *L. gibbosus* in Europe). We stress that further studies are needed to better assess the roles of these artificial structures in biodiversity in general and in breeding populations of amphibians, especially at the landscape scale.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2012.06.031.

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