The contribution of motorway stormwater retention ponds to the biodiversity of aquatic macroinvertebrates

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A B S T R A C T

Biodiversity conservation does predominantly focus on protected natural areas, but has to consider also the usually Human-dominated matrix in which these natural areas are embedded. Here we study highway stormwater retention ponds, which may act as refuges for native flora and fauna and contribute to the maintenance of biodiversity in Human-dominated landscapes. However, the biodiversity supported by such artificial ponds has received little attention so far. Using standardised methods, we addressed the potential role of highway stormwater ponds as refuges by comparing aquatic macroinvertebrate communities (Coleoptera, Heteroptera, Odonata and Gastropoda) in highway stormwater ponds with ponds in the wider landscape. As expected from their pollutant retention function, highway ponds differed in abiotic conditions from surrounding ponds. However, they supported aquatic macroinvertebrate communities at least as rich and diverse at the family level as surrounding ponds and exhibited similar variability in family community composition and structure. The main difference we observed was a higher abundance of small and/or short-lived invertebrates in the highway ponds. These similar community compositions and structures suggest that highway ponds contribute to the biodiversity of the pond network at a regional scale. Thus, road practitioners should consider highway ponds not only for their hydrological and pollutant retaining purposes but also as a possibility to increase the role of highway verges as a refuge and, consequently, landscape connectivity. The management of these water bodies should recognise their potential for biodiversity especially in Human-dominated landscapes.

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1. Introduction

During the last decade, conservation biology has focused on biodiversity hot-spots and/or rare and protected species. However, in major industrial countries, protected natural areas often represent only a small fraction of the total land area (for example 2–12% in France, depending on the protection criteria used), which is unlikely to be sufficient to conserve the majority of biodiversity, especially in a context of climate change (Pressey et al., 2007). A complementary emergent view, justified both by conservative goals and the social and economic value of biodiversity (Chapin et al., 2000; Millennium Ecosystem Assessment, 2005), highlights the need to consider biodiversity not only in protected natural areas, but also in the usually Human-dominated landscape matrix, to favour *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 been found to have a negative impact on biodiver-

sity (Trombulak and Frissell, 2000; McKinney, 2006), they may also provide important refuge and connectivity roles within the landscape (Savard et al., 2000; Le Viol et al., 2008; Vermonden et al., 2009), in addition to their primary technical function.

This approach may be of particular interest for aquatic ecosystems, which have dramatically decreased during the last century (wetland losses reached 40–90% in a number of northern European countries; Hull, 1997) due to fast anthropogenic changes in landuse. This is notably the case for ponds (E.P.C.N., 2007), which were found the most species-rich aquatic habitat (in comparison to lakes, rivers and streams) at the regional scale (Davies et al., 2008) and can be viewed as biodiversity hot-spots (Williams et al., 2004; Davies et al., 2008). The ecological network of ponds has in fact dramatically changed over the past decades due to the loss of numerous anthropogenically created and natural ponds, which resulted in increasing isolation of the remaining ponds (Tamisier and Grillas, 1994; Gibbs, 2000). Simultaneously, new ponds have been created in response to new uses: recreational (golf courses, green parks, fishing), safety (firefighting water supply) and pollution retention. Stormwater ponds along highways are now required by legislation (European Union directive 91/271/CEE, French law 92/3) to retain stormwater runoff and

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pollutants deposited on roads by traffic (heavy metals, sediments, nutrients, petroleum hydrocarbons, salts, pesticides: see Davis et al., 2001; Karouna-Renier and Sparling, 2001). This aims to retain polluted runoff, reducing its impact on other water bodies (Scher and Thiery, 2005).

As for other types of man-made ponds (see: Beja et al., 2003; Williams et al., 2004; Declerck et al., 2006; Céréghino et al., 2008; Ruggiero et al., 2008 for farmland ponds; Wood et al., 2001 for industrial ponds; Clements et al., 2006 for urban ponds), these new ponds support wildlife (Karouna-Renier and Sparling, 2001; Scher and Thiery, 2005; Snodgrass et al., 2008; Vermonden et al., 2009) and may serve as corridors and refuges for the native fauna and flora. This role of refuges, defined here as spatial structures providing alternative stable habitats where species can complete their life cycle when their habitats are degraded, likely depends on surrounding landscape. In natural or semi-natural habitats (i.e., not strongly affected by strong anthropogenic activity) generally supporting high species diversity, highway retention ponds may have negative effects on biodiversity due to their high level of pollution and because they promote the invasion of non-indigenous species (e.g. Jodoin et al., 2007: *Phragmites australis* in North America). In contrast, in Human-dominated areas, where wildlife habitats are critical for the conservation of biological diversity and ecological processes, highway stormwater ponds may play a crucial role because they form large networks, (e.g. one pond every 2 km along highways in France), often connected by ditches running along highways. Their presence may thus enhance regional diversity (by creating refuges) and connectivity (corridors, stepping stones) among aquatic ecosystems. However, despite many studies focusing on physical and chemical aspects of these ecosystems (Sriyaraj and Shutes, 2001), very few studies have examined the role of motorway stormwater ponds in biodiversity conservation (except see Scher and Thiery, 2005).

The aim of the present study is to evaluate the distribution of biodiversity within and among ponds and the potential role of highway stormwater retention ponds as refuges for biodiversity. Due to their pollutant retention function, highway stormwater ponds are expected (i) to shelter impoverished communities and (ii) to share similar community composition within a given geographic region, because they share a high number of abiotic characteristics: they were built simultaneously to retain pollutants, which constrains their age, shape, and artificial surroundings. We can thus expect that two highway stormwater ponds support more similar faunistic communities than a highway stormwater pond and another type of neighbouring pond (surrounding pond) or than two ponds in the landscape. To define relevant conservation policies, it is therefore crucial to characterise the spatial partitioning of regional γ diversity (Whittaker, 1972; Crist et al., 2003) between its different components (α and β diversity) instead of focusing on local species richness only (α diversity). To address this, we compared community richness and composition in highway stormwater ponds with those of other ponds located in the surrounding landscape using four taxonomic groups (Coleoptera, Heteroptera, Odonata, Gastropoda). These groups differ in their ecological requirements, life cycle, feeding mode, and dispersal abilities. Therefore, we believe (1) these groups are representative of the pond animal community, (2) they are highly complementary in the macroinvertebrate food web (Downing, 2005) and (3) are likely affected differently by environmental variables (pollution, watershed land-use; Oertli et al., 2005; Bilton et al., 2006; Karouna-Renier and Sparling, 2001). We specifically examined (i) whether highway stormwater retention ponds and surrounding ponds sheltered different taxonomic and functional trait diversity, (ii) whether community composition was more similar among highway ponds than among surrounding ponds (comparing β diversity), and (iii) in what way highway ponds may contribute to the overall pond biodiversity in Human-dominated areas (γ diversity).

2. Methods

2.1. Study area

This study was conducted along a 56 km section of highway A11 (1°39′30″E–48°29′15″N to 1°03′E–48°14′N), built in 1972 in France. The study area is characterised by a temperate climate and successively traverses landscapes dominated by urban, woodland and agricultural land covers. The traffic levels are among the highest in France, with an average of above 88,000 vehicles per day (Cofiroute, unpublished data).

2.2. Site selection and field survey

2.2.1. Site selection

We sampled all highway stormwater ponds ($n = 25$) containing water within 50 m of the carriageway edge along the 56 km of the study section, on both sides of the highway. Using geomorphic maps, aerial photographs, and field surveys, we sampled 18 additional permanent and accessible ponds within 15 km of the highway but at least 150 m from any road, by way of obtaining a comparable number of surrounding ponds and highway ponds in the different landscape types. All selected highway ponds were built to collect and retain highway water runoff but none were planted-up with plants to retain pollutants. In contrast, none of the sampled surrounding ponds received road runoffs. Also, surrounding ponds were not connected to the hydrographic network and did not collect agricultural drainage. The region in which the study was conducted is mostly flat. Although 6 among the 18 surrounding ponds do not actually meet a particular use, all surrounding ponds are likely anthropogenic ponds (10 for hunting, 2 for farm uses). Contiguous environments (within a 25-m radius) also differ among surrounding ponds: 5 of the 18 surrounding ponds studied were bordered by crops, while 7 by woodland, 3 by fallow and 3 by meadow. Although more than half of them were located in a Natura2000 area, surrounding ponds should not be considered as "unaltered", "natural" ponds, but rather as ponds representative of those located in the landscape crossed by the highway.

2.2.2. Field survey

In each pond, invertebrates were sampled at five sites evenly distributed around the pond, the first site being located at the Northern most point of the pond. In 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 (mesh-size: 250 μm). During each sweep, we gently agitated the bottom sediments to ensure the collection of both nektonic and benthic macroinvertebrates. All inventories were performed between June 15 and July 15, 2006.

To quantify the environmental differences between the two pond types, we recorded the following characteristics: pond perimeter (m), pond bottom type (clay, clay–gravel, clay–silt, clay–litter, litter, litter–silt, silt), presence/absence of fish (field observations and Cofiroute unpublished data), abundance of macrophytes (helophyte, hydrophyte, absence) and macrophyte diversity (Shannon diversity index), which were estimated according to the frequency of each vegetation type among the five sampled sites. We estimated the area of the different land-use types (artificial, farmland and woodland) within a 500-m radius buffer around each pond, using CORINE land cover mapping data and the Geographical Information System package ARCGIS 9 (ESRI, 2000). This buffer size corresponds to a compromise between the Corine land cover grain size and the known influence of landscape on pond

biodiversity at small scales (Declerck et al., 2006). We also measured chemical characteristics of each pond during a short period (March 15–March 26, 2007), a period characterised by low precipitations (average 0.8 mm per day) and temperatures (average 4 °C at 8 h 00 UTC): in three sites per pond, we recorded *in situ* the conductivity and salinity using CONSORT C500 equipment and collected water samples for further chemical analyses (concentration in PO_4, NO_2, NO_3, and pH).

2.3. Macroinvertebrates: taxa level

Due to economic and temporal constraints, all individuals of the four taxonomic groups studied (Coleoptera, Heteroptera, Odonata and Gastropoda) were identified at the family level, using recent key books (Gerken and Sternberg, 1999; Tachet et al., 2000; Heidemann and Seidenbuch, 2002). Of course, we cannot exclude that different results may be found at the species level. However, this approach allows considering more samples within ponds and between ponds. In addition, this choice takes into account a very large part of sampled individuals because early stages of development could be identified at the family level whereas only adults or late stages could be identified at the species level. The analyses carried out on abundance are thus based on nearly the total number of individuals collected. Moreover, many studies have shown a significant correlation with richness at the family and species level in several taxonomic groups (Williams and Gaston, 1994; Ricotta et al., 2002; Heino and Soininen, 2007; Lovell et al., 2007; see also Mandelik et al., 2007). For aquatic macroinvertebrates, the influence of a higher taxonomic level of identification has been studied mainly for classifying streams (Marshall et al., 2006; Heino and Soininen, 2007). Although more differences between locations might be revealed by analyses at species level, a higher taxon resolution should be sufficient to distinguish the greater between-site differences (Lenat and Resh, 2001). Hewlett (2000), focusing on Ephemeroptera, Plecoptera and Trichoptera, considered that genus-level and species-level identification is unnecessary in broad-scale monitoring, as identification at the family level only is sufficient. Note that we used the family diversity as a proxi for species diversity, but we did not compare family richness among the four taxonomic groups because the families did not include similar number of species. Finally, our study relies on the analysis of biological traits, which were mostly characterised at the genus-family level. Given their quite coarse resolution, these traits are rather consistent within a given family.

2.4. Taxa traits

To address the influence of pond type on community functional composition, we characterised taxa based on readily available functional traits using Tachet et al. (2000) and Usseglio-Polatera et al. (2000) information adapted to family level (Supplementary material 1). These functional traits include maximum adult size (<2.5 mm, 2.5–5 mm, 5–10 mm, 10–20 mm, 20–40 mm, 40–80 mm), life cycle duration (< or ⩾1 year), number of generations per year (<1, 1, >1), primary dispersal mode (aquatic passive, aquatic active, aerial passive, aerial active), main food source (detritus (<1 mm), dead plant (⩾1 mm), living microphytes, living macrophytes, dead animals (<1 mm), living microinvertebrates, living macroinvertebrates, vertebrates) and main feeding mode (shredder, scraper, filter-feeder, piercer, predator). Following Pavoine and Dolédec (2005), we assigned a percentage score to each taxon for each trait category using average family affinity measured from the Usseglio-Polatera database (2000) (Supplementary material 1) when a family could be characterised by several categories of a given trait (e.g. family Notonectidae is 82% in category life cycle duration >1 and 18% in category life cycle duration <1).

2.5. Data analysis

All analyses were conducted with R software (R Development Core team, 2007) except where otherwise indicated.

2.5.1. Abiotic characteristics

To assess environmental differences between highway ponds and surrounding ponds, we performed Fisher exact tests on contingency tables (qualitative variables) and Kruskall Wallis tests (quantitative variables). We also examined the correlations among environmental variables (quantitative variables) using Pearson correlation tests and, when two or more variables were strongly correlated, we retained only one of them in the subsequent faunistic analyses.

2.5.2. Faunistic composition
2.5.2.1. Richness. To study the influence of pond type on taxa richness at different spatial scales, we measured family richness at the site scale (S_{local}), at the pond scale (S_{pond}) and at the pond type scale, within each pond type (S_{type}, within Highway stormwater pond type – hereafter HP or Surrounding pond type – hereafter SP). Comparing observed family richness (S_{obs}) across ponds and habitats might not be valid in case of unequal family detection probabilities (Boulinier et al., 1998; Nichols et al., 1998). We therefore used statistical methods derived from the capture–recapture methodology to estimate family richness (S_{est}) and changes in community composition. As in recent studies addressing richness estimation and differences in community composition from species count data (Kerbiriou et al., 2008; Le Viol et al., 2008), we used the program COMDYN (Hines et al., 1999), based on the jack-knife estimator of Burnham and Overton (1979). To estimate family richness at the pond level (S_{pond}), we used site samples as replicates. Two ponds (one highway pond and one surrounding pond) were excluded due to insufficient number of sampled families (thus for COMDYN analyses, $n = 41$). To estimate richness at the pond type level (S_{type} for highway stormwater pond or surrounding pond type), we used ponds as replicates ($n = 18$): analyses were based on presence–absence data at the pond level, pooled across the five sites. As 18 replicates only were available for surrounding ponds, we sampled randomly without replacement 18 ponds out of 25 in the highway pond group; this sampling procedure was performed 55 times. Each of 55 pairs of (1) 18 sampled highway ponds plus (2) the 18 surrounding ponds was input into program COMDYN to obtain estimated richness per pond type. The estimated richness in each pond type was then characterised using the mean and standard error of the 55 outputs. We estimated family richness at the pond level (S_{pond}) and at pond type level (S_{type}) by pooling all families. For individual taxonomic group (Coleoptera, Heteroptera, Odonata, Gastropoda), we estimated family richness at pond type level (S_{type}) but not at the pond level (S_{pond}) because of insufficient data. So at the pond level, we focused on observed richness only.

Within the taxonomic groups, we analysed the influence of pond type on both family richness per site (S_{local}) and estimated richness per pond (S_{pond}), using linear models and analyses of variance, as follows: (i) we tested the effect of pond type on the dependent variable (S_{local} and S_{pond}), (ii) the effect of each environmental variable that differed significantly between the two pond types (see above: "pond characteristics"), and (iii) the effect of pond type adjusted to significant environmental variables. The nested structure of the data was taken into account (i.e. local richness per site nested within pond). Estimated richness was weighted by the inverse of its variance.

2.5.2.2. Diversity. We also analysed the effect of pond type on invertebrate diversity, using linear mixed models (lme) and

analyses of variance, where site Simpson's diversity index was used as a dependent variable.

In addition, we examined the partitioning of diversity between scales: (i) per site within ponds, (ii) per pond within pond types, and (iii) between pond types. This was done using the apportionment of quadratic entropy (APQE, Pavoine and Dolédec, 2005). This method links diversity and dissimilarity and allows the decomposition of diversity according to a given hierarchy (within and between: site, pond, pond type). Quadratic entropy has a critical advantage over usual diversity indices because it takes into account differences between species or families. The differences that can be incorporated in APQE may be either taxonomic or functional (taxa attributes). The significance of these diversity components is tested by comparing the observed distribution with those expected to arise by chance using a simulation approach.

As described in Pavoine and Dolédec (2005), we performed APQE analysis using (i) equidistance among families, (ii) taxonomic distance, and (iii) functional distances considering different functional traits (see above: "taxa attributes"). To compute taxonomic distance, we used the approach proposed in Pavoine and Dolédec (2005).

2.5.2.3. Composition. We first verified the absence of spatial autocorrelation in community composition using mantel tests (mantel.randtest) to assess the correlation between matrices of geographic vs. taxonomic distances among ponds. Matrices of family-specific distances across ponds were computed both with the Jaccard index on presence/absence matrix and with the Bray Curtis index on abundance matrix. This effect was also tested separately within both pond types. No spatial autocorrelation in aquatic invertebrate communities (neither across overall ponds nor within pond types) was found.

Second, we examined the effect of pond type on the composition of invertebrate communities using a Constrained Analysis of Principal Coordinates (CAP) followed-up by ANOVA-like permutation tests to assess significance of effects. CAP (capscale) is an ordination method similar to Redundancy Analysis (RDA), i.e. exploring the relationship between two sets of variables, but allowing non-Euclidean dissimilarity indices. It was used to examine whether family similarity among ponds depended on the pond type. It was performed (1) on presence/absence matrices across ponds, using the Jaccard index and (2) on abundance matrices across ponds, using the Bray Curtis index.

Third, we examined whether community β similarity among ponds differed across pond types. This was done using PERMDISP (Anderson, 2006), a computer program to compare the multivariate dispersions among groups (here pond type) on the basis of community similarity matrices. The test is based on (1) the calculation of the distances from observations to their centroid and (2) the comparison of the average of these distances among groups, using ANOVA. A *p*-value is then obtained using 999 permutations of the observations. Permutation dispersion analyses were performed using presence/absence (Jaccard similarity index) and frequency data (Bray Curtis similarity index).

Fourth, accounting for family detectability, we examined the complementarity of communities (Nichols et al., 1998) in each pond type using COMDYN with ponds as replicates (*n* = 18). In addition to estimating richness within each pond type (S_{type} within highway pond and surrounding pond type), we obtained the following estimators: estimated complement of "extinction probability" between the two types, Φ (i.e. proportion of surrounding pond families present in highway stormwater ponds), estimated complement of family "turnover", γ (i.e. proportion of highway stormwater pond families present in surrounding ponds). As for richness, we compared the mean and standard error (over 55 re-sampling

events) of these estimators between highway pond and surrounding pond types.

Finally, we analysed the influence of pond type on abundance of each sampled invertebrate family using generalized linear models and analyses of variance. As for richness, we tested independently (i) the effect of pond type, (ii) the effect of each environmental variable that differed significantly between pond types, and (iii) the effect of pond type adjusted to significant environmental variable. The nested structure of the data was also taken into account (abundance per site nested within pond).

3. Results

3.1. Abiotic characteristics of highway ponds

We found some differences in abiotic characteristics between highway ponds and surrounding ponds (Table 1): the land cover surrounding highway ponds was characterised by larger artificial areas, while the land cover surrounding ponds was characterised by a larger woodland area. Highway ponds exhibited higher salinity, conductivity, pH, and NO_3 concentration. In contrast, we found no difference in pond perimeter, pond bottom type, presence/absence of fish, presence of vegetation, frequency of macrophytes, abundance of helophytes and hydrophytes, agricultural area, nitrogen (NO_2) and phosphate concentrations (PO_4). As some of the variables that differ between pond types were correlated, we retained woodland area (correlated to conductivity and pH: Pearson test $t = -2.5$; $p = 0.015$), NO_3 concentration (correlated to NO_2: Pearson test $t = -10.8$; $p < 0.0001$; with PO_4: Pearson test $t = -2.1$; $p = 0.042$) and salinity (salt is usually deposited on car-

Table 1
Abiotic characteristics of highway stormwater ponds and surrounding ponds. (KW: Kruskall wallis test, F: Fisher exact test.)

	Test	Highway ponds	Surrounding ponds
Artificial area (ha)^{KW}	$\chi_1^2 = 3.8$ $p = 0.050$	9.14 ± 2.13	3.19 ± 1.48
Agricultural area (m²)$_{KW}$	ns		
Woodland area (m²)^{KW}	$\chi_1^2 = 4.5$ $p = 0.034$	24.65 ± 0.47	42.00 ± 6.70
Salinity (mg NaCl/L)^{KW}	$\chi_1^2 = 30.7$ $p < 0.0001$	0.45 ± 0.30	0.09 ± 0.01
Conductivity (mS/cm)^{KW}	$\chi_1^2 = 30.6$ $p < 0.0001$	0.96 ± 0.05	0.18 ± 0.02
pH^{KW}	$\chi_1^2 = 10.4$ $p = 0.001$	8.16 ± 0.22	7.24 ± 0.24
NO_3 (mg/L)^{KW}	$\chi_1^2 = 5.7$ $p = 0.017$	4.23 ± 1.24	1.27 ± 0.35
NO_2 (mg/L)^{KW}	ns	0.08 ± 0.03	0.02 ± 0.01
PO_4 (mg/L)^{KW}	ns	0.59 ± 0.13	0.77 ± 0.21
Pond perimeter (m)^{KW}	ns	163 ± 17	208 ± 31
Fish (presence/absence)^F	ns	7/18	5/13
Vegetation (presence/absence)^F	ns	18/7	11/7
Helophyte (frequency)^{KW}	ns	0.25 ± 0.07	0.14 ± 0.06
Hydrophyte (frequency)^{KW}	ns	0.29 ± 0.08	0.28 ± 0.09
Macrophyte structure diversity	ns	0.12 ± 0.05	0.06 ± 0.04
Pond bottom type^F	ns	Clay (2), clay–gravel (7), clay–silt (2), clay–litter (3), litter (3), litter–silt (1), silt (7)	Clay (5), clay–gravel (1), clay–silt (2), clay–litter (2), litter (5), litter–silt (3), silt (2)

riageways – correlated to conductivity and pH: Pearson test $t = -37.6$; $p < 0.0001$) for subsequent analyses.

3.2. Aquatic invertebrate communities of highway ponds

Across 43 sampled ponds, we observed a total of 34 macroinvertebrate families. We determined 28,047 individuals to family level; they belonged to Gastropoda (7 families – 9808 individuals), Odonata (6 families – 5670 individuals), Coleoptera (12 families – 2408 individuals) and Heteroptera (9 families – 10,161 individuals). Of these four groups, 7720 individuals were found in the 18 surrounding ponds and 20,327 in the 25 highway ponds.

3.2.1. Influence of pond type on macroinvertebrate family richness
We found no significant effect of pond type on the number of families observed at the local scale (site level, $S_{localHP} = 7.76 \pm 0.35$ SE; $S_{localSP} = 6.44 \pm 0.40$ SE), at the pond scale – accounting for detectability – ($S_{pondHP} = 19.87 \pm 4.24$ SE, $S_{pondSP} = 17.89 \pm 4.60$ SE, $F_{1,39} = 1.70$, $p = 0.20$), or at pond type scale ($S_{typeHP} = 30.54 \pm 3.06$ SE, $S_{typeSP} = 34.61 \pm 8.53$ SE). There was also no difference in detection probabilities between the two pond types regardless of scale (detectability at the pond scale surrounding ponds: 0.74; highway ponds: 0.74 and at the pond type scale, surrounding ponds: 0.89; highway ponds: 0.92).

The patterns in family richness varied however across taxonomic groups. The observed site richness of Gastropoda was significantly higher in highway ponds compared with surrounding ponds ($F_{1,41} = 12.2$; $p = 0.001$; $S_{localHP} = 1.70 \pm 0.10$ SE; $S_{localSP} = 0.73 \pm 0.08$ SE, analysis nested to pond), while it did not differ between pond types for the others groups (Coleoptera, Odonata, Heteroptera). However, the family richness of Gastropoda was significantly affected by salinity (positive effect, $F_{1,41} = 13.35$, $p < 0.001$, analysis nested to pond), so that the effect of pond type on Gastropoda disappeared when the salinity effect was accounted for. The estimated pond type richness (accounting for detection probability) did not differ between highway ponds and surrounding ponds for any taxonomic groups (Table 2). There was also no difference in detection probabilities (Table 2).

3.2.2. Influence of pond type on macroinvertebrate family diversity
A partitioning of diversity (APQE: Table 3) showed that Simpson diversity differed significantly between pond types, and across ponds within pond type, but not among sites within ponds. Note however that the diversity proportion explained between pond type was low, accounting only for 2.4% of total diversity, compared with 63% within sites, 8.6% between sites within ponds, and 24% between ponds. Overall, invertebrate diversity was higher in highway ponds than in surrounding ponds (average Simpson diversity per site, highway ponds: 0.60 ± 0.02 SE, surrounding ponds: 0.57 ± 0.03 SE). A similar pattern of diversity partitioning was observed when taxonomic distances among taxa were included in the measure of diversity and when accounting for functional dissimilarities among families (Table 3). Note that in the latter, diversity significantly differed between pond types (Table 3) linked with

Table 3
Partitioning of taxonomic and functional diversity (APQE analysis).

	Within site	Between sites within pond	Between ponds within type of ponds	Between types of ponds
Equidistance				
Diversity	0.55 (63%)	0.07 (8.6%)	0.22 (26%)	0.02 (2.4%)
p Value		$p = 1$	$p = 0.001$	$p = 0.001$
Taxonomic distance				
Diversity	1.34 (64%)	0.18 (8.5%)	0.51 (24%)	0.05 (2.5%)
p Value		$p = 1$	$p = 0.001$	$p = 0.001$
Functional distance				
Adult size				
Diversity	0.19 (58.7%)	0.03 (7.9%)	0.10 (30.9%)	0.01 (2.5%)
p Value		$p = 1$	$p = 0.001$	$p = 0.011$
Cycle duration				
Diversity	0.11 (59.9%)	0.02 (9.0%)	0.04 (22.9%)	0.02 (8.2%)
p Value		$p = 0.99$	$p = 0.001$	$p = 0.001$
Number of generation				
Diversity	0.11 (59.8%)	0.02 (9.2%)	0.05 (27.7%)	0.01 (3.3%)
p Value		$p = 1$	$p = 0.001$	$p = 0.011$
Dispersal mode				
Diversity	0.10 (59.7%)	0.01 (8.7%)	0.05 (28.3%)	0.01 (3.3%)
p Value		$p = 0.97$	$p = 0.001$	$p = 0.001$
Food source				
Diversity	0.17 (62.1%)	0.02 (8.0%)	0.07 (26.4%)	0.01 (3.5%)
p Value		$p = 1$	$p = 0.001$	$p = 0.001$
Feeding mode				
Diversity	0.21 (62.2%)	0.03 (8.4%)	0.09 (26.5%)	0.01 (2.9%)
p Value		$p = 1$	$p = 0.001$	$p = 0.005$

higher abundance (weighted by percentage score of affinity per trait category), in highway ponds than in surrounding ponds, of macroinvertebrates of small and intermediate sizes (<2.5, 2.5–5, 5–10, 10–20 mm), of short-lived macroinvertebrates, of invertebrates having one or more generations per year, of invertebrates with high affinity for passive dispersion, of invertebrates feeding on dead animals, on dead plants, on living microphytes, on living macrophytes, of shredders, piercers and scrapers.

3.2.3. Community composition
Highway ponds and surrounding ponds did not support significantly different macroinvertebrates communities, as shown by CAP performed on presence/absence data and on abundance data (ANOVA-like permutation tests: $F_{1,41} = 1.32$, n.perm = 100, $p = 0.14$; $F_{1,29} = 0.99$, n.perm = 200, $p = 0.10$ respectively). This was confirmed by the COMDYN analysis accounting for detection probabilities: theoretically, surrounding ponds did not exhibit any unique family, 99% of surrounding pond families were found in highway ponds and 95% of highway pond families were found in surrounding ponds. Note that, when considering observed richness, two and four families among the 34 were not observed respectively in the highway ponds (Odonata: Gomphidae, Coleoptera: Dryopidae) and the surrounding ponds (Odonata: Platycnemidae, Coleoptera:

Table 2
Family richness of the four taxonomic groups in highway stormwater and surrounding ponds. S_{obs} is the average observed richness at the pond level, S_{est} the estimated richness at the pond type level, SE the standard error and p the detection probability.

	Highway stormwater ponds					Surrounding ponds				
	$S_{obs(25)}$	SE	S_{est}	SE	p	$S_{obs(18)}$	SE	S_{est}	SE	p
Coleoptera	3.52	0.33	13.39	7.22	0.80	3.11	0.46	11.89	7.16	0.84
Heteroptera	4.12	0.44	8.50	0.46	0.98	4.56	0.35	8.94	3.29	0.89
Odonata	3.12	0.22	5.56	1.54	0.89	3.06	0.26	5.94	2.29	0.84
Gastropoda	3.08	0.26	7.78	2.27	0.89	1.78	0.31	7.00	0.00	1.00

Table 4
Comparison of invertebrate family abundances between highway stormwater ponds (HP) and surrounding ponds (SP), with or without adjustment to the main environmental variable (salinity, woodland, NO_3). All tests are nested within pond. [*]Families marked with an asterisk are found in only one pond type and cannot therefore be tested adjusted to environmental variables.

	Test non-adjusted	Abundance trend	Test adjusted to environmental variable
Gastropoda			
Physidae	$F_{1,41} = 8.85$; $p = 0.005$	HP > SP	$F_{1,39} = 9.13$; $p = 0.004$
Planorbidae	$F_{1,41} = 1.55$; $p = 0.22$		ns
Hydrobiidae	$F_{1,41} = 7.03$; $p = 0.011$	HP > SP	ns
Valvatidae	$F_{1,41} = 4.75$; $p = 0.035$	HP < SP	ns
Ferrissiidae	$F_{1,42} = 7.76$; $p = 0.008$	HP < SP	ns
Acroloxidae	$F_{1,41} = 1.53$; $p = 0.22$		
Lymnaeidae	$F_{1,41} = 15.49$; $p < 0.001$	HP > SP	$F_{1,39} = 8.66$; $p = 0.005$
Odonata			
Platycnemididae[*]	$F_{1,42} = 8.81$; $p = 0.005$	HP	
Coenagrionidae	$F_{1,41} = 9.04$; $p = 0.004$	HP > SP	ns
Lestidae	$F_{1,41} = 0.70$; $p = 0.40$		ns
Aeshnidae	$F_{1,41} = 0.17$; $p = 0.68$		ns
Gomphidae[*]	$F_{1,41} = 12.34$; $p = 0.001$	SP	
Libellulidae	$F_{1,41} = 8.85$; $p = 0.39$		ns
Coleoptera			
Dytiscidae	$F_{1,41} = 0.24$; $p = 0.63$		ns
Hydrophilidae	$F_{1,41} = 0.26$; $p = 0.61$		ns
Hydroscaphidae[*]	$F_{1,41} = 6.91$; $p = 0.010$	HP	
Curculionidae	$F_{1,41} = 2.24$; $p = 0.14$		ns
Haliplidae	$F_{1,41} = 0.45$; $p = 0.50$		ns
Elmidae	$F_{1,41} = 3.02$; $p = 0.08$		ns
Helophoridae	$F_{1,41} = 1.71$; $p = 0.19$		ns
Noteridae	$F_{1,42} = 0.57$; $p = 0.45$		
Hydrochidae	$F_{1,41} = 0.01$; $p = 0.91$		
Dryopidae[*]	$F_{1,41} = 12.34$; $p = 0.001$	SP	
Scirtidae[*]	$F_{1,41} = 8.14$; $p = 0.007$	HP	
Hygrobiidae	$F_{1,41} = 8.70$; $p = 0.005$	HP > SP	ns
Heteroptera			
Notonectidae	$F_{1,41} = 0.36$; $p = 0.55$		ns
Naucoridae	$F_{1,42} = 6.52$; $p = 0.014$	HP > SP	ns
Pleidae	$F_{1,41} = 0.22$; $p = 0.57$		
Hydrometridae	$F_{1,41} = 4.75$; $p = 0.035$	HP > SP	ns
Veliidae	$F_{1,41} = 9.23$; $p = 0.003$	HP < SP	$F_{1,39} = 7.29$; $p = 0.010$
Mesoveliidae	$F_{1,42} = 0.17$; $p = 0.68$		ns
Gerridae	$F_{1,42} = 0.03$; $p = 0.87$		ns
Nepidae[*]	$F_{1,42} = 14.80$; $p < 0.001$	HP	
Corixidae	$F_{1,41} = 4.89$; $p = 0.033$	HP < SP	$F_{1,39} = 4.27$; $p = 0.047$

Hydroscaphidae, Scirtidae, Heteroptera: Nepidae). In addition, using PERMDISP analysis, the β diversity within each pond type did not differ between surrounding ponds and highway ponds as shown by the permutation dispersion analysis test with presence/absence data (overall test for differences in dispersion among pond types: $F_{1,42} = 0.07$; $p = 0.80$) and abundance data (overall test for differences in dispersion among pond types: $F_{1,42} = 0.04$; $p = 0.83$).

Finally, we found that the abundance of 11 of 28 families detected in both types of ponds were significantly different between highway ponds and surrounding ponds (Table 4): seven were significantly more abundant in highway ponds (Physidae, Lymnaeidae, Hydrobiidae, Coenogrionidae, Naucoridae, Hydrometridae, Corixidae), while four were more abundant in surrounding ponds (Valvatidae, Ferrissiidae, Hygrobiidae, Veliidae). Note that the pond type effect remained significant for four of them only, when tested adjusted to the retained environmental variables (NO_3, woodland area, salinity): Physidae, Lymnaeidae, Corixidae in highway ponds, Vellidae in surrounding ponds.

4. Discussion

We addressed the potential role of highway stormwater ponds as refuges through a comparison of aquatic invertebrate communities (Coleoptera, Heteroptera, Odonata and Gastropoda) between highway stormwater ponds and ponds located in the surrounding landscape. Diversity partitioning analyses suggested that our sample design (five sites systematically distributed within ponds) gave an accurate description of the macroinvertebrate community with limited bias, because no significant differences were detected within ponds whereas significant differences were found among ponds. We showed that, although highway ponds differed in abiotic conditions from surrounding ponds, they supported aquatic invertebrate communities at least as rich and as diverse at the family level (α diversity). Highway ponds also exhibited similar variability in family community composition and structure across ponds to surrounding ponds (β diversity). In fact, highway ponds did not greatly differ from surrounding ponds in family community composition and structure, and thus may contribute to reinforcing the pond network and consequently the abundance of such habitats on a regional scale. Note however that small, short-lived invertebrates were more abundant in highway ponds. Below we discuss how these results may help to inform biodiversity conservation policies in Human-dominated landscape and derive the consequences in terms of highway ponds management.

4.1. Highway ponds exhibit different abiotic characteristics

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 urbanisation, which implies a high percentage of impervious cover increasing the pollution rate in ponds. In contrast, surrounding ponds were located in landscapes with more woodland, which may explain e.g. lower pH: litter decomposition is known to contribute to a decrease in pH via a discharge of humic acids (Sauer et al., 2006). The higher salinity in highway ponds can be attributed to road management as salt (NaCl) is a common de-icing agent and high concentrations of chlorides are often considered specific pollutants from motorways (Scher and Thiery, 2005). Salt inflow is likely to result in increased conductivity in highway ponds (Scher and Thiery, 2005). In addition, the higher nitrate concentration in highway ponds is likely due to traffic as motor vehicles are known to be a major source of oxides nitrogen (nitric oxide is converted into nitrates when exposed to water – rainfall, atmospheric water – see Cape et al., 2004; Faus-Kessler et al., 2008). These results were overall in accordance with previous studies on chemical and physical characteristics of urban stormwater runoff, which reported higher concentrations of heavy metals, petroleum hydrocarbons, pesticides, sediments and nutrients (Davis et al., 2001; Karouna-Renier and Sparling, 2001).

4.2. Highway ponds and surrounding ponds have similar macroinvertebrate communities

Our results suggest that highway ponds contribute significantly to the maintenance of biodiversity at the landscape scale, which has been previously suggested (Scher and Thiery, 2005) but never verified. Highway ponds did not differ from surrounding ponds with respect to invertebrate community composition and did not support particular families, hence their presence is unlikely to increase regional biodiversity in terms of family identities, but it may nonetheless favour the maintenance of biodiversity via increased habitat availability. Interestingly, highway ponds appeared to shelter all macroinvertebrate families sampled at the regional scale, as suggested by COMDYN analyses. In addition, at the pond and site scales, they supported aquatic macroinvertebrate communities as rich and as diverse as surrounding ponds, in terms of families. These findings are partly counterintuitive: as highway ponds were characterised by distinct abiotic conditions (salinity, pollutants), one would expect that they support fewer families, different communities or at least a lower diversity than surrounding ponds. Note however that aquatic organisms are generally salt-tolerant, unless salt concentration reaches values where osmotic stress is too high (Blasius and Merritt, 2002; Mayer et al., 2008). Highway ponds exhibited a slightly higher site diversity than surrounding ponds. Note however that in terms of diversity partitioning, this contribution to the overall diversity is low (2.5% between the two pond types) in comparison to the diversity supported by ponds (25% among ponds within pond type), and by sites (63%: within sites). In fact within the highway pond type, highway ponds greatly differed from one another both in terms of family composition and diversity. Interestingly, these differences in family composition (presence/absence) and structure (abundance) were not higher among highway ponds than among surrounding ponds, although highway ponds were expected to have more similar family composition between ponds due to their homogeneous technical functions and consequently their characteristics (shape, bottom, age, highway proximity, maintenance, etc.). This finding is likely due to a great variability of abiotic conditions, as already shown by studies focusing on physical and chemical characteristics (Robertson and Taylor, 2007; Novotny et al., 2009) and also possibly to historical effects of colonisation (Chase, 2007).

The abiotic environmental conditions might be responsible for observed higher diversity in highway ponds. The taxonomic differences in diversity of invertebrate communities between surrounding ponds and highway ponds were also associated with differences in invertebrate functional traits. We believe that these differences associated with the higher abundance of some invertebrates in highway ponds (invertebrates of small and intermediate sizes, short-lived invertebrates, invertebrates having one or more than one generation per year, invertebrates with a passive dispersal mode, invertebrates feeding on dead plants, on dead animals, on living microphytes, on living macrophytes, shredders, piercers and scrapers) can be explained by the greater productivity in highway ponds, a direct consequence of the observed and known higher nutrient concentration (see above). Contrary to other groups, gastropods mainly comprise primary consumers, whose abundance is expected to be more sensitive to primary productivity than the abundance of organisms located at higher levels in the food web. Higher productivity should impact the different levels of the trophic web (Long et al., 2007; Duffy et al., 2007), but due to the pyramidal shape of the latter, these effects may be detectable only at lower levels. Highway ponds, which exhibit higher nutrient concentrations and are subject to episodic salt deposition, might also be characterised by a greater variability in environmental conditions over time (Mykrä et al., 2008), resulting in higher abundance of short-lived invertebrates (Townsend and Hildrew, 1994; Usseglio-Polatera et al., 2000; Angélibert et al., 2004; Statzner et al., 2008) and thus in invertebrates having one or more than one generation per year. Eutrophic habitats experience phytoplankton blooms in summer, which causes increased abundance of primary consumers, many of which are short-lived invertebrates. Note that abiotic variables (nitrates, salinity) explained only a small proportion of the variation in abundance between highway ponds and surrounding ponds: four of eleven families still exhibited a significant difference in abundance between surrounding ponds and highway ponds when adjusted to abiotic variables (Table 4). Other variables such as pollutants, or range and frequency of abiotic variation may contribute to differentiate surrounding ponds and highway ponds.

4.3. Implications for the management of stormwater retention ponds to enhance biodiversity

Our results contribute to a better understanding of diversity partitioning in Human-dominated landscapes and have implications in defining biodiversity-friendly management in such landscapes. However, these results should be interpreted and used carefully due to inherent limits of the study. First, we worked at the family level and our results may differ if obtained at the species level. Note however that the use of a higher taxon (especially families), as surrogates for species diversity, has been shown to be relevant in freshwater community analyses (Heino and Soininen, 2007). Secondly, the main risk with higher taxa analyses is to find no significant differences between sites while such differences actually exist. However, in our study, we found differences in the partitioning of diversity (APQE) between ponds. We also detected differences at the functional diversity level. We thus expect that our analyses are reliable and informative about the distribution of a diversity level at the landscape scale, but of course it would be interesting to complete this approach with studies accounting for species level and examining the distribution of rare species.

Second, these results concerned relatively old highway ponds (built 34 years ago) that have natural bottoms and they might differ from more recent stormwater ponds with synthetic bottoms (Poly-Ethylene High density membrane), which aim to limit pollutant infiltration. Third, the collected pollutants particularly heavy metals (Pb, Cu, and Zn) have been shown to accumulate in wild organisms in urban stormwater ponds (fish: Campbell, 1994; macroinvertebrates: Karouna-Renier and Sparling, 2001). Thus, even if heavy metals are in low concentration in urban ponds (Karouna-Renier and Sparling, 2001), highway ponds management

choices that may be adopted to conserve biodiversity in Human-dominated landscape, have to take into account the probability of pollutant accumulation (heavy metals, hydrocarbons, etc.) in the food web and its possible consequences in terms of fecundity and mortality (see for amphibians: Snodgrass et al., 2008). For species that are not tolerant to pollutants, highway ponds will not provide additional habitat and could even act as traps (Snodgrass et al., 2008), whereas for pollutant-tolerant species these highway ponds could provide suitable habitats within the pond network.

Despite these limits, our findings have important implications in the context of biodiversity conservation, especially with the need to consider spatial issues when developing strategies for pond conservation (Briers and Biggs, 2007). Man-made ponds may have substantial conservation value (Ruggiero et al., 2008; Herzon and Helenius, 2008). In accordance with previous studies on other taxonomic groups (e.g. fish; Hazell et al., 2004), we found that habitat characteristics were likely the most important factors shaping the assemblages, whatever the origin of the ponds. As for other artificial anthropogenic ponds (urban domestic ponds: Gaston et al., 2005; Vermonden et al., 2009; farmland ponds: Ruggiero et al., 2008; Herzon and Helenius, 2008; Davies et al., 2008), highway ponds may increase regional biodiversity: first, as one of the main factors influencing invertebrate diversity in ponds is the degree of connectivity among ponds (Gee et al., 1997), a network of ponds is likely to the maintenance of high diversity. This role may be especially of interest in Human-dominated landscapes, such as agricultural landscapes with intensive cereal production, where highway ponds often constitute the only pond type. In Mediterranean region, their contribution to biodiversity may be also stronger: being often the only permanent ponds in the area (Beja and Alcazar, 2003; Grillas et al., 2004; Scher et al., 2004), they likely support distinct fauna and flora from surrounding temporary ponds. Given the urge to conserve biodiversity, especially in the context of climate change, road practitioners should consider highway ponds not only for their hydrological and pollutant retaining purposes but also as a possibility to increase the role of highway verges as a refuge and, consequently, landscape connectivity. Thus the management of these water bodies (frequency and temporal distribution of sediments bottom dredge that act as disturbance to wildlife communities, slope definition of pond banks, macrophytes and surrounding vegetation management) should integrate these potentialities for biodiversity (for management recommendations, see Declerck et al., 2006; Vermonden et al., 2009), especially in Human-dominated landscapes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.08.018.

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