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THE ROLE OF PONDS

Level-dependence of the relationships between amphibian biodiversity and environment in pond systems within an intensive agricultural landscape

**Alienor Jeliazkov · François Chiron ·
Josette Garnier · Aurélien Besnard ·
Marie Silvestre · Frédéric Jiguet**

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Abstract Wetlands, especially ponds, and their associated amphibian biodiversity are threatened by agricultural intensification. To improve conservation planning of these ecosystems, we need to understand at which scales biodiversity responds to human-induced disturbances. This study aims to assess the level-dependence of environment-amphibian biodiversity relationships in 150 ponds in an intensive agricultural landscape in Seine-et-Marne (France). Amphibian diversity surveys, site characteristic measurements and landscape descriptions are analysed. The hierarchy of the effects of local and regional variables on species richness, regional heterogeneity of species composition and species occurrences is investigated at three spatial levels: pond level, 1-, and 4-km^2 level. Species richness is negatively influenced at all levels by the fish presence. Water quality and pond density, which emphasize level-dependent effects, significantly increase species richness at the local and regional levels, respectively. With few exceptions, species occurrence analysis shows similar patterns, confirming, locally, the importance of fish avoidance, and, regionally, the need for increasing pond density. Environmental variables have no effect on the regional heterogeneity of species composition, questioning the potential existence of dispersal processes at scales above 1 km^2. This study highlights the relevance of a pond-group-centred approach compared to a pond-centred approach with regard to pond conservation in agricultural landscapes.

Keywords Agricultural landscape · Ponds · Amphibians · Habitats · Biodiversity · Spatial scales

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A. Jeliazkov (✉) · F. Chiron · F. Jiguet
Département Ecologie et Gestion de la Biodiversité,
Laboratoire Conservation des Espèces, Restauration et
Suivi des, Populations, UMR 7204, MNHN & CNRS,
Muséum National d'Histoire Naturelle, 55 rue Buffon,
75005 Paris, France
e-mail: jeliazkov@mnhn.fr; alienor.jeliazkov@gmail.com

J. Garnier · M. Silvestre
Laboratoire Sisyphe, UMR 7619, UPMC & CNRS,
Université Pierre et Marie Curie, 4 place Jussieu,
Tour 46-56, 75005 Paris, France

A. Besnard
UMR 5175, CEFE & CNRS, Centre d'Ecologie
Fonctionnelle et Evolutive, , Campus CNRS 1919, route
de Mende, 34293 Montpellier Cedex 5, France

M. Silvestre
FR3020, UPMC & CNRS, Fédération Ile-de-France de
Recherche sur l'Environnement, Université Pierre et
Marie Curie, 4 place Jussieu, Tour 56-55, 75005 Paris,
France

Introduction

Human disturbances and agricultural intensification, in particular, are a major driver of habitat loss (Saunders et al., 1991), especially for wetlands. Because they are small and sparse, ponds are particularly affected by this process of habitat erosion (Wood et al., 2003). However, ponds, which are one of the richest types of wetlands in terms of biodiversity (Williams, 2004), act as shelters of plant and animal biodiversity, and favour their persistence at different spatial, biological, and temporal scales (Oertli et al., 2002; Semlitsch, 2002). Moreover, because they are at the interface between terrestrial and aquatic habitats (Schneider et al., 2002), pond systems provide many ecological functions that can be of benefit to water quality, such as protection from intensive fertilisation (Zedler, 2003).

More and more research has taken up the challenge of wetland conservation, notably in Europe (Biggs et al., 2005; Céréghino et al., 2008). Wetland restoration and creation actions have led to encouraging results in terms of biodiversity conservation (Williams et al., 2007), especially for amphibians in altered landscapes (Rannap et al., 2009; Brand & Snodgrass, 2010; Shulse et al., 2010). To improve the efficiency of such management plans, we need to better understand species and community responses of aquatic biota to human-induced disturbances.

Amphibian communities raise important conservation issues (Houlahan et al., 2000). Due to the biphasic life cycle—aquatic and terrestrial—of some species, and their migration and dispersal ability, amphibians are sensitive to both local and regional environmental conditions (Werner et al., 2007). At the local level, some species are more or less sensitive to abiotic conditions such as water chemistry (Knutson et al., 2004). In some human-dominated areas, amphibians can be more sensitive to the structure of the surrounding habitat than to water quality (Scher & Thièry, 2005). As for the biotic factors, the presence of predatory fish has detrimental effects on the amphibian presence and diversity (Hecnar & M'Closkey, 1997; Smith et al., 1999). At the regional level, numerous studies have shown the influence of habitat quality, landscape composition and connectivity on amphibian diversity (Houlahan & Findlay, 2003; Ficetola et al., 2009). The availability of terrestrial habitats is crucial (Semlitsch & Bodie, 2003), as is their configuration. Indeed, in agricultural areas, the distance to the nearest woodlands can be limiting even for open-habitat species (Da Silva & Rossa-Feres, 2011). Pond isolation and pond density have also been pinpointed as important drivers of amphibian diversity (Brodman et al., 2003; Ficetola & De Bernardi, 2004) and of meta-population dynamics in some species (Gibbs, 1993). Thus, amphibian responses to the environment are multi-factorial and depend on the level of study. Since these relationships result from processes potentially acting at different spatial scales (Levin, 1992), multi-scale studies are highly recommended, allowing a holistic and integrative comprehension of ecosystem functioning.

Traditionally, *scale*-dependence of amphibian diversity-environment relationships is studied by testing links between a local measure of diversity and measures (or aggregates) of environmental variables at varying metric radii around ponds (Pellet et al., 2004; Simon et al., 2008). This method, though efficient, only focuses on local diversity, i.e. at the pond level. In contrast, we proposed to test a *level*-dependence of biodiversity-environment relationships through a systematic approach based on a pragmatic discretisation of the space into three structural levels. Our objective was to determine the key environmental variables that influence amphibian diversity and occurrence in an intensive agricultural landscape, and to compare these patterns according to: (i) pond level; (ii) 1-km^2 cell level; and (iii) 4-km^2 cell level. These *spatial levels* remain relevant in terms of the dispersal/migration distances of amphibians (Smith & Green, 2005) and are coherent with conservation objectives.

We proposed to study different *levels of biological diversity* across the three spatial levels: a local component of 'inventory diversity', i.e. species richness measured at the pond level (α), a regional (*sensu lato*) component of 'inventory diversity', i.e. species richness measured at coarser levels (γ) and a component of 'differentiation diversity', which corresponds to measured dissimilarities between ponds in terms of species composition within coarser levels (D, often referred to as β diversity) (for the levels of biological diversity, see Whittaker, 1972, as well as Jost, 2007; for the notions of 'inventory' and 'differentiation' diversity, see Jurasinski et al., 2008). In addition, we provided a focus on the species level by comparing occurrence patterns of the five species most frequently found in the area studied at the three spatial levels.

By combining statistical methods, we tested and hierarchised the effects of the environmental variables that most commonly in the literature appear to structure amphibian diversity, occurrence and community composition (Table 1).

In general, we assumed that the response of amphibian diversity to environmental variables might differ according to the structural and biological level we focused on. In particular, we proposed two groups of hypotheses:

(i) At the community level, we assumed that local inventory diversity is mainly driven by local variables linked to the quality of aquatic habitat (Van Buskirk, 2005), whereas differentiation diversity may instead be a function of habitat availability around ponds, i.e. pond density and the presence of semi-natural habitats in the landscape (Ficetola & De Bernardi, 2004). As a derived hypothesis of (i) regional diversities would vary according to the differentiation diversity rather than the local diversity in landscapes characterised by higher habitat diversity. Given the different ecological requirements of amphibian species (Cushman, 2006), heterogeneous landscapes may actually host a variety of species.

(ii) At the population level, we aimed to assess species response variability to local and regional environmental variables. Although we did not use a trait-based approach, we discussed species

Table 1 Hypotheses of species response traits to environmental disturbances and to the surrogate variables of the study, according to a non-exhaustive review of the literature

	Response trait	*Bufo bufo*	*Triturus helveticus*	*Triturus vulgaris*	*Pelophylax* sp.	*Rana dalmatina*
Water pollution	Tolerance to chemical pollutions, nutrient loads, or acidification **Water Quality Index**	+[1] –[2,3] ~[4,5]	~[1,3]	~[1,4]		
Fish stocking	Tolerance to fish predation **Fish presence**	+[1,6] ~[7]	–[1,8,9]	–[1,6,10]	+[11,12] –[9] ~[7]	+[6,11,12] ~[7]
Landscape alteration	Dependence on woodland habitats **Landscape gradients**	+[13] –[14]	+[1,8,9]	+[1,13] –[14]	+[9] –[14]	+[15]
	Tolerance to urbanisation/ development of infrastructures **Landscape gradients**	+[14]		–[14,16]	–[14]	–[15,17]
	Dependence on large pond area **Pond area**	–[13,18]	–[1,8,18]	+[16] –[1,18]	–[18]	–[16]
	Dependence on pond density or connectivity **Pond density**	+[13]	+[8]	+[10,13]	+[19] –[10]	+[19]
	Ranges of maximum dispersal distances (m) **Spatial dependence**	118–3621[20] 500–1000[22] <1600[21]	150–1000[22]	80–182[20]	1200–15000[20]	300[20] <1000[22]

+ / - / ~: positive/negative/mitigated response

Missing hypotheses are due to a lack of information for the species considered

The Bold fonts indicate surrogate variables tested in the study

Reference samples: [1]Beebee (1981); [2]Rouse et al. (1999); [3]Mann et al. (2009); [4]Cooke (1977); [5]Freda (1986); [6]Hartel et al. (2007); [7]Gunzburger & Travis (2005); [8]Joly et al. (2001); [9]Le Viol et al. (2012); [10]Ficetola & De Bernardi (2004); [11]Teplitsky et al. (2003); [12]Teplitsky et al. (2004); [13]Piha et al. (2007); [14]Van Buskirk (2005); [15]Hartel et al. (2009); [16]Santi et al. (2010); [17]Lesbarrères et al. (2003); [18]Oertli et al. (2002); [19]Kolozsvary & Swihart (1999); [20]Smith & Green (2005); [21]Semlitsch & Bodie (2003); [22]ACEMAV coll. (2003)

responses across levels in light of their main ecological and behavioural characteristics presented in Table 1.

Materials and methods

Study area, pond selection and environmental characterisation

The area studied is located in Brie, within the Seine-et-Marne department of France (Eastern Ile-de-France; 48.6°N/3.2°E). This site is representative of an intensive agricultural landscape since 80% of its area (~430 km^2) is covered by crops, and mainly cereals (Fig. 1).

We selected 150 ponds out of a total of some 300 ponds in this area on the basis of three main criteria: (1) ponds were surrounded by more than 50% of agricultural land within a radius of 200 m to remain in a context of intensive agriculture while optimising our cross-scale representativeness of all of the ponds in the area; (2) ponds were permanent to avoid major discrepancies in ecological functioning linked to the hydrological regime; and (3) to test the effect of pond density on amphibians, we chose ponds within clusters of different pond densities in which inter-pond distances did not exceed 2000 m.

Site selection and characterisation of the ponds and their surrounding landscape for the three spatial levels were processed using the GIS tools, ArcView9.3® and ETGeoWizard10®.

For landscape characterisation, we combined the complementary databases MOS (Mode d'Occupation du Sol, IAU IDF, 2008) and Ecomos (Atlas des Milieux Naturels en Ile-de-France, IAU IDF, 2005). We considered six categories to describe the landscape composition: crops (agricultural areas), urban and inhabited areas (including transport infrastructures), meadows (including grasslands and natural pastures), woodland areas, wetland areas and rural areas (including remaining areas, i.e. non-urban, wasteland, bare rock and sparse vegetation areas). We calculated the cover proportions of each landscape category for all levels.

For more accurate information on pond location and characteristics, we used the database BD TOPO®v2 (Base de Données Topographique, IGN, 2008). These data were supplemented by two complementary pond censuses (2009–2012 and 2009–2010) (Département de Seine-et-Marne, 2011; SNPN, 2012).

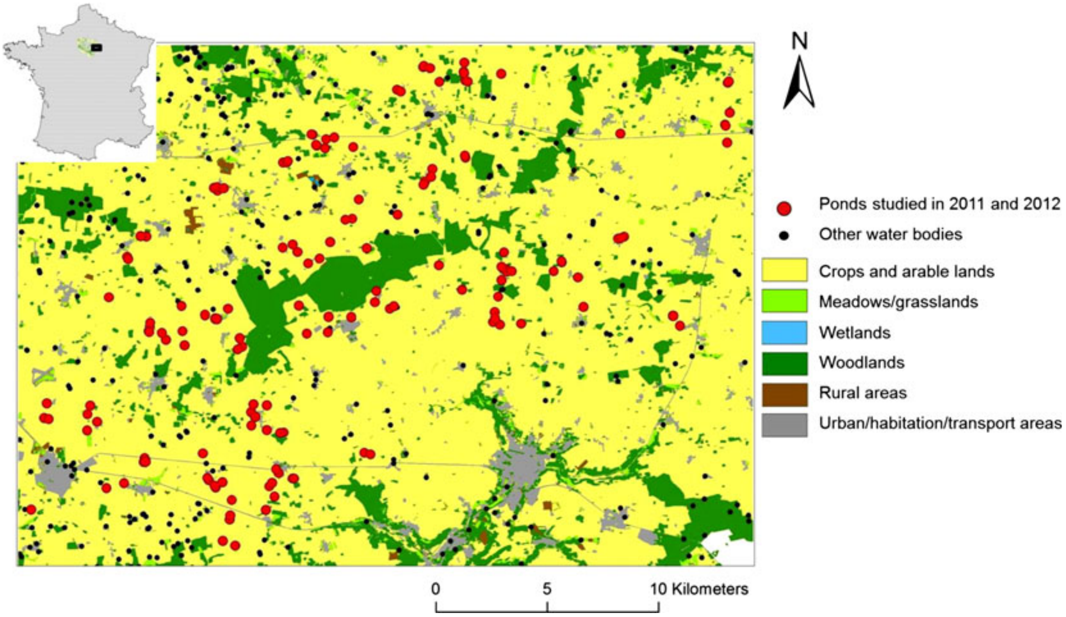

Fig. 1 Map of the study area with the 150 ponds surveyed in 2011 and/or 2012

Finally, to describe water quality, we conducted four sessions of physico-chemical measurements of the water in June 2011, July 2011, March 2012 and June 2012. The following variables were directly measured on site: dissolved oxygen (O_2, mg/L), water temperature (°C) and pH. Water samples were analysed in the laboratory to assess concentrations of ammonium (NH_4^+, mg/L), ammonia (NH_3, mg/L), nitrates (NO_3^-, mg/L), nitrites (NO_2^-, mg/L), silica (Si, mg/L), phosphates (PO_4^{3-}, mg/L) and chlorophyll *a* (chl a, µg/L). Phosphate, silica and nitrogen forms were determined spectrophotometrically on glass-fibre filtered water, according to the protocols of Eberlein & Kattner (1987), Rodier (1984), and Slawyk & MacIsaac (1972), respectively. Chlorophyll *a* was analysed according to Lorenzen (1967).

Since many of these variables were correlated, we calculated a Water Quality Index adapted from Pesce & Wunderlin (2000) and initially developed for stream waters, to give an integrative view of the water quality. This index relies on a compilation, rescaling, and standardisation of the parameter values according to 11 classes of water quality, ranging from 0% (very bad quality) to 100% (very good quality) (see Pesce & Wunderlin, 2000; Sánchez et al., 2007), and is calculated as follows

$$\mathrm{WQI}(\%) = \frac{1}{S}\sum_{i=1}^{S}\left(\frac{1}{N_i}\sum_{j=1}^{N_i} C_j\right)$$

where WQI (%) is the mean Water Quality Index of a pond over the four measurement sessions, i the number of the session (1st, 2nd, 3rd or 4th), S the total number of sessions, N_i the total number of variables measured at the session i, j the parameter itself, C_j the rescaled and standardised value of the parameter j in percentage according to Sánchez et al. (2007, p. 319, Table 3).

Amphibian survey and biotic information

We assessed species richness and abundance of amphibians for all 150 sites in 2011 and 2012, using a standardised protocol. A total of 52 ponds were surveyed in 2011, 65 ponds in 2012, and 33 ponds in both years, to assess an eventual year effect. There was no or a negligible year effect in the species richness and occurrence data, allowing us to not include the year as a co-factor in the analyses of this study (Supplementary analyses and results shown in Appendix 1). We conducted two 2-week exclusively nocturnal sessions per year during the main reproductive seasons: in March and in June.

To avoid detection biases as much as possible (Schmidt & Pellet, 2005), we combined three complementary methods to detect the target taxa, while minimising habitat destruction. First, we identified and counted calling males during a point-count lasting for 5 min. Second, we visually identified and counted individuals using lamps in five equidistant and equidistributed plots measuring approximately 5 × 5 m along the banks of the ponds. Third, dip-netting (one time per plot) allowed us to detect, identify and count individuals, especially tadpoles and larvae, which could have previously been undetected. Several species of the subgenus *Pelophylax* are present in the department: *Rana ridibunda*, *Rana lessonae* and *Rana kl. esculenta*, which were grouped together as *Pelophylax* sp. due to the ambiguity of their identification.

For each site, we also recorded the presence or absence of fish on the basis of visual observations, by dip-netting and/or according to the information provided by pond owners.

Data processing and methods for analysing ecological relationships and their level-dependence

All statistical analyses were performed with the statistical computing software R 2.12.1. We considered three spatial levels of analysis: (1) the ponds and their close surroundings materialised by a buffer zone with a 200-m radius centred on focal ponds (‘pond level’); (2) the cells of 1000 × 1000 m (or 1 km^2) (‘Level 1000’); and (3) the cells of 2000 × 2000 m (or 4 km^2) (‘Level 2000’). To form Level 1000 and Level 2000, we applied regular grids of 1-km^2 cells and of 4-km^2 cells, respectively, on the study area (Appendix 2 in Supplementary Material). These grids were adjusted according to the layer of all water bodies encountered in the study area, and a cell was defined if it provided at least one sampled pond within its limits.

Three types of response variables were studied across the levels. For inventory diversity, we used the species richness (number of species) for all three levels, designated as α_{Pond}, γ_{1000} and γ_{2000} (Fig. 2). For differentiation diversity, we studied the mean inter-pond dissimilarities at Level 1000 and Level 2000, designated as $\overline{D}_{1000}$ and

$\overline{D}_{2000}$, respectively. To do this, we calculated Jaccard dissimilarities (package {ade4}) based on the presence/absence data (Koleff et al., 2003). These values were then averaged at each regional level, giving one mean value of dissimilarity per cell (Fig. 2). For statistical purposes in the analyses, we used the transformed variables $\overline{S}_{1000}$ and $\overline{S}_{2000}$, where $\overline{S}_{1000} = \sqrt{1 - \overline{D}_{1000}}$ and $\overline{S}_{2000} = \sqrt{1 - \overline{D}_{2000}}$, corresponding to the square roots of similarities. Finally, we analysed binary variables of occurrences (presence/absence) for the five species—*Bufo bufo*, *Triturus helveticus*, *Triturus vulgaris*, *Pelophylax* sp. and *Rana dalmatina*—at the three levels, referred to as PA_{bufbuf}, PA_{trihel}, PA_{trivul}, PA_{pelosp}, PA_{randal}, respectively, with a mention of the level when necessary (Fig. 2).

For the analyses of inventory diversities α_{Pond}, γ_{1000} and γ_{2000}, we had 150 entities (ponds), 84 entities (1-km^2 cells), and 57 entities (4-km^2 cells), respectively. For the differentiation diversities $\overline{S}_{1000}$ and $\overline{S}_{2000}$, we had 39 entities at both levels (excluding cells of <2 ponds/cell). The pond level is thus nested in the two higher levels, but Level 1000 is not necessarily nested in Level 2000 (Fig. 2 and Appendix 2 in Supplementary Material).

The spatial dependence of response variables was tested by the analysis of spatial correlograms. We measured spatial dependence using Moran's Index for different distance classes (package {ncf}) with increments of 200, 500 and 1000 m, for the variables $PAPond_{sp}/\alpha_{Pond}$, $\gamma_{1000}/\overline{S}_{1000}$ and $\gamma_{2000}/\overline{S}_{2000}$, respectively. The statistical significance was assessed by a permutation test (1000 permutations) for a confidence limit of 5%. Only first distance classes carrying a spatial dependence (Moran's I) significantly higher than zero were considered. According to the mean distance of the last significant distance class, an autocovariate term, referred to as *Autocov*, was calculated and included as an additional covariable in the models to take spatial auto-correlation into account (see Augustin et al., 1996; Betts et al., 2009).

For the analyses of inventory diversity at Level 1000 and Level 2000, we aggregated environmental variables by averaging values measured at the pond level (Table 2). For the analyses of differentiation diversity, the mean Euclidean distance (MeanEuclDist) (Legendre & Legendre, 1998) was calculated between values of local environmental variables of ponds within cells, as a surrogate of the heterogeneity of local conditions. Principal Component Analyses were performed on the proportions of the six categories of landscape cover to summarise landscape collinear information and identify main landscape gradients (referred to as *CompoPay1* and *CompoPay2*) at each level. The final set of tested variables for each analysis is presented in Table 2.

We applied the statistical method of hierarchical partitioning associated with a randomisation procedure on the proportions of independently explained variances (in contrast to jointly explained variances) to assess their significance and classify the effects of environmental variables on response variables (1000 repetitions for each analysis) (package {hier.part}) (Chevan & Sutherland, 1991). The statistic Z is calculated from the observed values compared to the generated distribution of randomised values, and statistical significance is based on an upper 0.95 confidence limit, implying that $Z \geq 1.65$. Because the distribution of response variables was not normal (except for the mean similarities $\overline{S}_{1000}$ and $\overline{S}_{2000}$), we used a log link function for α_{Pond}, γ_{1000} and γ_{2000} (as species counts), and a logit link function for PA_{sp} variables (as binary variables) in the models.

A complementary step of Generalised Linear Model fitting (package {stats}) allowed us to estimate the regression coefficients and assess the sign of the relationships revealed by the analyses of hierarchical partitioning. To assess the goodness-of-fit of Poisson and Gaussian models used for the inventory and differentiation diversities, we applied a Chi squared test on the model deviance against degrees of freedom (package {epicalc}), and a Shapiro test on the model residuals, respectively.

Results

PCAs defining landscape gradients

At the three levels, the first two axes of PCAs explained from 91% up to 99% of the total inertia of the landscape composition data (Fig. 3 and Appendix 3 in Supplementary Material). Pond coordinates along these two axes were used in the models as landscape variables; *CompoPay1* and *CompoPay2*. At the pond level, landscape characteristics varied along a first gradient (Axis 1) of land artificialisation caused by an increase of

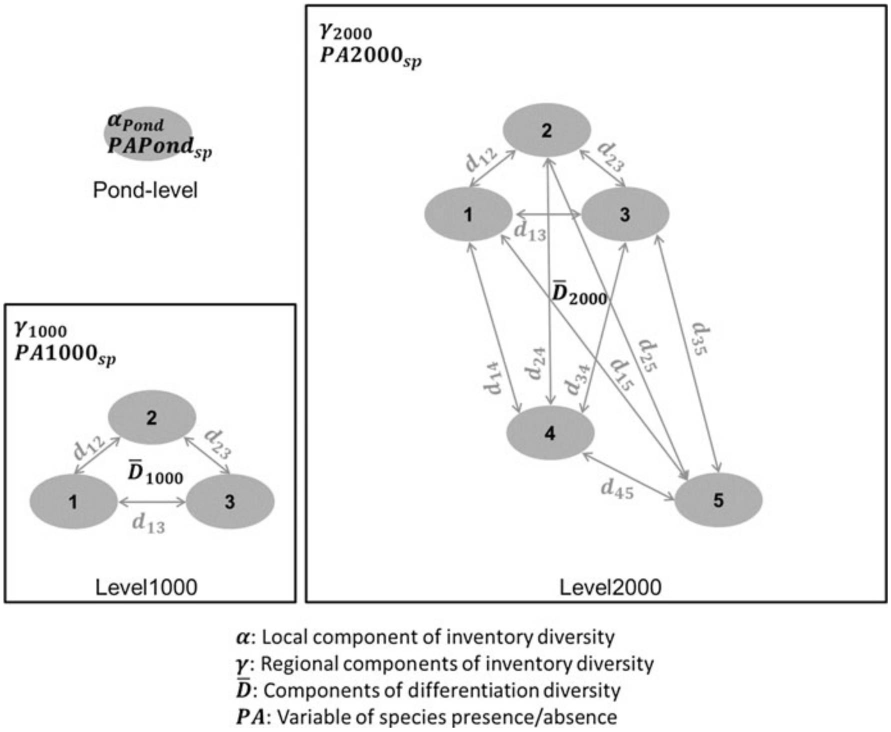

Fig. 2 Scheme of the three structural levels considered in the study: pond level (entity = pond), Level 1000 (entity = 1-km^2 cell) and Level 2000 (entity = 4-km^2 cell). The response variables of interest for each level are represented: species richness of ponds/1-km^2 cells/4-km^2 cells ($\alpha_{Pond}/\gamma_{1000}/\gamma_{2000}$ respectively), mean differentiation diversity within 1-km^2 cells/4-km^2 cells ($\bar{D}_{1000}/\bar{D}_{2000}$ respectively) (resulting from the mean of inter-pond dissimilarities ($d_{Pond\text{-}to\text{-}Pond}$)), and occurrence of the five species in ponds/1-km^2 cells/4-km^2 cells ($PAPond_{sp}/PA1000_{sp}/PA2000_{sp}$ respectively). According to the concept of α/β/γ diversities founded by Whittaker (1972), and adapted by Jost (2007) and Jurasinski et al. (2008)

either agricultural areas or urbanised lands, and along a second gradient of habitat diversification (Axis 2) in favour of semi-natural habitats such as woodlands and meadows (Fig. 3a). For Level 1000 and Level 2000, we observed two main landscape gradients: a first gradient of agricultural intensification characterised by a loss of woodlands, and a second gradient of urbanisation and a slight diversification of habitats (Fig. 3b, c and Appendix 3 in Supplementary Material).

Spatial dependence

Spatial dependence of response variables was significant only at the pond level, with different distance thresholds depending on the variable (t): α_{Pond} ($t = 1509$ m, $I = 0.33$, $P = 0.009$), $PAPond_{bufbuf}$ ($t = 700$ m, $I = 0.42$, $P = 0.004$), $PAPond_{trihel}$ ($t = 503$ m, $I = 0.36$, $P = 0.01$), $PAPond_{trivul}$ ($t = 503$ m, $I = 0.24$, $P = 0.04$), $PAPond_{pelosp}$ ($t = 299$ m, $I = 0.29$, $P = 0.03$), $PAPond_{randal}$ ($t = 299$ m, $I = 0.32$, $P = 0.03$). No significant spatial dependence was observed for the other response variables. Thus, autocovariate covariables were calculated for the maximum neighbourhood distances of 2000, 700, 500 and 300 m, and were added to the analyses of the variables α_{Pond}, $PAPond_{bufbuf}$, $PAPond_{trihel}/PAPond_{trivul}$ and $PAPond_{pelosp}/PAPond_{randal}$, respectively.

Fish occurrence, and inventory and differentiation diversities of amphibians

Field surveys revealed that 66 out of 150 ponds hosted fish (44% fish ponds *vs* 66% fishless ponds). We observed a total of 11 amphibian species with a varying raw occupancy over the study area: *Pelophylax* sp. (57%), *Bufo bufo* (46%), *Rana dalmatina* (35%), *Triturus vulgaris* (23%), *Triturus helveticus* (16%), *Alytes obstetricans* (11%), *Triturus cristatus* (8%), *Triturus alpestris* (6%), *Hyla arborea* (5%), *Pelodytes punctatus* (4%) and *Rana temporaria* (3%).

Table 2 Set of environmental variables tested on response variables with the different aggregation modes used depending on the level considered, namely pond level (pond, or local surroundings in a radius of 200 m), Level 1000 (1-km^2 cells), and Level 2000 (4-km^2 cell)

Environmental variables	Response variables		
	Pond level	Level 1000/2000	
	α_{Pond} and $PAPond_{sp}$	$\gamma_{1000/2000}$ and $PA1000/2000_{sp}$	$\overline{S}1000/2000$
WQI	Pond WQI (%)	Mean pond WQI (%)	MeanEuclDist between pond WQIs (%)
Area	Pond area (m^2)	Mean pond area (m^2)	MeanEuclDist between pond areas (m^2)
Fishes	Fish occurrence in the pond (1/0)	Fish occupancy in the cell	MeanEuclDist between pond fish occurrences
CompoPayl	1st landscape gradient at pond level	1st landscape gradient at Level 1000/2000	1st landscape gradient at Level 1000/2000
CompoPay2	2nd landscape gradient at pond level	2nd landscape gradient at Level 1000/2000	2nd landscape gradient at Level 1000/2000
DensPond	Number of surrounding ponds (from 0 to 4 ponds, without focal pond)	Total number of ponds per cell (from 1 to 7/10 ponds)	Total number of ponds per cell (from 2 ponds to 7/10 ponds)

Fish occupancy is calculated as the ratio of the number of ponds occupied by fish out of the total number of ponds per cell

α_{Pond}: species richness of ponds

$PAPond_{sp}$: species occurrence in ponds

$\gamma_{1000/2000}$: species richness of 1-km^2 cells/4-km^2 cells

$PA1000/2000_{sp}$: species occurrence in 1-km^2 cells/4-km^2 cells

$\overline{S}1000/2000$: square root of the mean inter-pond similarities in terms of species composition within 1-km^2 cells/4-km^2 cells

MeanEuclDist: Mean Euclidean Distance

See Appendix 4 in Supplementary Material for a graphical visualisation of the response variables of inventory and differentiation diversities.

Concerning the inventory diversity (Figs. 4a–c, 5a, c, e), we observed that fish occurrence significantly and negatively affected species richness at all levels, explaining 22% ($Z = 4.88$), 13% ($Z = 1.78$) and 30% ($Z = 4.18$) of the species richness at pond level, Level 1000 and Level 2000, respectively. However, a larger proportion of species richness variance was explained by the spatial component (46%, $Z = 10.66$), followed by the Water Quality Index (27%, $Z = 6.14$) at pond level (Figs. 4a, 5b), both with positive effects (Appendix 5 in Supplementary Material). We found identical patterns at Level 1000 and Level 2000, with a positive effect of pond density (71%, $Z = 13.37$ and 64%, $Z = 9.54$, respectively), counteracting the negative effect of fish occurrence (Figs. 4b, c, 5d, f). As for the differentiation diversity (Fig. 4d, e), we observed no significant effect of the environmental variables.

The GLMs built with the significant explanatory variables revealed by the hierarchical partitioning satisfied the test of goodness-of-fit, except—albeit marginally—for the Gaussian models fitted on the differentiation diversities ($W = 0.93$, $P = 0.02$ for $\overline{S}_{1000}$ and $W = 0.94$, $P = 0.04$ for $\overline{S}_{2000}$).

Species occurrences

Fish occurrence had a significant negative effect on all species at almost all levels, except on *Pelophylax* sp. (no effect) and on *B. bufo* (positive effect) (Table 3). These two species were also the only ones to be highly and positively influenced both by WQI and pond area at pond level and/or Level 1000. The pond density had a positive effect on all species—except *T. vulgaris*—and varied depending on the species (from 27 up to 71% of explained variance). The effect of the spatial component was positive and predominant for newts (*T. helveticus* and *T. vulgaris*) and for *Pelophylax* sp. The occurrence of *B. bufo* was negatively correlated to *CompoPay1*, indicating a negative effect of urbanised areas. At upper levels, where *CompoPay1* represented a Crops versus Woodlands gradient (Fig. 3), we noted

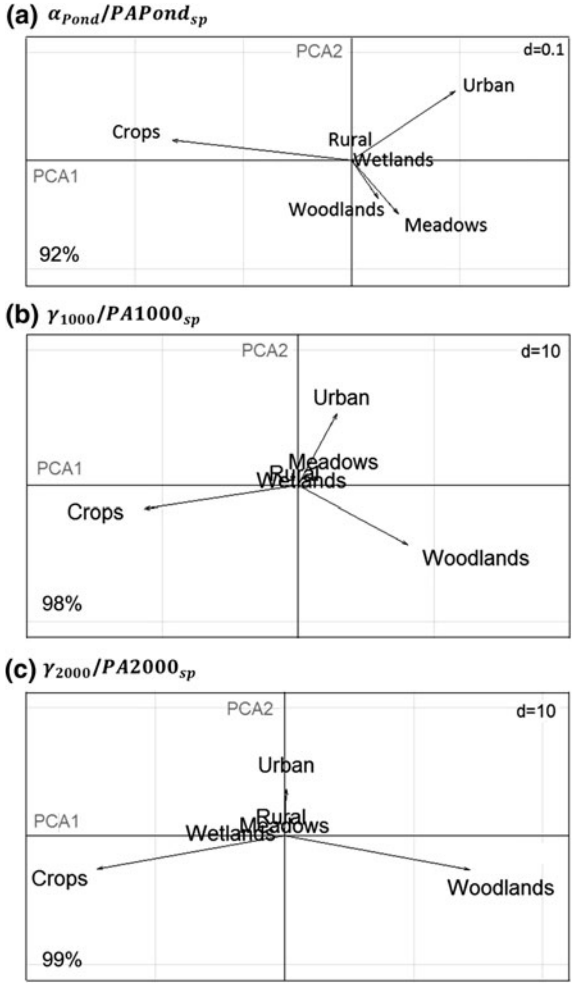

Fig. 3 Plots representing the landscape gradients according to PCA analyses performed on cover proportions of each landscape category (Crops, Meadows, Urban, Woodlands, Wetlands and Rural areas) according to the different levels of data aggregation. The first two axes (PCA1 and PCA2) were retained, together explaining a major part of the landscape inertia as indicated in the bottom left corner within the plots. Because the PCAs at the regional level provided redundant information, we only show PCAs associated with the study of **a** $\alpha_{Pond}/PAPond_{sp}$ (150 entities), **b** $\gamma_{1000}/PA1000_{sp}$ (84 entities), and **c** $\gamma_{2000}/PA2000_{sp}$ (57 entities). d = mesh unit. (For the PCAs associated with $\overline{D}_{1000}$ and $\overline{D}_{2000}$, see Appendix 3 in Supplementary Material)

a positive effect of woodlands increase on the three species *B. bufo*, *T. helveticus* and *R. dalmatina*. The variable *CompoPay2*, representing an urbanisation increase, had no effect except for *R. dalmatina* at Level 2000 for which this effect was negative (Table 3, Appendix 5 in Supplementary Material).

Discussion

The Seine-et-Marne department includes a total of 15 amphibian species (considering the three species of *Rana pelophylax* grouped together) (Renault, 2012). The total species richness of the study area (11 species) thus represents 73% of the department diversity. Although several species were particularly scarce (e.g. *Rana temporaria* and *Hyla arborea*), this suggests that at least some agricultural ponds, or groups of ponds, may be valuable in terms of amphibian conservation given the department diversity.

Level-dependence in ecological relationships for inventory and differentiation diversities at the community level

We demonstrated that the species richness at the pond level was influenced by local conditions, negatively by the fish presence, and positively by water quality. Although the effects of water chemistry on amphibians remain minor according to Hecnar & M'Closkey (1997), the effects of nitrogen levels are often incriminated (Boyer & Grue, 1995; Rouse et al., 1999). In our study, we were not able to determine if the positive effect of the water quality is linked to a negative effect of nitrogen concentrations (Houlahan & Findlay, 2003) and/or of a trophic state (Hinden et al., 2005). The surrounding landscape within 200 m showed no effect, despite the expected influence of the quality of nearby terrestrial habitats (Gibbons, 2003; Ficetola et al., 2009). However, 200 m would approximately define the 'core habitat' of amphibians (Semlitsch & Bodie, 2003), and additional larger buffer zones would be necessary to protect the sites against edge effects (Lidicker & Koenig, 1996). In the area studied, regulatory uncultivated buffer zones have a minimum width of 5 m and untreated strips should not exceed 100 m in width from the pond shoreline, according to the regulations of the European Common Agricultural Policy (Grenelle II, article 52, 2010). It is therefore very unlikely that the optimal size of undisturbed semi-natural habitats and their connectivity can be achieved. Detailed information about the pond micro-habitats or the punctual features of the adjacent landscape would shed light on the effect of neighbouring terrestrial habitats (Marnell, 1998).

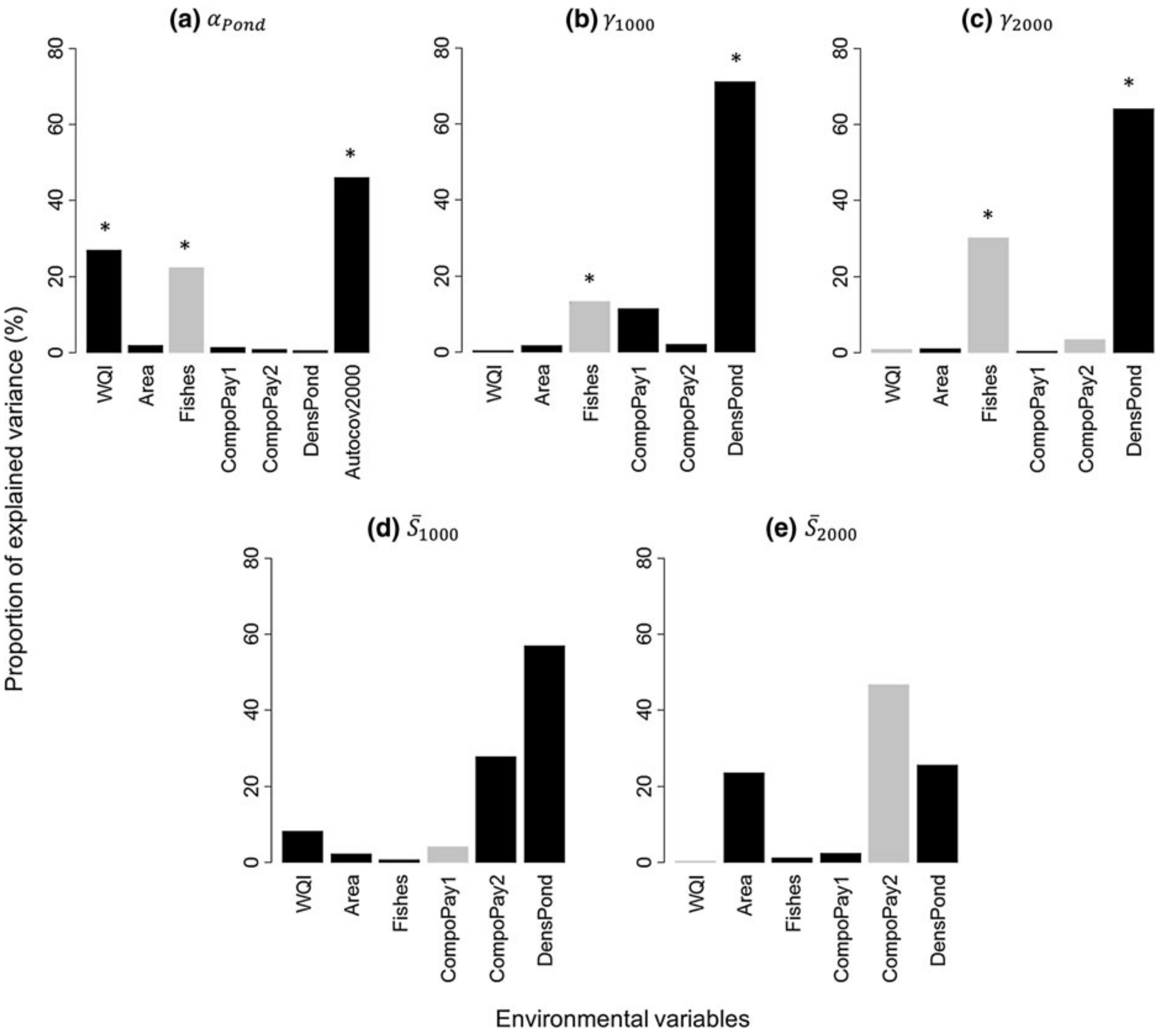

Fig. 4 Proportions of variance, independently explained by the six environmental predictors (+ the autocovariate component for α_{Pond}): in the inventory diversity with **a** the pond species richness, **b** the 1-km^2 cells species richness, **c** the 4-km^2 cells species richness; and in the differentiation diversity with **d** the mean between-pond similarities within 1-km^2 cells, **e** the mean between-pond similarities within 4-km^2 cells. *Asterisks* indicate significant effects ($P < 0.05$), *grey bars* refer to negative effects and *black bars* to positive effects according to complementary GLM analyses (Appendix 5 in Supplementary Material)

We found that species richness was essentially and positively influenced by pond density at the regional level, as predicted by the simple species-area relationship (Arrhenius, 1921), as well as, indirectly, by other studies showing the negative effect of pond isolation (Lehtinen et al., 1999; Ficetola & De Bernardi, 2004). Yet, even at these levels, the negative effect of the fish presence remains significant, despite any expected influence of the landscape. This suggests that the regional species richness in this study area is primarily dependent on local richness and, by extension, on local aquatic conditions. The limiting factor would instead be the availability of favourable sites for colonisation, i.e. sites that are uninhabited by fish. As highlighted by Marsh & Trenham (2001), pond isolation can play a strong role in disturbed areas because, without necessarily being breeding sites, ponds at least offer terrestrial habitats. This observation is reinforced by our results on the differentiation diversity where we found no effect of the environmental variables on community homogenisation, especially in spite of our expectations about the

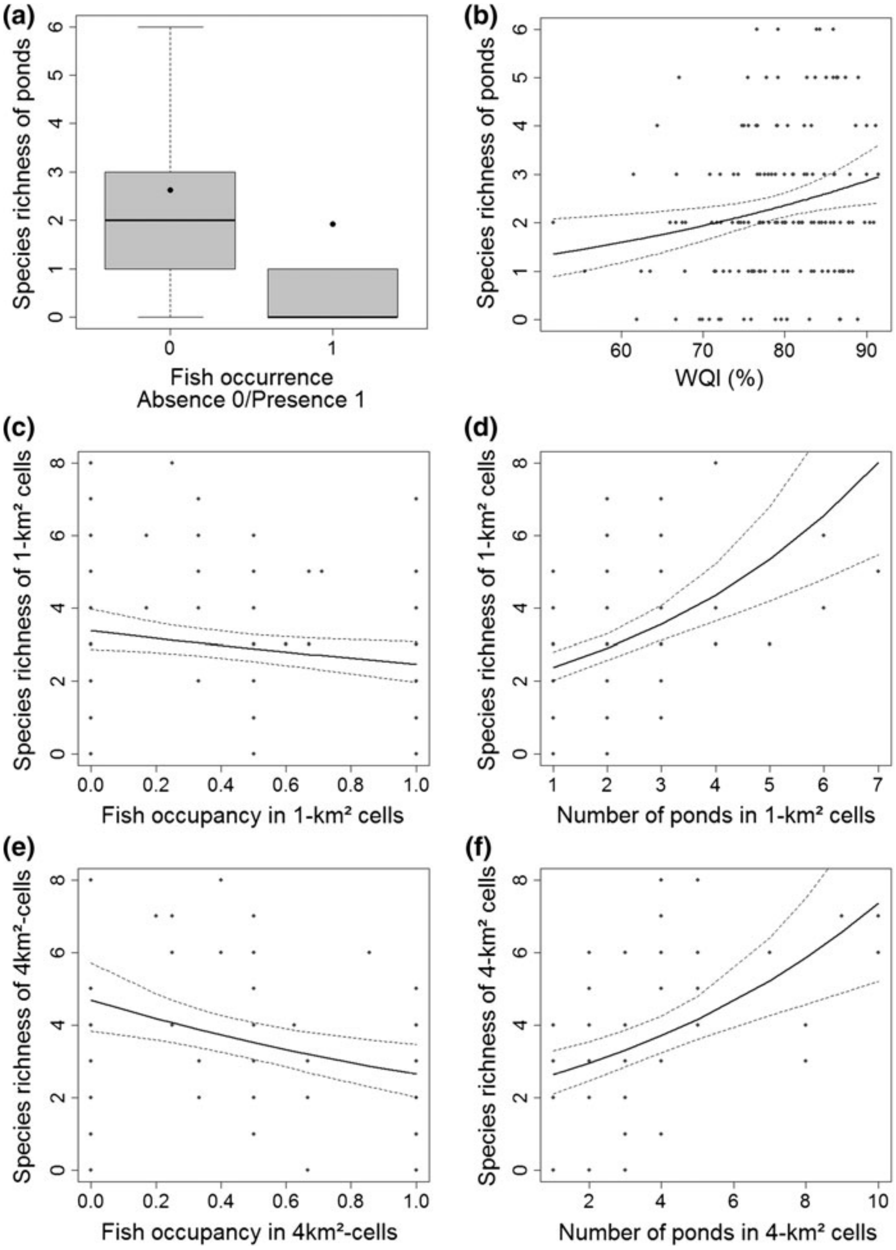

Fig. 5 Plots of the key relationships between inventory diversity and environmental variables revealed by the analyses of Hierarchical Partitioning and Generalized Linear Modelling at the three levels: species richness at pond level depending on **a** fish presence and **b** WQI; species richness at Level 1000 depending on **c** fish occupancy and **d** pond density; and species richness at Level 2000 depending on **e** fish occupancy and **f** pond density. *Solid black lines* on plots and *bold black dots* on the boxplot represent the model predictions; *dashed black lines* on plots and *solid black intervals* on the boxplot represent the 95% confidence intervals

landscape effects. This raises serious uncertainties about potential migration/dispersal processes at the 1- and 4-km^2 levels in such intensive agricultural landscapes. Indeed, when the landscape connectivity is low, the distances amphibians travel are probably limited and, as a result, the structural units of 1 and 4 km^2 may be too large here to encompass eventual migration or dispersal processes. This is partly confirmed by our results on the spatial dependence of species occurrence. Indeed, except for *T. vulgaris*, the maximum spatial auto-correlation was at least two times lower than the maximum displacement capacities usually recorded for these species (Table 1). Thus, in such intensive agricultural landscapes, it may be necessary to downwardly revise amphibian travel distances, assuming dispersal actually occurs. However, our results concerning spatial dependency can also be interpreted as a strict spatial synchrony, i.e. ponds belonging to the same clusters (thus, ponds spatially close) are more likely to present similar

Table 3 Results from hierarchical partitioning for the five most frequent species in the study showing the proportions of variance in the occurrence of each species at pond level, Level 1000 and Level 2000, explained independently by the six environmental predictors + the autocovariate term for pond level. Only significant results are shown ($P < 0.05$ with $Z \geq 1.65$); proportions of explained variance (%) are in bold; the sign of the effects is represented by an exponent + for positive effect and—for negative effect (for detailed GLM results, see Appendix 5 in Supplementary Material)

Species	Levels	Environmental variables						
		WQI	Area	Fishes	CompoPay1	CompoPay2	DensPond	AutocovSp
Bufo bufo	Pond level	**27**$^+$ $Z = 2.93$		**24**$^+$ $Z = 2.73$	**22**$^-$ $Z = 2.19$			
	Level 1000		**15**$^+$ $Z = 1.75$	**17**$^+$ $Z = 1.76$	**18**$^+$ $Z = 2.19$		**32**$^+$ $Z = 4.24$	–
	Level 2000							–
Triturus helveticus	Pond level			**31**$^-$ $Z = 6.08$				**46**$^+$ $Z = 8.23$
	Level 1000			**27**$^-$ $Z = 3.5$	**20**$^+$ $Z = 2.24$		**38**$^+$ $Z = 4.85$	–
	Level 2000			**42**$^-$ $Z = 4.63$			**43**$^+$ $Z = 4.78$	–
Triturus vulgaris	Pond level			**40**$^-$ $Z = 8.89$				**41**$^+$ $Z = 8.93$
	Level 1000			**65**$^-$ $Z = 4.96$				–
	Level 2000			**59**$^-$ $Z = 7.04$				–
Pelophylax sp.	Pond level	**30**$^+$ $Z = 4.33$	**16**$^+$ $Z = 2.20$					**32**$^+$ $Z = 4.19$
	Level 1000		**28**$^+$ $Z = 2.51$				**42**$^+$ $Z = 4.44$	–
	Level 2000						**71**$^+$ $Z = 5.93$	–
Rana dalmatina	Pond level			**61**$^-$ $Z = 4.28$				
	Level 1000			**23**$^-$ $Z = 2.19$	**32**$^+$ $Z = 3.07$		**27**$^+$ $Z = 2.64$	–
	Level 2000			**36**$^-$ $Z = 2.88$		**24**$^+$ $Z = 1.7$		–

Bold numbers show the proportions of explained variance (%); in exponent, the sign of the effect (positive/negative: +/−)

Z: Z statistics (level of significance: $Z \geq 1.65$); −: no autocovariate component for Level 1000 or Level 2000

habitat types (Petranka et al., 2004) and, consequentially, similar biological communities, according to processes of habitat selection. Moreover, diversity indicators such as species richness or mean community similarities may not be sensitive enough to the landscape variables of the system of interest and its spatial extent (Whittaker et al., 2001). The landscape gradients that summarise the landscape variability might not be appropriate to detect the effect of land uses on regional community variations. Since amphibians show variable and specific ranges of ecological requirements (Cushman, 2006), an explanation might be that contemporary amphibian communities are composed of the species, that are more resistant and resilient to land-use change. Those species thrive, whereas species highly sensitive to urbanisation and agriculture have relict populations or have already disappeared.

Level-dependence in ecological relationships for species occurrence

Species occurrence was generally locally influenced by the fish presence and regionally influenced by pond density. At the pond level, the fish presence had a negative effect on all species except the most frequent ones, *Bufo bufo* and *Pelophylax* sp. This might be explained by the unpalatability of their eggs (Kats et al., 1988) although this possibility has recently been subject to debate; our results may perhaps be due to the ability of these species to avoid predation in the particular case of permanent ponds (Gunzburger & Travis, 2005). Moreover, *Rana pelophylax ridibunda* is able to develop morphological defences at larval stages against predation (Teplitsky et al., 2003). Less sensitive to predation and good competitors due to their comparatively larger clutches (ACEMAV coll., 2003), *Pelophylax* sp. and *Bufo bufo* may instead be limited by habitat area and water quality. Concerning the occurrence of *Bufo bufo*, the positive effect of the fish presence could be interpreted as a competition release mediated by the predation on potential competitors of toads, if any competitive phenomenon ever occurs (e.g. Morin, 1983; Alford & Wilbur, 1985). In any case, competition seems to remain less important than site availability and quality (Van Buskirk, 2005), and the co-occurrence of toads and fish are probably due to similar criteria of habitat selection: pond area and water quality. The surrounding landscape within 200 m showed almost no effect on species occurrence, probably for the same reasons as previously discussed for inventory and differentiation diversity. Notwithstanding, *B. bufo* was still affected by urbanisation increase, which is consistent with the negative effect of road density (Hels & Buchwald, 2001). Local pond density had no effect on species occurrence while site quality was predominant. This is consistent with Denoël & Ficetola (2008) who showed that the local occurrence of newts depended on site quality and woodland proximity rather than local pond density.

However, species occurrence was highly dependent on pond density at the regional level in anurans and newts, consistently with Trenham et al. (2003), and Joly et al. (2001), respectively. In addition, the three species, *B. bufo*, *T. helveticus* and *R. dalmatina*, were highly and positively responsive to the proportion of woodland cover. This illustrates the importance of the regional availability of terrestrial habitats for these species (Denoël & Lehmann, 2006; Hartel et al., 2008; Hartel et al., 2009), which potentially act as wintering sites (Regosin et al., 2005) or as corridors (Roe & Georges, 2007).

Conclusions concerning level-dependence and implications for conservation biology

Overall, this study confirms that environment-amphibian biodiversity relationships in pond located in intensive farmland landscape are level-dependent, except the fish presence-amphibian relationships. Such a strong and cross-level effect is probably due to anthropogenic origins, e.g. introductions of carnivorous fishes for fishing activities. As fish stocking is unlikely to be avoided, especially in private ponds, an alternative local solution would be to maintain or restore some shallow and vegetated areas in the pond that would provide shelter against predation. Moreover, as expected, water quality only operated at the local level, whereas woodland cover and pond density, at regional levels. This multi-level approach stresses a decoupling between local and regional effects, and is consistent with pond-centred studies of e.g. Knutson et al. (2004) and Van Buskirk (2005). Therefore, conservation plans have to consider the environmental influences emerging from both local and regional levels to improve inventory and differentiation diversities. For the latter one, especially in such homogeneous landscapes, it is crucial to promote regional pond density and proximity, but also inter-pond connectivity, notably by large uncultivated corridors between ponds (Joly et al., 2001).

Landscape effects were only revealed by studying ecological relationships at the species level (i.e. for each individual species), as observed by Kolozsvary & Swihart (1999). Nonetheless, species occurrence determined at a given level can be responsive to environmental variability arising from several levels. Thus, in such small communities, species occurrence appears to be a convenient indicator to study amphibian responses to spatial level change.

Our results on the multi-specific approach showed that there was no antagonism in the species-environment relationships investigated. Except for the particular positive effect of fish on most frequent species, environmental drivers conserve the same effect whatever the species. As a consequence, some species-centred conservation strategies can even be satisfactory at the community level in altered landscapes, notably through the protection of 'umbrella' species.

Conclusion

Our study again confirms the necessity of multi-scale and species-specific approaches for the study of amphibians in pond systems (Cushman, 2006), especially in human-dominated landscapes where actions for biodiversity conservation are required and where data are lacking (Renault, 2012). We pointed out the key factors that must be considered for the conservation of inventory diversities and species occurrence of amphibians, e.g. predator fish avoidance at the local level and an increase in pond density at the regional level.

In this context, it seems crucial to aggregate local data to identify the main drivers of and threats to biodiversity (Mattson & Angermeier, 2006). The strong contribution of local diversity to regional diversity was found in many other biological groups, e.g. birds (Flohre et al., 2011) and macro-invertebrates (Thiere et al., 2009). These patterns are necessarily identified through multi-scale approaches where investigations are not just carried out on contrasting perimeters of environmental influences, but on contrasting scales of biodiversity assessment as well, which is essential in conservation (Willis & Whittaker, 2002). Such landscape-centred investigations (Fahrig, 2003; Mimet et al., 2013) can be conducted according to any types of structural levels or administrative scales (Flohre et al., 2011) and even at nested spatial scales (Gabriel et al., 2010), provided that these scales are coherent in terms of biodiversity conservation, since agri-environment measures are usually decided according to such pragmatic *scales*. In pond restoration ecology, Kentula (2000) highlights the need of 'landscape success' criteria for evaluating restoration plans, in contrast with local standards.

Moreover, it is very likely that pond systems in fragmented and disconnected areas do not function according to meta-population processes (Smith & Green, 2005) at levels above approximately 1 km. Indeed, if conditions such as one wetland/km^2 and a distance of less than 500 m to the nearest wetland are effectively required (Gibbs, 2001), then intensive agricultural areas are often likely to be out of the question due to the impossibility of ensuring these processes. Thus, in such landscapes, conservation efforts should be focused on pond groups and on associated buffer zones and corridors rather than on isolated ponds (Roe & Georges, 2007). Furthermore, to supplement our understanding about the ecological relationships in pond systems and to identify decisive scales of conservation (Poiani et al., 2000), we need to model animal displacement possibilities in an explicit framework. In this respect, analyses of landscape connectivity (Joly et al., 2003; Zanini et al., 2008) and of pond networks (Fortuna et al., 2006) appear to be particularly promising.

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