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Amphibian pond loss as a function of landscape change – A case study over three decades in an agricultural area of northern France

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ABSTRACT

Agricultural reform and infrastructural development are among the major drivers of biodiversity loss and landscape homogenization worldwide. Ponds and other small stagnant water bodies are crucial for maintaining regional biodiversity, yet they are vulnerable to human induced landscape change. We investigated for 199 ponds in the 'département' Pas-de-Calais in north-western France if pond persistence ($n = 86$, 43%) or disappearance ($n = 113$, 57%) was related to wider changes in the landscape, over the period 1975–2006. Landscape data were obtained from aerial photographs (1963), two ASTER satellite images (2001 and 2003) and observations on the ground (1975 and 2006) and land use around the ponds was described over concentric circles with five different radii in the 100–1000 m range. Overall, pond disappearance was associated with a decrease in grassland and an increase in arable fields around the ponds. We found that the small, man-made cattle ponds, with either natural substrate or concrete drinking troughs, were more often affected than the larger, semi-natural ponds. Since the cattle ponds are regularly used for amphibian reproduction, their massive abandonment therewith weakens the population network and puts the local occurrence of some of the rarer species at risk. Spatial extrapolation of models on pond persistence allowed the identification of areas most at risk of further pond loss. We suggest that local amphibian conservation efforts will be the most effective if the focus is on the marshes and dune areas and on pond preservation in the remaining grasslands.

1. Introduction

At the present *ca.* 45% of surface area of the European Union is covered by farmland (http://faostat.fao.org/). If managed in an environmentally friendly way, farmlands may be spatially heterogeneous (Beaufoy et al., 1994) and support a high level of biodiversity, including species rich plant, butterfly (Schmitt and Rákosy, 2007), amphibian (Hartel et al., 2010a) and bird (Pain and Pienkowski, 1997; Moga et al., 2010) communities. However, the increasing demand for agricultural products triggers the intensification and change of land use, resulting in habitat loss and fragmentation, spatial homogenization and, ultimately, a reduction in biodiversity (Tilman et al., 2002). Understanding the relationship between land use and its dynamics and the occurrence and condition of wildlife in farmlands is an important challenge for conservation biologists and natural resource managers (Löfvenhaft et al., 2004; Stoate et al., 2009).

Ponds and amphibians are important model systems to explore the effect of land use change on habitats and wildlife. It was only recently recognized that these small sized wetlands may make a significant contribution to the biodiversity of entire landscapes (Scheffer et al., 2006). When compared to larger water bodies, such as lakes, rivers and ditches, ponds may support considerably more species, including endemic and protected ones (Williams et al., 2004; Scheffer et al., 2006; Davies et al., 2008; Oertli et al., 2009). However, due their small size, ponds are prone to destruction and to increased isolation through structural changes in the surrounding landscape (Boothby, 2003). Agricultural intensification, urban development and forest clearing are particularly common in regions with strong human presence and it has been estimated that *ca.* half of the ponds in western Europe have disappeared between 1900 and 1990 (Hull, 1997). The recognition of the biodiversity value of ponds – often neglected in research and policy in favour of lakes, rivers and streams – has prompted calls for action towards their conservation (Semlitsch and Bodie, 1998; Céréghino et al., 2008).

Most species of Palearctic amphibians are dependent on ponds and other small, stagnant water bodies for their reproduction. A low dispersal capability (Bowne and Bowers, 2004; Semlitsch,

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2008) implies that an amphibian metapopulation is easily disrupted by increasing population isolation through the loss of aquatic and terrestrial habitats (Halley et al., 1996; Semlitsch, 2000; Jehle et al., 2005). As strings of suitable terrestrial habitat can act as corridors for amphibian movement (Semlitsch, 2008), so can ponds act as stepping-stones for dispersal and reproduction, increasing the connectivity in the landscape over distances larger than the dispersal per generation distance (Semlitsch, 2000). The loss of ponds can therewith lead to not just smaller overall population sizes but also reduce genetic diversity, and the chance for pond repopulation (the so-called rescue effect), with concomitant effects on (decreased) population fitness and (increased) chances for local extinction (Brown and Kodric-Brown, 1977; Halley et al., 1996).

Several studies have indicated that changes in land-cover and in the habitat configuration in the surroundings of breeding ponds may have a substantial impact on amphibian abundance (Price et al., 2006; Hartel et al., 2009), population dynamics (Gibbs et al., 2005) and species richness (Gagné and Fahrig, 2007; Simon et al., 2009). Similar findings have been reported for other taxonomic groups, such as dragonflies (Kadoya et al., 2008) and plants (Palik et al., 2007). Studies which address the persistence of ponds related to land use and landscape structure are scarce. So far most work has been theoretical (Boothby, 2003; Wood et al., 2003) or directed at pond environmental quality (Houlahan and Findlay, 2004; Declerck et al., 2006) while few empirical studies have focused on pond presence as a function of the landscape (e.g. Boothby and Hull, 1997).

We here explore the effects of landscape change on the persistence of ponds over a three decade temporal window in a rural area in the 'département' (department) Pas-de-Calais in north-western France and we determine to what extent pond loss affects the breeding possibilities for the locally occurring 12 amphibian species (five urodeles and seven anurans). Our study is timely because of the lack of empirical data and because it captures a period that witnessed major changes in the local landscape, due to changes in land use and intensification, infrastructural and urban development as well as land abandonment.

2. Methods

2.1. Study area, data collection on ponds and amphibians

The study area of *ca.* 300 km^2 is located in north-western France, in the coastal zone of the department Pas-de-Calais (Fig. 1). The landscape is diverse, dominated by agriculture fields used for crops and pasture for cattle raising and the dairy industry. Other extensive landscape features are two dune areas along the west and the north coast and associated inland marshland and an area of open cast mining in the east. As ponds we consider all clearly distinguishable water bodies, natural or man-made, that potentially serve as breeding habitat for one or more species of amphibians.

The first dataset was compiled over the spring and early summer in 1974 and 1975 through field surveys by teams from the Zoological Museum of the University of Amsterdam (now NCB Naturalis; Zuiderwijk and Hooghiemstra, 1975; Arntzen and Gerats, 1976) and included 207 ponds that were categorized as (i) field ponds (n = 159), (ii) drinking troughs (n = 27) and (iii) (semi-)natural ponds (n = 21). Field ponds are small (up to *ca.* 200 m^2) water bodies on natural soil substrate that are man-made for the purpose of watering the cattle. Cattle drinking troughs have an artificial substrate (cemented bricks or concrete) with a surface of up to *ca.* 50 m^2. The semi-natural ponds are mostly large (>200 m^2) dug-out water bodies in marshy areas, created for the purpose of

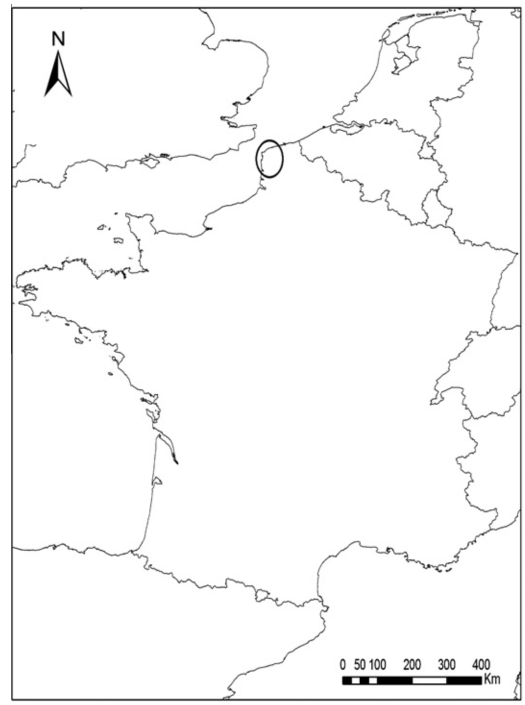

Fig. 1. Location of the study area (encircled) in the department Pas-de-Calais at the Atlantic coast of north-western France.

the duck hunt. Two inundated fields and one brook in which we observed amphibian reproduction were also placed in this category.

Ponds observed in 1974-'75 were re-surveyed in May 2006 and April 2008. A pond was considered 'persisting' after visual confirmation of its existence and considered 'destroyed' when its old location had been found but the pond itself was no longer in existence. Observed ponds were compared in type and location to the 1975 description, to ascertain that it was the same. Locations were all marked with a GPS device (accuracy <10 m) therewith improving upon the spatial accuracy of the 1975 data. Eight ponds locations we were unsure about were excluded from the analysis.

The 1974–'75 survey included the search for amphibians. Most ponds were visited multiple times from early spring to late summer. The presence of amphibian species was recorded as either eggs, embryos, larvae, metamorphs, juveniles and adults, supplemented in anurans with observations on calling adults. The presence of the water-bound life stages was taken as evidence that the pond served as a reproduction site.

2.2. Landscape data

To reconstruct the landscape pattern of the past a series of panchromatic aerial photographs (1:25,000) were obtained from the Institut Géographique National, France. The 31 partially overlapping photos covered an area of approximately 4.5 × 4.5 km each and were recorded in June 1963. The paper prints were scanned to digital format (300 dpi), imported in ArcMap 9.3 (a module of ESRI ArcInfo 9.3, 2006) and georeferenced using coordinates of known points, together with sections that overlapped with georeferenced images. The spatial resolution of the photos in the resulting composite was 2.2 m. The landscape features of interest were manually digitized using ArcMap 9.3, through on-screen interpretation (Jensen, 2007) in which we distinguished the following ten classes: arable fields, grasslands and pasture fields, forests and woods, urban areas, transport routes including main roads and railways, marshlands, quarries, bare sand, dune grassland and dune shrubs.

Recent landscape information was obtained from two ASTER satellite images that were recorded on 14 February 2001 and 5 November 2003, with a post-georeferencing spatial resolution of 18.8 m. Both images were classified in 20 classes using the unsupervised ISODATA algorithm of Erdas Imagine 9.1 (Leica Software, 2006) that we then clustered in the following five groups: water, bare soil, low herbaceous vegetation cover, high herbaceous vegetation cover and forest. Arable fields were subsequently distinguished from pasture based on the variations in vegetation cover throughout the year (Cyr et al., 1995). Bare arable fields were distinguished from the class 'bare sand' on the basis of topographical information. Similarly, grasslands and forest areas falling within the dune areas were assigned to new 'dune-grassland' and 'dune-shrub' classes, respectively. Open cast mining, marshes, urban areas and the main transportation lines were taken from a 1:25,000 digital topographic map of the area (CartoExploreurII, 2000) and superimposed to the map.

Classification accuracy was assessed for both periods with a stratified random protocol using 562 points for the 1963 map and 547 points for the 2003 map. These points were selected randomly with the majority within a 1000 m radius of the ponds and a minimum of 30 points for each mapped class. Mapped classes were compared with ground truth data gathered during the fieldwork (including unpublished data from JWA in 1975), supplemented with recent aerial imagery from Google Earth^{TM}. Overall classification accuracy, kappa statistics, and user and producer accuracy were calculated for each landscape class.

2.3. Data analysis

The rate of pond loss was assessed by computing the delta statistic $\Delta N = (\log N)t_2 - (\log N)t_1$, where N = the number of ponds, t_2 is the second (i.e. 2006–'08) and t_1 is the first (i.e. 1974–'75) survey period. To explore land use effects on pond persistence, we used a pond-centred approach over circular areas with five different sizes. These radii allowed to compare effects of landscape change on pond persistence at three different scales: local – 100 m and 250 m, intermediate – 500 m, and large – 750 m and 1000 m. This range reflects a compromise between data accuracy (that is more readily obtained over larger surfaces) and data independence (i.e., non-overlap of radii, also affected by the non-random distribution of ponds over the landscape). The difference in area occupied by each of the landscape classes during this period was calculated for every pond individually, for all the radii considered. To test the hypothesis that pond disappearance versus pond persistence is a function of the landscape we assessed if the variation in area of each landscape class occurred differently around both categories of ponds with the Mann–Whitney *U*-test.

Binary logistic regression with forward stepwise addition of the independent variables was used to identify landscape classes that might be used as predictors for pond persistence versus disappearance over the 30 year period. A weighting variable was introduced to obtain a balanced dataset with virtually equal numbers of ponds that persisted or disappeared. The fit of the models obtained was quantified with the area under the curve (AUC) of the receiver operation characteristics plot (Fielding and Bell, 1997; Pearce and Ferrier, 2000). We carried out a 'forward' analysis in which the landscape classification of 1963 was used as the source of the independent variables, with the aim of 'predicting' pond loss observed in 2006. We also applied a 'backward' analysis in which the landscape pattern of 2003 was used as the source of the independent variables, with the aim of reconstructing the landscape effects on pond loss since 1975 to extract the variables conditioning future pond persistence. The results obtained with the latter approach – since these are based on current landscape conditions – were applied to the entire study area, using the 'focal statistics' function in ArcMap 9.3, to create a map that would visualize areas in risk of pond loss and areas where ponds are expected to persist. The maps of the various spatial scales were combined into a single one by multiplying the probability values of each cell.

The potential consequence of pond destruction on amphibian breeding habitat loss was assessed by using the 1974–1975 data on pond and amphibian occurrence and the pond destruction over three decades. We used the *G*-test with Williams's correction to analyse if the occurrence of amphibians was significantly different across pond types and to explore if the occurrence of amphibians differed for persisting versus destroyed ponds.

We assumed that species richness follows a Poisson distribution and we tested the relationship between species richness and pond type (i.e. 'field ponds', 'drinking troughs' and 'semi-natural ponds') by Generalized Linear Models. The feasibility of the model was assessed by the dispersion parameter. Three species with low occurrence (*Salamandra salamandra*, *Pelodytes punctatus* and *Pelophylax* kl. *esculentus*) were excluded from pond type analysis but counted for the amphibian species richness estimate. Statistical analyses were all carried out with SPSS 17 (SPSS Inc. 2008) and R (R Development Core Team, 2009).

3. Results

3.1. Pond loss as a function of landscape

Of the 199 ponds recorded in 1974–'75, 86 (42%) were found to be present in 2006–'08. Of these, 67 were field ponds, six were

Table 1
User and producer accuracy (in percentages) across reconstructed landscape classes for 1963 and 2003 in the coastal area of department Pas-de-Calais, France (see Fig. 2) from N randomly selected points. Overall classification accuracy and Kappa coefficients for both dates are shown at the bottom.

Landscape class	1963			2003		
	N	User	Producer	N	User	Producer
Agriculture	113	94.7	93.9	132	97.7	94.2
Dunes-grass	40	85.0	75.6	32	96.9	73.8
Dunes-shrubs	32	68.8	73.3	41	80.5	100
Forest	48	95.8	93.9	36	80.6	93.5
Grassland	137	92.7	90.1	113	91.2	91.2
Marsh	31	92.3	100	32	100	85.7
Quarry	30	100	100	34	92.9	100
Sand	64	92.2	98.3	38	89.5	94.4
Transport	31	84.6	100	30	100	100
Urban	36	88.9	97.0	59	89.8	91.4
Overall accuracy	91.5			91.9		
Kappa ± SE	0.897 ± 0.016			0.903 ± 0.015		

Table 2
Total area occupied by each of the recognized landscape classes in 1963 and in 2003 (see also Fig. 2) and the amount of change during this period.

Landscape class	Surface in Km^2		
	1963	2003	Change
Arable	153.10	148.57	−4.53
Dune-grass	1.65	1.47	−0.18
Dune-shrubs	0.93	1.83	0.90
Forest	22.03	32.92	10.89
Grassland	91.10	73.58	−17.52
Marsh	0.67	0.77	0.10
Quarry	3.02	7.20	4.19
Sand	3.55	2.63	−0.92
Transport	2.99	4.09	1.11
Urban	10.61	16.59	5.97

drinking troughs and 13 were natural ponds. Pond loss (58%) was more pronounced for field ponds and drinking troughs ($\Delta N = -0.36$ and $\Delta N = -0.61$ respectively) than it was for natural ponds ($\Delta N = -0.18$).

Overall landscape classification accuracy was of 92% for both surveys, with Kappa scores around 0.9 (Table 1). User and producer accuracy for individual landscape classes was generally above 90%, and always higher than 68%. Between 1963 and 2003, the study area underwent a decrease in the area occupied by arable fields, grasslands, dune grasslands and bare sand and an increase in the area of forests, marshes, quarry, urban and dune shrubs (Table 2, Fig. 2). The largest differences were observed for grasslands, which lost a total of 17.5 km^2, and in forest, which increased by 10.9 km^2. The area occupied by quarry and dune shrubs doubled in this period but their surface areas were still small in an absolute sense.

The area of grassland decreased significantly more around destroyed ponds than around persisting ponds whereas bare sand surface decreased more around persisting ponds at all radii except at 100 m (Fig. 3). The increase in arable land was higher around destroyed pond sites in the 250 m radius, while the 500 m, 750 m and 1000 m radii showed an increase in arable around destroyed ponds and a decrease around persisting ponds. The area of dune-grasslands and dune-shrubs increased more around persisting ponds at all distances. The increase in urban and transport was higher around destroyed ponds, at 250 m and 750 m, respectively. No sig-

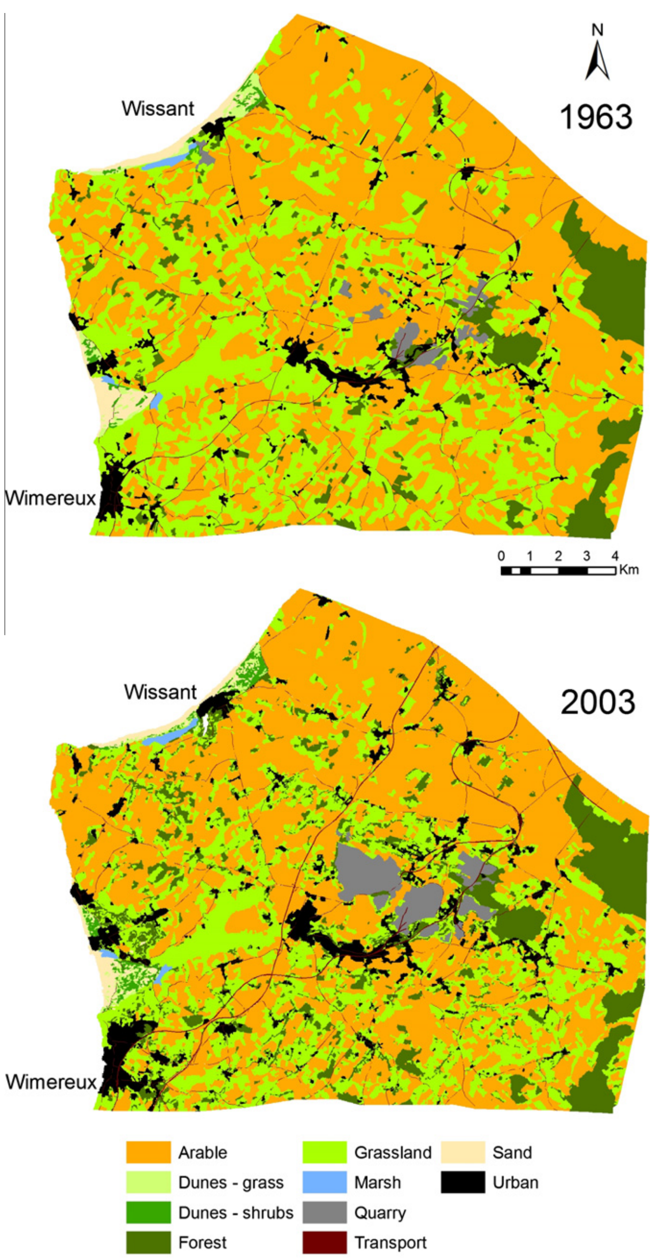

Fig. 2. Landscape composition in the coastal area of department Pas-de-Calais, France in 1963 and 2003, reconstructed from the classification of the aerial photographs and two ASTER satellite images, respectively.

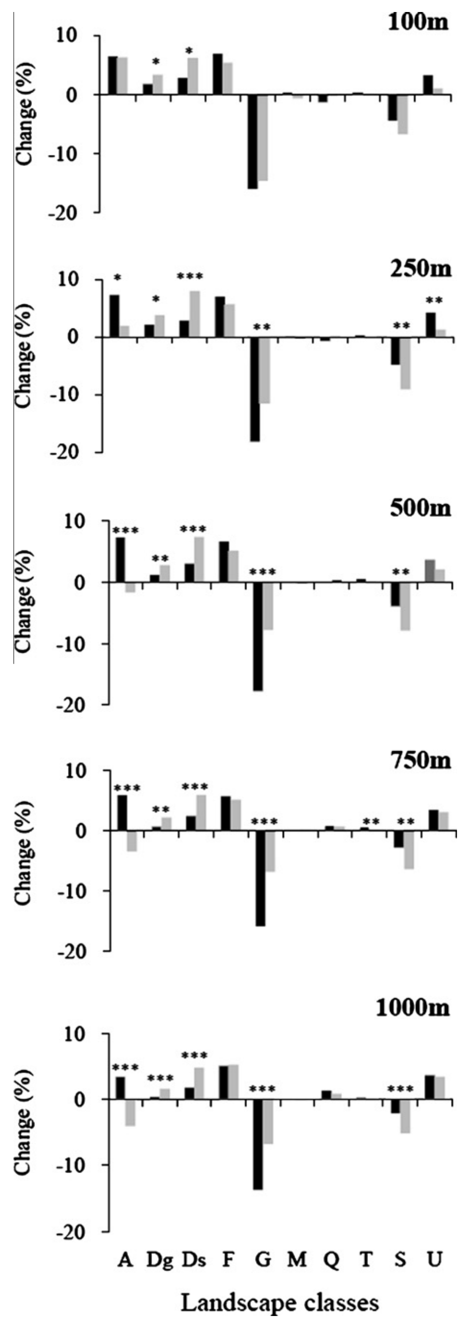

Fig. 3. Variation in the area occupied by each landscape class over the 1963–2003 period, around persisting ponds (heavy shading) and destroyed ponds (light shading) for five surfaces with radii of 100–1000 m around pond localities. Significant differences in landscape composition are marked as $^{*}p \leqslant 0.05$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$, analyzed with the Mann–Whitney *U*-test. A – arable, Dg – dune grassland, Ds. – dune shrubs, F – forest, G – grassland, M – marsh, Q – quarry, T – transport network, S – bare sand and U – urban.

Table 3
Logistic regression based pond persistence models derived from the landscape conditions in the coastal area of department Pas-de-Calais, France in 1963 (top panel) and 2003 (bottom panel), for five circular radii around the ponds. Model accuracy is expressed by the 'area under the curve' statistic (AUC).

Landscape class	Radius				
	100 m	250 m	500 m	750 m	1000 m
Arable	−56.064				
Dune-grass					
Dune-shrub					
Forest					
Grassland					1.135
Marsh	148.085	33.654	30.489	16.009	13.311
Quarry					
Sand					
Transport	−652.912	−123.025	−67.450	−35.335	
Urban	−190.851	−58.405			
Constant	0.440	0.267	0.187	0.285	−1.818
AUC ± SE	0.738 ± 0.035	0.687 ± 0.037	0.694 ± 0.038	0.708 ± 0.037	0.717 ± 0.039
Arable	−33.924	−7.753	−4.841		
Dune-grass					
Dune-shrubs				6.274	1.588
Forest			−8.438		
Grassland				2.166	1.494
Marsh	130.665	27.268	22.420	12.666	7.872
Quarry				4.482	
Sand			−12.299	−4.154	
Transport	−502.552			−33.445	
Urban	−148.516	−35.450	−8.957		
Constant	0.441	0.630	2.419	−1.070	−1.855
AUC ± SE	0.734 ± 0.035	0.722 ± 0.036	0.774 ± 0.034	0.794 ± 0.033	0.754 ± 0.036

nificant amounts of change were found for forest, marsh and quarry.

Under the forward approach marshes were selected as viable predictors of pond persistence in the regression results of all the distances used. The class 'transport' was also selected for every distance, except at 1000 m, where the class 'grasslands' was selected. 'Urban' was selected further as a local-scale predictor, as were arable fields at 100 m (see Table 3 for the magnitude and direction of the effect). AUC values of the models ranged from 0.687 ± 0.037 at the 250 m radius to 0.738 ± 0.035 at the 100 m radius. Under the backward approach marshes were selected as in the forward approach. Arable and urban were selected at the local and intermediate scales while dune-shrubs and grasslands were selected at the large scales. AUC values ranged from 0.722 ± 0.036 at the 250 m radius to 0.794 ± 0.033 at the 750 m radius. Pond persistence was consistently positively affected by marsh, grasslands and dune shrubs and negatively affected by arable, urban and transport in both forward and backward approaches. A spatial extrapolation of the results illustrates this dichotomy (Fig. 4).

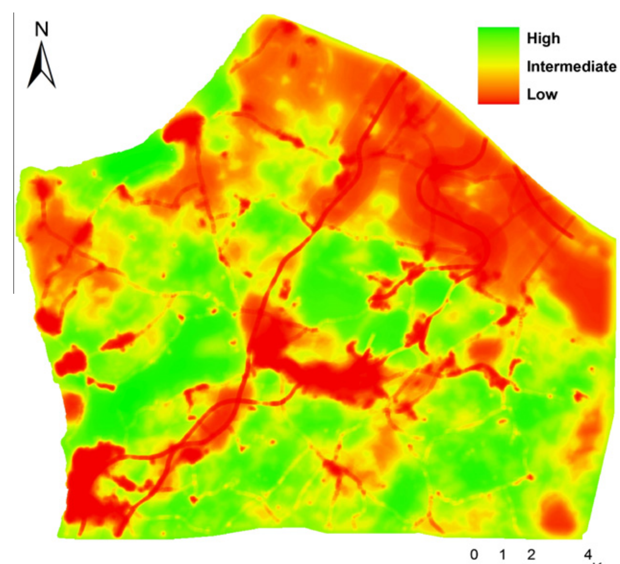

Fig. 4. Current suitability of the landscape for pond conservation as determined from models of pond loss, in the coastal area of department Pas-de-Calais, France (details see text). (For interpretation of the colors mentioned in this figure, the reader is referred to the web version of this article.)

3.2. Pond destruction and amphibian breeding habitat loss

The twelve amphibian species observed in the 1974–'75 survey period included the newts *Ichthyosaura alpestris* (108 ponds), *Lissotriton helveticus* (101), *L. vulgaris* (71), *Triturus cristatus* (56), the salamander *Salamandra salamandra* (5), the frogs *Rana temporaria* (114), *Hyla arborea* (33), *Pelodytes punctatus* (4) and *Pelophylax* kl. *esculentus* (1) and the toads *Bufo bufo* (119), *Alytes obstetricians* (66) and *Bufo calamita* (29).

For *A. obstetricans*, *I. alpestris, L. helveticus* and *L. vulgaris* occurrence was highest in drinking troughs and lowest in semi-natural ponds (Fig. 5). For *T. cristatus* the pattern was similar but only marginally significant. *Bufo bufo* and *R. temporaria* had the highest occurrence in semi-natural ponds followed by field ponds. *Hyla arborea* was found absent from drinking troughs. Amphibian species richness significantly decreased with the character of the ponds, from 3.92 ± 1.80 in drinking troughs to 3.69 ± 2.15 in field ponds and 2.52 ± 1.66 for the class of semi-natural ponds (Table 4).

The species *A. obstetricians, I. alpestris*, *L. helveticus, L. vulgaris* and *T. cristatus* showed a significantly higher occupancy in field ponds that would become destroyed than in persisting ones (Fig. 6a). Conversely, *Bufo bufo* and *R. temporaria* show high occupancy (>50%) in persisting field ponds. The destruction of drinking troughs strongly affected the urodeles: more than 80% of these were breeding sites of *L. helveticus*, more than 50% were used by *L. vulgaris*, more than 30% by *T. cristatus* and all destroyed drinking troughs were used by *I. alpestris*. Breeding habitat loss for anurans

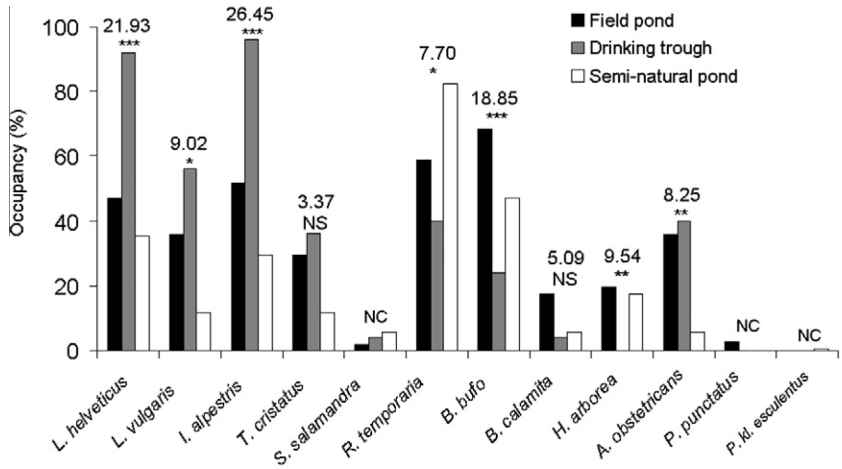

Fig. 5. Pond occupancy of amphibian species across three pond categories in 1974–1975. The values above bars represent the *G*-test statistic. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$, NS = not significant and NC = *G*-test not calculated. The ponds surveyed were 159 field ponds, 27 drinking troughs and 21 of semi-natural ponds.

Table 4
The relationship between amphibian species richness and pond type (i.e. 'drinking trough', 'field pond' and 'semi-natural pond') tested with Generalized Linear Models. The dispersion parameter was estimated at 1.19.

	Estimate	SE	*Z* value	Pr (>|*t*|)
Intercept	1.306	0.042	31.052	<0.0001
Drinking trough	0.059	0.109	0.546	0.58
Semi-natural	−0.378	0.158	2.392	0.01

was less severe at <30% for *B. bufo* and <45% for *R. temporaria* and *A. obstetricans* (Fig. 6b). The disappearance of semi-natural ponds resulted in breeding habitat loss for *L. vulgaris*, *T. cristatus*, *A. obstetricans* and *L. helveticus*. The loss also affected *R. temporaria* and *B. bufo* but these two species have a higher occurrence in the persisting ponds than in destroyed ones (Fig. 6c).

4. Discussion

4.1. Pond loss as a function of land use

We documented extensive land use change and a marked reduction in the number of ponds in the coastal area of department Pas-de-Calais, France over the 1975–2006 period. Field ponds and drinking troughs were more affected than the (semi)-natural ponds used for duck hunting. In parallel to this, over the three decades considered, land conversion was mostly from grassland to arable, reducing the need for cattle watering holes: the grassland cover experienced the largest reduction in department Pas-de-Calais and the decline is logically associated with the disappearance of ponds by active destruction or gradual infilling and neglect. Persisting ponds also experienced a reduction in surrounding grassland, although significantly less than for lost ponds. This type of agricultural change, together with the extension of urban areas and the extension of the transportation network had the strongest effect on pond loss at low spatial scales (100 m buffer around the ponds). At large-scale (1000 m radius) a positive effect of grassland cover and dune-shrubs was evident. The positive effect of grassland (pasture) cover on pond persistence at large spatial scales (750–1000 m buffers – see Table 3) may be explained by the fact that the large grassland covers are still under (e.g. grazing) management, as supported by our field observations. Lack of grazing can reduce the pond hydroperiod through the development of the shoreline and aquatic vegetation and increasing evapo-transpiration (Pyke and Marty, 2004; Voldseth et al., 2009). Boothby (2003) and Boothby and Hull (1997) point to succession as a cause of pond disappearance but in Pas-de-Calais this appeared of minor importance.

The increase in arable lands was also associated with pond destruction and this is likely to be the mirror-image of pasture decrease (i.e., conversion from pasture to arable). The third strongest impact on pond persistence comes from urbanization. Urban encroachment was observed already in 1975 near ponds that would not make it to the present day. Since urban development seems ongoing, most ponds close to agglomerations are at risk. These results run parallel to those of Boothby and Hull (1997) who observed that pond loss in north-western England (UK) was caused by land development, in particular agricultural reform (two ponds out of three) and urbanization (one pond out of four). Similarly, Gibbs et al. (2005) reported that destroyed amphibian ponds in the state of New York, USA were linked to land development, for in particular residential, commercial and crop cultivation purposes. Moreover, land conversion may affect amphibians not only directly through the loss of breeding and terrestrial habitats, but also indirectly through the increased application of pesticides and fertilizers (Beebee and Griffiths, 2005). The consistency of interpretation among the several studies would point to a general pattern with perhaps a common cause, i.e., common practices in land development in the industrialized regions of the Holarctic.

The increase in forested area in Pas-de-Calais, from natural succession of traditional grasslands into woodlands and from plantations, was the second largest change observed; however, this change was not related to pond persistence. The marshes in the study area have undergone little change over the period of investigation, including the ponds that come with it and that are maintained for the purpose of duck-hunting. In 1963 the dune areas, especially the 'Dunes de la Slack' north of Wimereux, were largely bare sand as a side effect of military action in the Second World War. Since then natural succession took its place, with a marked overall increase in grassland and shrubs. Land cover change in the dunes was most pronounced around persisting ponds that are mostly man-made and maintained, either for duck-hunting, as watering holes for deer, or as part of a recently established Natura 2000 Reserve.

4.2. Loss of ponds as amphibian breeding habitats

With the pond disappearance over three decades a large number of amphibian breeding sites were also lost. On average, amphibian species richness was higher in field ponds and drinking

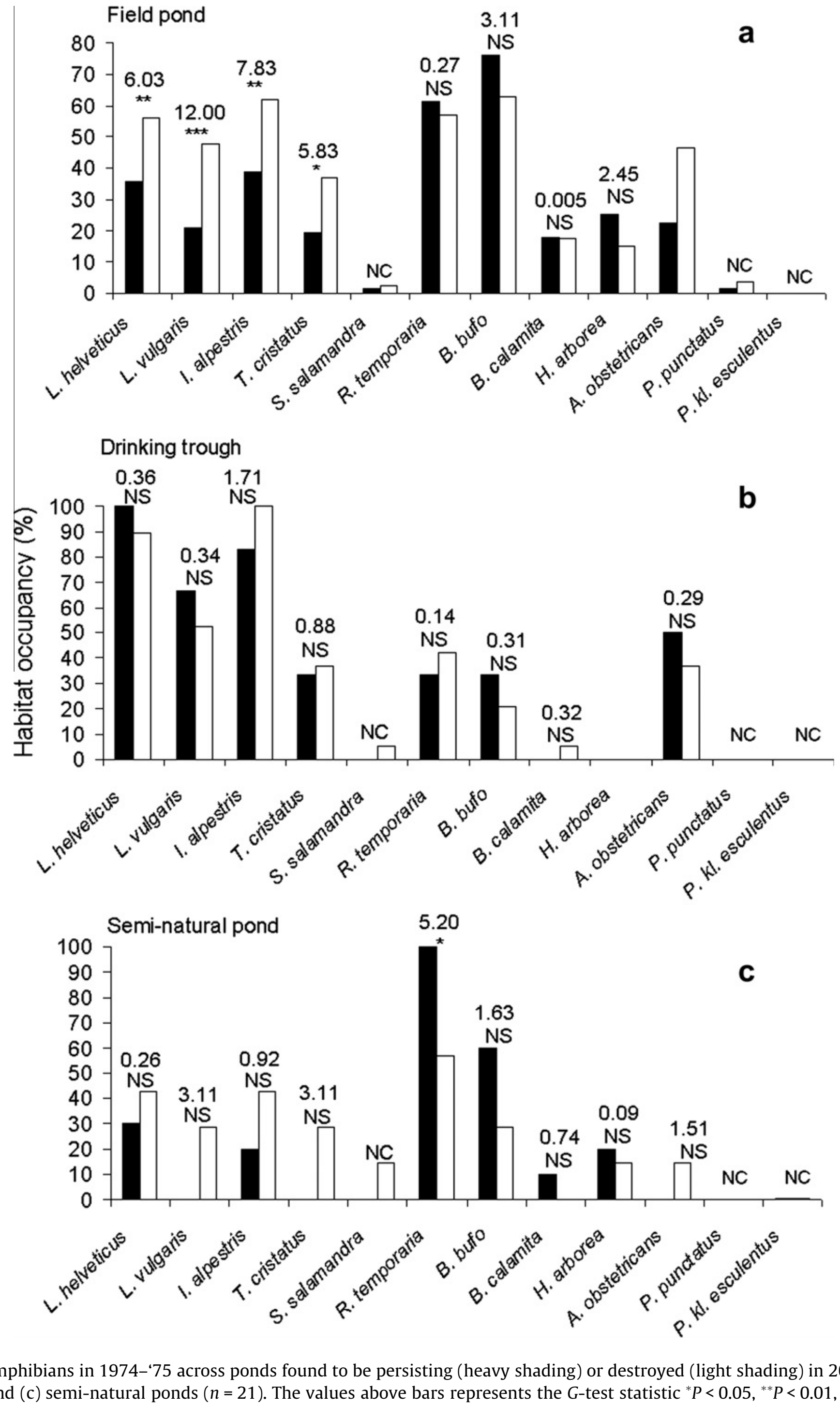

Fig. 6. Habitat occupancy of amphibians in 1974–'75 across ponds found to be persisting (heavy shading) or destroyed (light shading) in 2006–'08. (a) field ponds ($n = 159$), (b) drinking troughs ($n = 27$) and (c) semi-natural ponds ($n = 21$). The values above bars represents the G-test statistic $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$, NS = not significant and NC = G-test not calculated.

troughs than in the semi-natural ponds. As the former category is more frequently affected than the latter one, amphibian richness has declined more strongly than the number of lost ponds would indicate. Similarly, amphibian occupancy in 1974/'75 was higher in lost ponds than in persisting ponds for most species.

Our findings are in line with observations that man-made ponds may play a crucial role for amphibian persistence in farmlands (e.g. Beebee, 1997; Crochet et al., 2004; Hartel et al., 2010a) and one can wonder what the amphibian fauna would be like in the natural landscapes preceding the advent of agriculture. Unless conservation action is taken, ponds will tend to disappear when they are no longer needed. Farmland ponds therewith depend on the continuation of cattle grazing and land use change will tend to destroy them, as observed by others elsewhere. The decline in dewponds over two decades in a farming area in the United Kingdom, could be attributed to intensified agriculture practice and the lack of maintenance (Beebee, 1997). Loman and Anderson (2007) reported the loss of amphibian breeding ponds and negative population trends of *R. temporaria* in agricultural fields in Sweden in a study over 17 years. In southern France man-made cattle ponds tended to persist under continued regime of extensive management over a 30 year period (Crochet et al., 2004). Finally, Löfvenhaft et al.

(2004) observed structural changes in the landscape from urban and infrastructural development during to 50 years in Sweden with concomitant effects on the number of amphibian breeding sites and a reduction in the strength of the metapopulation network. These authors inferred a time lag of several decades between the habitat loss and population response (see also Findlay and Bourdages, 2000 and Piha et al., 2007).

The amphibian occurrence data was available for the first (1974–1975) survey period and not for the second one (2006–2008). In the second survey we locally observed some newly created ponds (mostly for duck hunting) but we did not document this precisely. This limits our ability to infer consequences of breeding habitat lost on amphibian population and metapopulation dynamics and regional persistence. However, given the massive decline in pond number and the observation that the richest ponds were affected the most, we conclude that the breeding habitat availability for amphibians sharply reduced over the three decades.

The massive breeding habitat loss may have consequences on breeding habitat selection for species and may influence reproductive success. For example, in a ten year study on pond selection by amphibians, Petranka and Holbrook, 2004 showed that some amphibian species may intensively move between neighboring ponds (in order to avoid predation and competition) whereas other species showed high pond fidelity. Similarly, Sinsch and Seidel (1995) showed a high variability in breeding pond use by the temporary pond breeding anuran, *B. calamita*. As such, pond loss will affect the availability of alternative breeding sites for amphibians and decrease connectivity between populations (e.g. Zanini et al., 2009; Hartel et al., 2010b) negatively affecting metapopulation dynamics. Our field observations carried out in 2006–2008 suggested that new ponds also appeared in the past three decades, and this was the case in the Slack valley where the number of wildfowl ponds has gone up (JWA, *personal observation*). These ponds, often with fish, are qualitatively different from the small field- and concrete ponds for watering the cattle. They may have little value for amphibians as breeding sites but they may serve as stepping stones, especially for the two mobile anurans (*B. bufo* and *R. temporaria*, Beebee, 1997).

It was also noticed that the extent of arable land around ponds increased. This represents a threat for amphibians through the destruction of terrestrial habitat used for feeding and shelter. Our study therewith contributes to a growing body of literature suggesting that agricultural intensification (e.g. Joly et al., 2001; Denoël and Ficetola, 2007) and urban development (e.g. Pellet et al., 2004) may be harmful for pond breeding amphibians, even if the breeding ponds themselves are not destroyed. Another negative effect of the pasture to arable conversion may be a reduction in dispersal movements through decreasing matrix permeability (Ray et al., 2002; Mazerolle and Desrochers, 2005). Furthermore, our study underlines the importance of considering multiple scales when evaluating the effect of land-use on pond biological qualities and pond persistence (see also Houlahan and Findlay, 2004; Declerck et al., 2006).

5. Conservation implications

We documented a sharp reduction in the number of ponds in an agricultural-urban area that underwent a major land in use change over three decades. A summary of results is in a map (Fig. 4) that highlights the areas in risk of further pond loss versus areas where chances for pond persistence are higher. The presence of marshes, grasslands and dune shrubs and the absence of arable, transport and urbanization is beneficial for pond persistence. We suggest that local amphibian conservation efforts will be the most effective if the focus is on the marshes and dune areas and on pond preservation in the remaining grasslands. The prime places to create new ponds would be in those landscape classes where pond loss has been most pronounced, where the network structure of ponds has been most affected and where the maintenance of new ponds can be secured.

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