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Amphibian diversity in farmlands: Combined influences of breeding-site and landscape attributes in western France



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ABSTRACT

Agricultural intensification is responsible for major habitat degradation and is a primary cause of biodiversity loss. Amphibians are currently facing a global decline induced by multiple pressures, including notably habitat degradation and land conversion. In western Europe, traditional farming systems involve a dense hedgerow network with a mosaic of pastures, cultivated fields, ponds, and small woods. These heterogeneous landscapes are particularly favorable for biodiversity but their role for amphibian conservation remain understudied.

We studied the amphibian community (15 species) of a hedgerow network landscape in western France. We described 79 cattle ponds and tested the influence of ponds characteristics as well as the surrounding landscape composition on species occurrence. Amphibian diversity was positively influenced by breeding site vegetation and also ponds density in the surrounding landscape. We also found positive effects of wood patches and hedgerow linear at a small spatial scale. In turn, crop cover and road linear negatively influenced amphibian richness at large spatial scale. Important variation were detected among species reflecting contrasted life history traits. Our results underline that traditional pastoral landscapes provide a high density of breeding sites and habitats favorable for a diversity of amphibian species.

1. Introduction

Habitat loss and degradation are the primary causes of biodiversity decline associated to the Anthropocene (Potts et al., 2010; Tscharntke et al., 2005; Vitousek et al., 1997). Understanding the impact of land use on biodiversity is therefore a key conservation issue (Foley et al., 2005; Newbold et al., 2016). A major impact of human land use results in habitat fragmentation and the altered functional connectivity between habitat patches (Wiens, 2009). Reduced connectivity is known to alter organisms movements, gene flows, and in turn affects population dynamics (Crawford et al., 2016). Landscape heterogeneity is important and recent studies have demonstrated that biodiversity responds to both landscape composition and configuration (Collins and Fahrig, 2017; Dufлот et al., 2017). Meanwhile, biological functions such as reproduction may depend on specific microhabitat features that condition species persistence (Botzat et al., 2013; Smith et al., 2017). Therefore it is critical to combine multiple spatial scales (from microhabitat to landscape) to understand the effects of anthropic disturbance on biodiversity patterns (Humphrey et al., 2015; Razgour et al., 2011).

Farmlands represent a vast surface area of the planet, and

agricultural landscapes consist of a variety of land uses where natural and anthropized habitats are interspersed. The intensification of agricultural practices is observed at a global scale (Foley et al., 2005; Matson et al., 1997) translating to habitat loss, reduced landscape heterogeneity, and altered connectivity (Stoate et al., 2001). A massive decline in farmland biodiversity has been reported (Krauss et al., 2010; Robinson and Sutherland, 2002) and understanding the role of agro-systems for biodiversity conservation is now of critical importance (Fahrig et al., 2011). Amphibians are currently facing a global decline both in natural and anthropized habitats (Collins and Storfer, 2003; Stuart et al., 2004). Most amphibian species depend on aquatic habitats for breeding and larval development but also on the surrounding landscape for the terrestrial phase (Quesnelle et al., 2015). Due to this dual life cycle, amphibians are particularly sensitive to habitat structure and thereby offer a relevant group for studying the impact farming practices intensification on biodiversity (Collins and Fahrig, 2017).

In western Europe, traditional hedgerow landscapes consist of networks of linear structures (i.e. hedgerows) and mosaic of pastures, cultivated fields, ponds, and small woods (Burel and Baudry, 1995). These landscapes offer an extreme level of imbrication between natural

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and anthropized habitats and diversity of contact zones (ecotones) and corridors (Baudry et al., 2000; Bennett, 1998). Hedgerow landscapes are favorable to a vast diversity of organisms with contrasting ecological affinities including both vertebrates and invertebrates (Boughy et al., 2011; Hinsley and Bellamy, 2000; Michel et al., 2007; Ouin and Burel, 2002). However, they have been profoundly affected by the intensification in land use since World War II (Robinson and Sutherland, 2002). Changes in farming practices have resulted in a dramatic increase in field size (Tscharntke et al., 2005), the replacement of permanent pastures with croplands (Robinson and Sutherland, 2002), the removal of wetlands and ponds (Wood et al., 2003), and increased pollutions (Stoate et al., 2001). A synchronic decline has been reported in biodiversity and notably birds population, in relation with hedgerow loss (Chamberlain et al., 2000; Cornulier et al., 2011). Heretofore only few studies have investigated the impact of hedgerow network landscape degradation in amphibians (Boissinot, 2009).

The determinants of amphibians richness attracted considerable interest either in natural (Quesnelle et al., 2015), agricultural (Collins and Fahrig, 2017) or urban landscapes (Hamer et al., 2015). The quality of breeding sites is a critical aspect because it directly supports reproduction (Arntzen et al., 2017; Wells, 2007). Because of limited ground mobility, surrounding habitat structure will constraint amphibians movements and activity (Semlitsch and Bodie, 2003) with important variation among species depending on their vagility (Hillman et al., 2014; Koumaris and Fahrig, 2016). The density of breeding habitat is also essential because it is related to functional connectivity with terrestrial habitat (Ribeiro et al., 2011; Wells, 2007). A number of studies demonstrated that species richness is influenced by both breeding habitat and landscape structure (Cushman, 2006; Van Buskirk, 2005). These effects are not restricted to species richness, but also involve population dynamics and gene flow (Angelone et al., 2011; Cushman, 2006). Overall, increasing human activities have multiple impacts on amphibians including habitat loss, altered connectivity but also increased mortality from road traffic or pesticide use (Arntzen et al., 2017; Bokony et al., 2018; Jackson and Fahrig, 2011).

We studied amphibian occurrence in 79 ponds in western France in a traditional hedgerow farmland landscape characterized by a mosaic of habitats and land use. Given the importance of aquatic habitat for reproduction and because the study site is still well preserved, we hypothesize that species richness should primarily depend on breeding-site attributes (Hartel et al., 2010). A progressive transition towards crop farming is occurring in the area (Gamache, 2006). Therefore the occurrence of amphibians should also depend on landscapes attributes and notably be favored by typical hedgerow landscape features that reflect high habitat connectivity and breeding site availability. The structure of each pond (depth, surface, vegetation cover, mud depth) as well as the surrounding landscape (8 concentric buffers from 100 to 3000 m) were described to test the following predictions:

- 1) Species richness should be positively influenced by pond vegetation cover that provides multiples benefits for reproduction and against predation
- 2) Hedgerow landscape features (high pond density, wood cover and hedge linear) should positively influence species richness. In turn crop farming and road density should have a negative impact on amphibian diversity
- 3) The contribution of local (breeding site) and landscape attributes should vary among taxa reflecting contrasted breeding requirements and mobility.

2. Materials and methods

2.1. Study area

The study was conducted in Gâtine Poitevine, in the northern part of Deux-Sèvres department in western France. This area is mainly

Table 1
Species distribution in the 79 agricultural ponds.

Species	Number of positive ponds	Proportion (%)
Anurans:		
<i>Alytes obstetricans</i>	2	2.53
<i>Bufo spinosus</i>	7	8.86
<i>Epidalea calamita</i>	0	–
<i>Hyla arborea</i>	59	74.68
<i>Pelodytes punctatus</i>	0	–
<i>Pelophylax kl. esculentus</i>	48	60.76
<i>Pelophylax lessonae</i>	10	12.66
<i>Pelophylax ridibundus</i>	47	59.49
<i>Rana dalmatina</i>	66	83.54
<i>Rana temporaria</i>	0	–
Urodeles:		
<i>Salamandra salamandra</i>	17	21.52
<i>Triturus marmoratus</i>	59	74.68
<i>Triturus cristatus</i>	5	6.33
<i>Hybrid marmoratus x cristatus</i>	1	1.27
<i>Lissotriton helveticus</i>	74	93.67

composed of traditional hedgerow farmlands (54% of land use). The landscape is a mosaic of pastures for cattle and sheep grazing and cultivated fields delimited by hedges. The most distinctive aspect of this agrosystem is a dense network of hedgerows (average density of 140 m/ha) that are connected by wood patches (surface ranging from 0.01 to 416 ha) and a high density of cattle ponds (total number > 5000, average density 3.5/km²) (Boissinot, 2009). This traditional landscape has been affected by the intensification in land use (Gamache, 2006) and 27.5% of hedgerows were removed between 1950 and 2002 in this region (Boissinot, 2009). In the study area, 15 amphibian species (10 anurans and 5 urodeles, see Table 1) are present (Thirion et al., 2002).

2.2. Pond selection and sampling method

We selected 79 cattle ponds with contrasted structural features (4 descriptors) and landscape attributes (5 variables). Pond surfaces area varied from 37.84 to 537.6 m² (mean = 217.46 m²) and the water depth from 0.5 to 2 m (mean = 1.44 m). The ponds were selected without previous information on the presence of amphibians. We excluded ponds harboring fishes as they negatively affect amphibian communities (Denoël et al., 2005; Hartel et al., 2007; Hecnar and M'Closkey, 1997). We monitored each pond over three nocturnal surveys between March and June 2007, which encompassed all species breeding period. Each survey was separated by one month on average and combined three methods to detect amphibians. First, an acoustic monitoring was conducted over 5 min at a distance of 5 m from the pond. This method is effective for detecting most male anuran species through their breeding calls (Pellet and Schmidt, 2005). Second, a close visual inspection of the pond banks was carried out using an halogen light (100 W). The number of observed individuals was recorded for each species, as well as the presence of anuran egg masses. Finally, we carried out direct sampling using a fishing net with a 4-mm mesh size, allowing to capture adults as well as larvae and tadpoles of the different species. For each visit, a total of 15 consecutive net sweeps were carried out per pond. The combination of these three methods is widely used to study amphibian communities (Ficetola and De Bernardi, 2004; Petitot et al., 2014). The three sampling visits allowed detecting all species of a given pond with a high degree of confidence (Petitot et al., 2014; Sewell et al., 2010).

2.3. Breeding sites description

We considered four pond descriptors that show important variation in the area and therefore possibly influence the presence of amphibians as well as species richness. They included: a) percentage of aquatic

Table 2

Results from the model selection procedure testing the influence of breeding sites and landscape attributes on species richness and occurrence. The relative importance (*I*) of each variable retained was based on the sum of AIC weights of models including the targeted variable. We also provide the number of models (*N*) in which the variable was selected. The model averaging procedure was applied considering only the best models (delta AIC to the best model < 4). Significant effects are bolded.

	Breeding-site attributes								Landscape attributes									
	SURF		D-MAX		%VGT		MUD		NB-POND		%WOOD		%CROP		L-HEDGE		L-ROAD	
	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>	<i>I</i>	<i>N</i>
Species richness	0.03	1	0.03	1	0.61	9	0.05	2	0.33	7	0.18	5	0.21	5	0.16	4	0.30	5
<i>R. dalmatina</i>					0.12	2			0.06	1	0.60	5	0.71	4			0.39	2
<i>P. lessonae</i>	0.10	5	0.07	3	0.33	9	0.12	5	0.47	9	0.15	5	0.20	8	0.17	7	0.09	4
<i>P. kl. esculentus</i>					0.56	5	0.49	4	0.54	4	0.11	2	0.14	2	0.13	2	0.04	1
<i>P. ridibundus</i>	0.31	5	0.04	1	0.18	2	0.64	5	0.18	3	0.04	1			0.49	4	0.12	1
<i>H. arborea</i>	0.08	1							0.51	1	0.28	1	0.13	1			1	4
<i>B. spinosus</i>	0.05	2	0.54	9	0.05	2	0.13	3	0.48	9	0.12	3	0.11	2	0.11	4	0.25	5
<i>S. salamandra</i>			0.44	2	0.24	1					0.38	2	0.06	1			0.87	4
<i>T. marmoratus</i>											0.71	1	0.18	1	0.11	1	1	3
<i>T. cristatus</i>	0.49	10	0.83	15	1	19	0.29	8	0.94	17	1	19	0.65	14	0.58	11	0.50	11

SURF: pond surface area (m²); D-MAX: maximum water depth (cm); MUD: mud depth (cm); %VGT: percentage of aquatic vegetation. Nb-POND: the number of ponds; %WOOD: the surface proportion of wood cover; L-HEDGE = the hedgerow linear (m); %CROP: surface proportion of crop fields; L-ROAD : the road linear (m). See text for statistics.

vegetation (%VGT), which was visually estimated and categorized according to four different classes: < 5%, 5–25%, 26–75%, and > 75%; b) surface area (SURF, m²), measured using a diameter tape; c) maximal water depth (D-MAX, cm), measured in the center of the pond using a graduated stick and d) organic mud depth (MUD, cm), obtained from the mean of four different measurements located at a distance of 1 m from the edge of each cardinal point of the pond. These parameters were recorded for each pond between April and June. Vegetation surveys were all carried out in June to reflect optimum plant development.

2.4. Landscape attributes

Amphibians are sensitive to habitat structure, but its influence depends on the spatial scale considered (Cushman, 2006; Ficetola et al., 2009). To take this into account, we characterized landscape structure using concentric circles (or buffer zones) centered on the middle of the focus pond. This method is widely used to study amphibian presence and abundance (Ficetola et al., 2009; Hartel et al., 2010; Pellet et al., 2004). We defined eight concentric circles with a radius ranging from 100 m to 3000 m and thus corresponding to a surface area ranging from 3.13 to 2813 ha. This large range was needed as the species occurring in the studied area differ sharply in migration and movement patterns (Joly et al., 2001; Smith and Green, 2005; Trochet et al., 2017).

We considered three variables reflecting hedgerow landscapes composition: the number of ponds (Nb-POND); the surface proportion of wood cover (%WOOD); total sum of hedgerow length (L-HEDGE, m.). We also considered two variables reflecting habitat degradation: the surface proportion of crop fields (%CROP); the road linear (L-ROAD, m, including unpaved roads). These variables were recorded at the 8 concentric scales, leading to an overall total of 40 landscape variables per sites. These variables were extracted by photo interpretation of the geographic database BD Ortho® 2002 and BD Topo® 2002 (IGN). The geographical spatial analyses were performed using ARCGIS 9.2 (ESRI).

2.5. Statistical analyses

We used Generalized Linear Models (GLM hereafter) to examine the determinants of species occurrence (0 or 1) and species richness per pond (Ficetola et al., 2011; Hartel et al., 2010). The probability of occurrence (i.e. detection of the species at least once whatever the sampling method or date versus no detection in the target pond) was modeled for species with a minimum of five occurrences, using a

binomial distribution (logistic regression) and a logit link function. Therefore, we excluded the midwife toad *A. obstetricans* and the Blasius newt for the occurrence analyses. As the palmate newt *L. helveticus* was found in nearly all ponds (74 occurrences over across the 79 surveyed ponds), it was also excluded from the species occurrence analysis (no statistical power due to no contrasting occurrences). All species were considered when addressing species richness.

In order to identify at which scale each landscape variables were explaining the most deviance of the occurrence probability or richness, we fitted simple GLM for each species separately (using binomial distribution and logit link function) and richness (using Poisson distribution and log link function). For each landscape variable separately, we fitted one model at each scale. We then selected for each landscape variable the scale explaining the most percentage of deviance. This specific scale was retained for a model selection procedure (see below).

We developed a model selection procedure to identify variables that were significantly correlated to the occurrence probability or richness. We fitted all GLM models combining a maximum of two variables either landscape or breeding-site variables. The landscape variables were tested at the previously retained scale. We kept the number of variables relatively low in the models because the number of ponds was relatively small (79) and because the occurrences were also pretty low for most species.

A model averaging procedure was applied considering the best models (deltaAIC to the best models below a threshold of 4) to get average slopes for each variables (Burnham and Anderson, 1998). We only discussed variables for which the p-value after model averaging was below 0.10. Model averaging was also used to calculate the relative importance of each variable (using sum of AIC weights of models including the targeted variable).

Several landscape variables were transformed to meet normality assumptions (Sokal and Rohlf, 1995). Specifically, we used square root transformation (number of ponds), Log(X + 1) transformations (hedgerow and road length) or arcsin transformation (percentage of crop and wood cover). All analyses were carried out using R 3.1 software (R Core Team, 2016), MASS package (Venables and Ripley, 2002), MuMIn package (Barton, 2015), mgcv package (Wood and Wood, 2013) and boot package (Canty and Ripley, 2012).

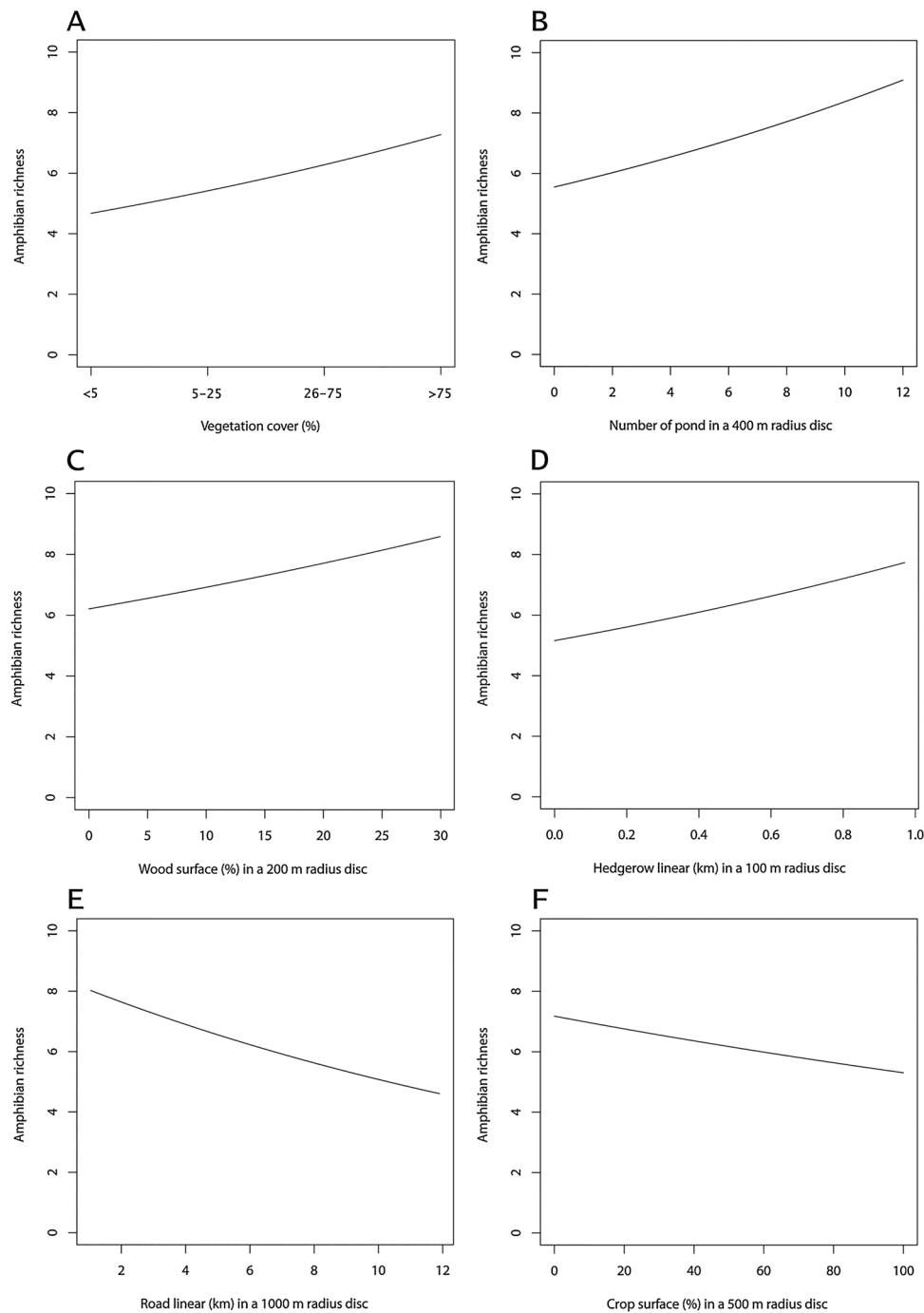


Fig. 1. Determinants of amphibian richness in the 79 sampled ponds. For this analysis, all detected species (12) were considered. Influences of A: pond vegetation cover (%), B: pond density, C: wood cover (%). D: hedgerow linear (Km), E: percentage of crop field: F: road linear (Km).

3. Results

3.1. Amphibian diversity

We detected 12 amphibian species (7 anurans and 5 urodeles) of the 15 known to occur in the study area (Table 1). On average we found 5 ± 1.7 species per pond and no pond was found unoccupied. Most ponds ($n = 34$; 43%) hosted 4–5 species. The maximum diversity was 8 species, but this was the case in only 12 ponds. One species, the palmate newt *L. helveticus*, was found in nearly all ponds ($n = 74$, see Table 1). The midwife toad *A. obstetricans* was found in only two ponds, and the Blasius newt in only one pond (Table 1).

3.2. Determinant of amphibian richness and species occurrence

Species richness was primarily associated to pond vegetation that was retained in 9 models (Table 2). The relative influence of this trait (sum of AIC weights) was high (0.61) when compared to other parameters (Table 2). Vegetation cover had a positive effect on amphibian richness (Fig. 1A). In turn the influence of other pond attributes was not significant (Table 2). The second parameter that contributed to species richness was pond density (sum of AIC weights 0.33) and was retained in 7 models in the averaging procedure. The four other landscapes variables had intermediate contributions (sum of AIC weights ranging from 0.16 to 0.3) and were retained in only 4 or 5 models (Table 2). Only limited correlation existed among landscape variables at the

Table 3

Estimates extracted from the model averaging procedure for breeding site (A) and landscape attributes (B) on species richness and occurrence. We provide the sign of the relation and the p value for the selected variable. We also provide the spatial scale retained for landscape attributes. Models were retained when delta AIC value from the best model were < 4. Significant effects are bolded.

A)	Breeding-site attributes							
	SURF		D-MAX		%VGT		MUD	
	Sign	P	Sign	P	Sign	P	Sign	P
Species richness	–	0.47	+	0.43	+	0.01	+	0.27
<i>R. dalmatina</i>					+	0.15		
<i>P. lessonae</i>	–	0.58	–	0.75	+	0.15	+	0.38
<i>P. kl. esculentus</i>					+	0.01	+	0.03
<i>P. ridibundus</i>	–	0.02	+	0.05	+	0.03	+	0.03
<i>H. arborea</i>	+	0.05						
<i>B. spinosus</i>	+	0.69	+	0.04	–	0.75	–	0.25
<i>S. salamandra</i>			–	0.01	+	0.03		
<i>T. marmoratus</i>								
<i>T. cristatus</i>	+	0.75	+	0.69	+	0.75	–	0.96

B)	Landscape attributes														
	NB-POND			%WOOD			%CROP			L-HEDGE			L-ROAD		
	Scale	Sign	P	Scale	Sign	P	Scale	Sign	P	Scale	Sign	P	Scale	Sign	P
Species richness	400	+	0.04	200	+	0.08	500	–	0.07	100	+	0.09	1000	–	0.05
<i>R. dalmatina</i>	3000	+	0.15	500	+	0.03	3000	–	0.02				200	–	0.04
<i>P. lessonae</i>	2000	+	0.08	100	–	0.38	200	–	0.29	100	+	0.30	100	+	0.59
<i>P. kl. esculentus</i>	400	+	0.01	200	+	0.08	2000	–	0.03	100	+	0.05	500	–	0.08
<i>P. ridibundus</i>	400	+	0.05	2000	–	0.06				400	+	0.01	2000	+	0.02
<i>H. arborea</i>	100	+	0.99	100	+	0.08	500	–	0.02				1000	–	0.004
<i>B. spinosus</i>	500	+	0.05	1000	+	0.19	500	+	0.21	2000	+	0.29	300	–	0.11
<i>S. salamandra</i>				200	+	0.02	1000	–	0.09				2000	–	0.01
<i>T. marmoratus</i>				200	+	0.02	500	–	0.006	200	+	0.01	3000	–	0.005
<i>T. cristatus</i>	500	+	0.72	100	–	0.74	3000	+	0.84	1000	+	0.77	100	+	0.76

SURF: pond surface area (m²); D-MAX: maximum water depth (cm); MUD: mud depth (cm); %VGT: percentage of aquatic vegetation. NB-POND: the number of ponds; %WOOD: the surface proportion of wood cover; L-HEDGE = the hedgerow linear (m); %CROP: surface proportion of crop fields; L-ROAD: the road linear (m). See text for statistics.

spatial scale retained in the model. Therefore, these effects may reflect independent landscape influences.

Important variations from this general pattern were found when looking at species responses (Table 2). The occurrence of two species (*R. dalmatina* and *T. marmoratus*) was primarily driven by landscape attributes (notably wood cover and road density). In turn the occurrence of five others (*Pelophylax* sp., *S. salamandra*, *B. spinosus*) was influenced by both landscape and pond attributes. The response of the crested newt *T. cristatus* was more complex to interpret because of the limited number of occurrences (5 among 79 ponds).

When focusing on the influence of pond attributes, the positive relation to vegetation cover was detected for *S. salamandra*, *P. kl. esculentus*, *P. ridibundus* (Table 3, Fig. 2E & F) and was marginal for *P. lessonae* and *R. dalmatina* (p-value: 0.15). *Pelophylax* sp. occurrences also tended to be positively associated to mud depth. Opposite responses to breeding site attributes were also detected. Pond depth had a positive influence on *B. spinosus* occurrence but a negative influence on *S. salamandra* (Fig. 2A & B). Similarly pond surface had a negative influence on *P. ridibundus* but a positive effect of *H. arborea* (Fig. 2C & D).

3.3. Landscape influences and spatial scales involved

The influence of pond density on amphibian richness was detected at a 400 m radius (Table 3, Fig. 1B). The relation was consistently positive for 4 species but involving contrasted spatial scales (Fig. 3A–D). Wood cover and hedges linear had a positive effect on specie richness at a rather small scale (respectively 200 and 100 m, Fig. 1C & D). The influence of wood coverage was positive for 5 species at small spatial scale (200 or 500 m see Fig. 3E to I). The relation was negative for only

one species (*P. ridibundus*). Hedge linear had a positive effect for 3 species at small scale (100–400 m radius, Fig. 3J–L).

Crop surface and road linear had a negative influence on species richness and these effects were found at medium and large scales (respectively 500 and 1000 m, Table 3, Fig. 1E & F). This pattern was also confirmed when looking at species response with negative responses ranging from 500 to 3000 m for crop cover in 5 species (Table 3, Fig. 4A to E). Similarly the negative effect of road linear was found in 5 species with scales ranging from 200 to 3000 m, Table 3, Fig. 4F–J). A positive effect of road cover was found for one species (*P. ridibundus*) and at large spatial scale (2000 m, Table 3, Fig. 4K)

4. Discussion

Amphibians are currently facing a global decline, notably because of habitat degradation, pollutants, or pathogens (Arntzen et al., 2017; Beebee and Griffiths, 2005; Stuart et al., 2004; Temple and Cox, 2009). Our study in a traditional farmland underlines the importance of breeding site quality and hedgerow landscapes attributes (high pond density and habitat compositional heterogeneity) on species presence and richness.

4.1. Proximate influence of breeding sites

Supporting our first prediction, we found that breeding-site (aquatic vegetation cover) primarily contributed to amphibian richness. Aquatic vegetation is critical for amphibians as it influences invertebrate productivity and thus food (Oertli et al., 2002), offers a physical support for egg-deposition and provides protection from predators (Gustafson et al., 2006; Miaud, 1995, 1993; Orizaola and Braña, 2003). These

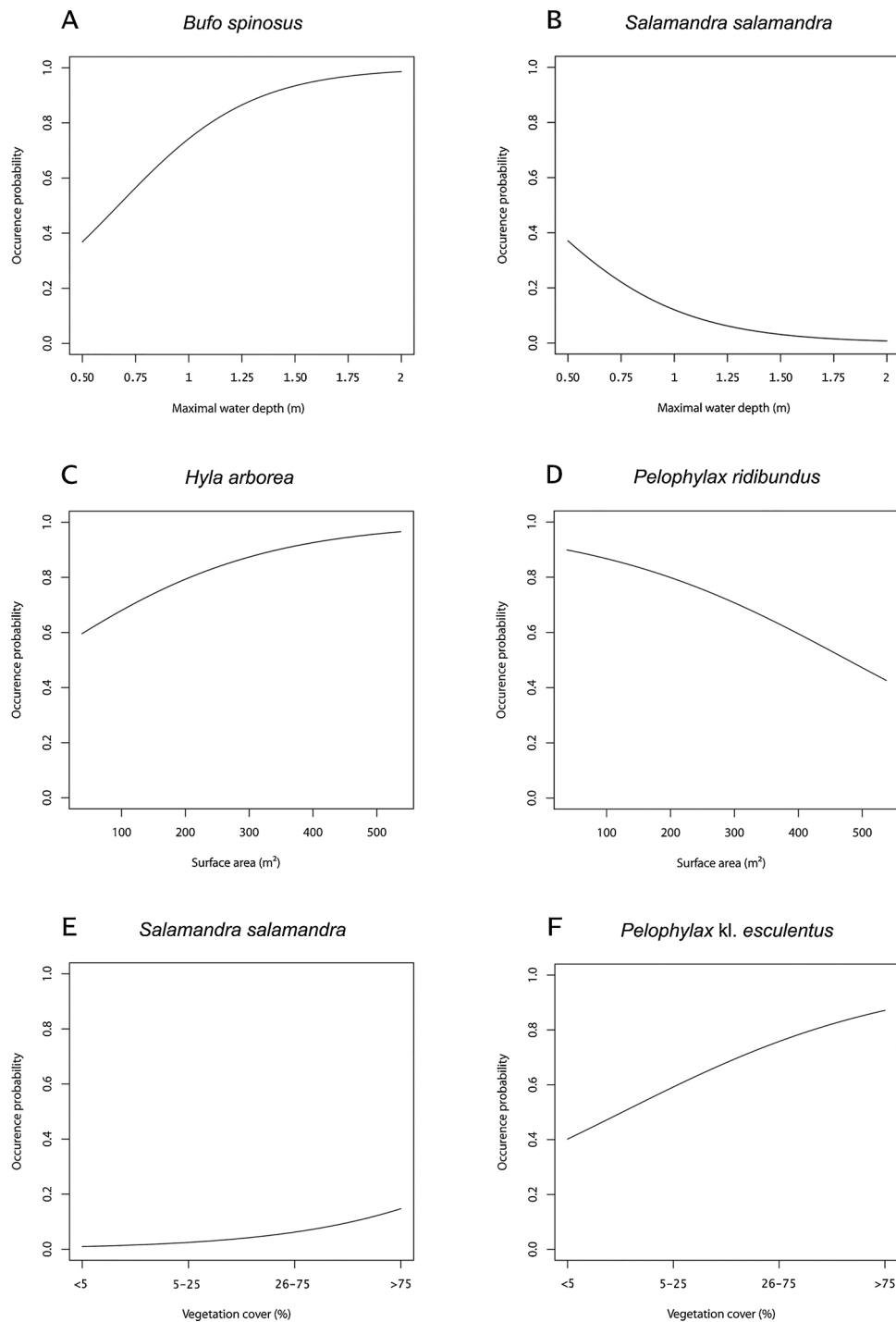


Fig. 2. Influence of ponds attributes on species occurrence. A & B: Maximal water depth (m). C & D: Pond surface area (m²). E & F: Vegetation cover (%).

multiple benefits likely explain why this parameter was the most important among the breeding-site covariates we tested. The positive influence of aquatic vegetation cover was also found for two species (*P. ridibundus* and *S. salamandra*). Despite this general pattern, important interspecific variation were found. For example, pond depth positively influenced *B. spinosus*, likely reflecting the adaptation of this species to large waterbodies (Duguet and Melky, 2003). In contrast, pond depth negatively influenced *S. salamandra*, which prefers shallow ponds for larvae deposition (Manenti et al., 2009). Mud depth had a positive influence on *Pelophylax* species, possibly reflecting the importance of this habitat characteristic for hibernation (Michaelidis et al., 2010). These

various influences reflect contrasting life history and breeding requirements among species. Pond diversity is known to favor species richness (Knutson et al., 2004). Other aquatic habitats occurs in the study area (large waterbodies, temporarily flooded pastures) are used by certain species (respectively *B. spinosus* and *R. temporaria*, see Boissinot et al., 2015). We posit that the diversity and quality of breeding habitats in hedgerow landscapes plays a crucial role in shaping the amphibian community.

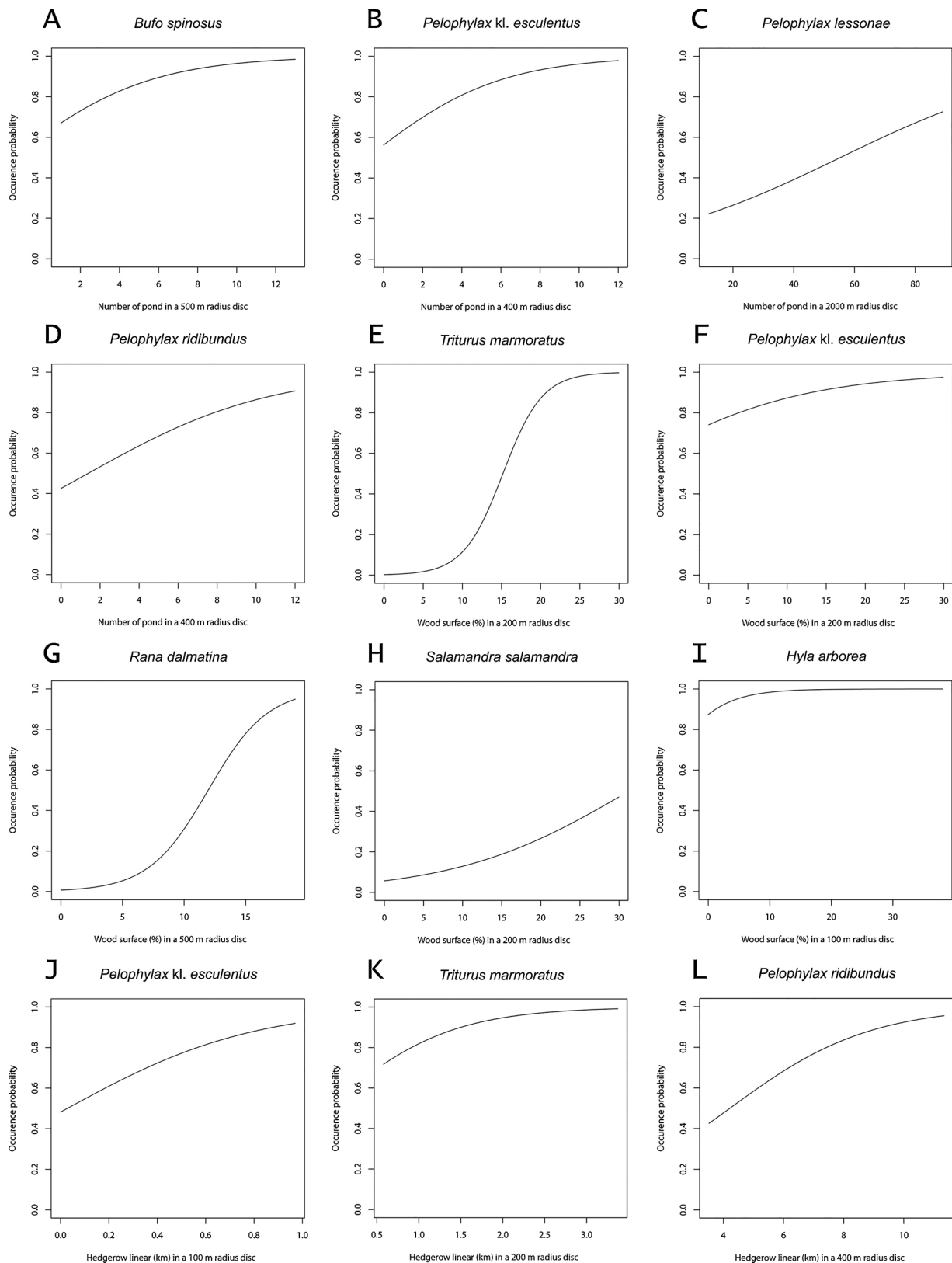


Fig. 3. Influence of hedgerow landscape attributes on species occurrence. A–D: number of ponds; E–I: wood surface (%); J–L: hedgerow linear (km).

4.2. Landscape effects and spatial scales involved

We found that landscape attributes also explained variation in amphibian richness but with a lower relative importance than breeding site (Table 2). Supporting our prediction, we detected a positive effect

of hedgerow network components. Notably we found that pond density in a 400 m radius had a positive influence on species richness and this variable was retained in 9 models (sum of AIC = 0.33). Similar influences were detected for wood cover and hedgerow linear although the relative importance was lower. Overall these effects were found at

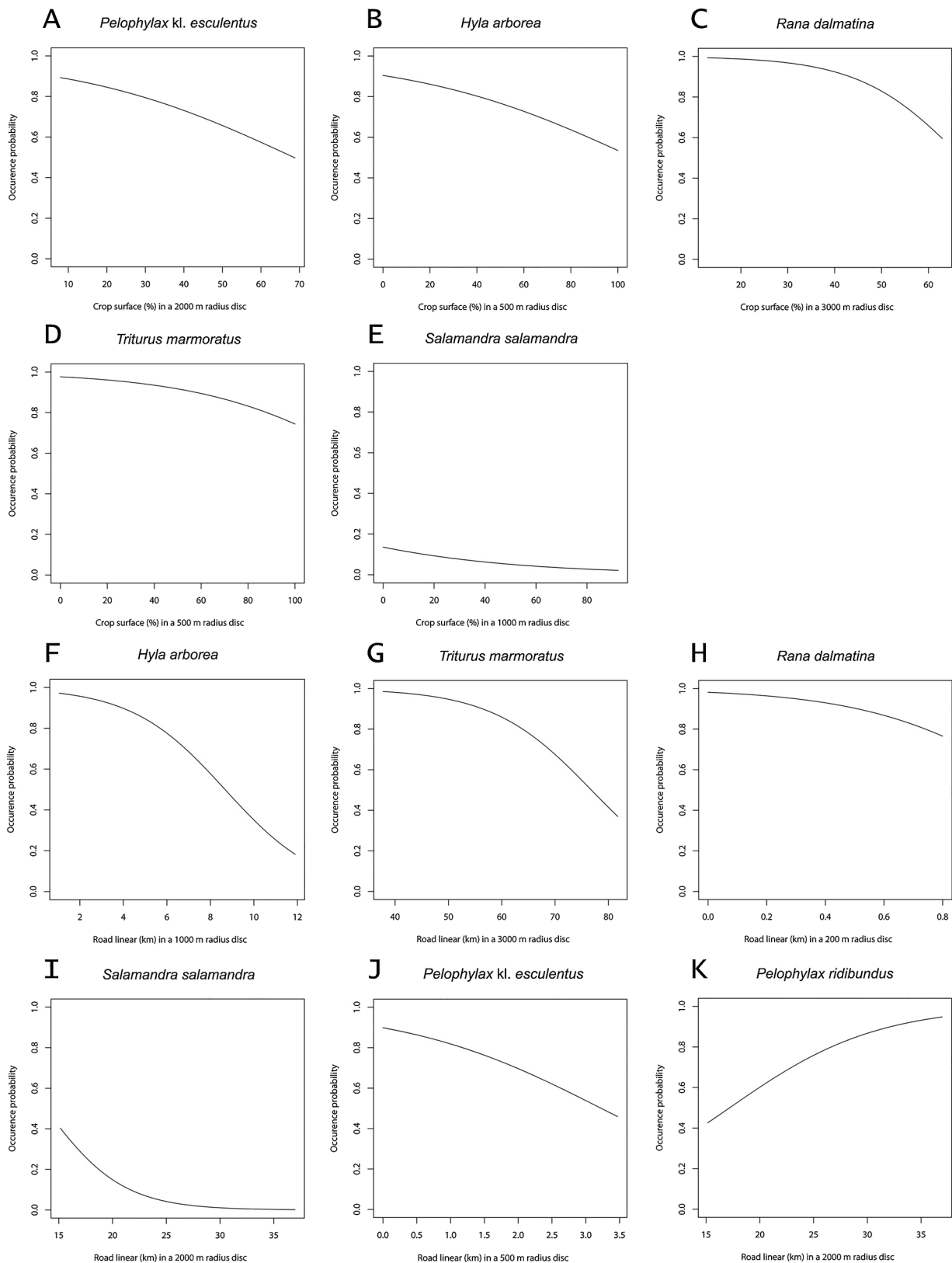


Fig. 4. Influence of land use intensification on species occurrence. A–E: percentage of crop surface. F–K: road linear (Km).

spatial scales inferior to 500 m. Therefore high pond densities, important wood cover and dense hedgerows at a rather small spatial scale are favorable for amphibian diversity. These landscape influences can result in proximate effects on i) population dynamic and/or ii) habitat connectivity and individual movements. For instance high pond density

is important to support population dynamic and facilitates movement among breeding habitats (Arntzen et al., 2017; Ribeiro et al., 2011). Woods are also essential for many amphibian species, particularly during the terrestrial phase, as woods provide significant trophic resources, shelter opportunities and suitable microclimates (Denoël and

Ficetola, 2007; Denoël and Lehmann, 2006). The positive influence of forest cover has also been demonstrated even within degraded farmlands (Cushman, 2006) and the importance of forest cover in proximity (< 500 m) of aquatic sites to prevent species loss.

The influence of hedges linear on amphibians has attracted only little attention and available studies provide conflicting results. Amphibian displacements are based on rectilinear movement and may be constrained by hedgerows. For example, Joly et al. (2001) found a negative influence of linears on newts' abundance. Other studies in tree frog suggest that hedgerows are not used during annual migration (Jehle and Arntzen, 2000) but possibly influence dispersal (Angelone et al., 2011). On the opposite, a study the common frog revealed a marked preference for hedgerow linears with higher adult densities and they seem particularly important for juvenile dispersal (Vos et al., 2007). Agricultural hedges can provide important microhabitats for wintering or aestivation, and daily activity. Amphibians are exposed to water loss and desiccation risks notably during activity in open environment (Köhler et al., 2011; Watling and Braga, 2015). Structured vegetation in hedges can provide humid microhabitats that will minimize the physiological conflict between water loss and thermoregulation. Finally, dense hedgerow networks tend to be associated to smaller field size, numerous ponds, and provide an index of landscape heterogeneity and connectivity. The functional roles of linear hedgerows for amphibians clearly require detailed attention (addressing both hedges density and structure) and should not be perceived as physical barriers.

We found that crop farming and road linear exerted negative influences on species richness. These effects were detected at larger spatial scales possibly resulting from altered meta-population dynamics with extinction not compensated by new settlements (Jackson and Fahrig, 2012). Crop farming is associated to a simplification of habitats (Tschamtko et al., 2005), a reduction in species richness and altered community composition as demonstrated in other groups (Burel et al., 2004; de la Peña et al., 2003). The shift from traditional pastoral practices to crop farming is associated with the abandonment of cattle ponds, and therefore a loss of breeding habitats (Curado et al., 2011). The use of pesticides and fertilizers is likely an aggravating factor (Bokony et al., 2018). Such effects can be expressed at large spatial scale through the circulation of contaminant in surface water systems (Selene Babini et al., 2018) with pervasive effects even at low concentration. Similarly, increased secondary road traffic associated with human activities is likely to affect amphibian species assemblage at a large spatial scale by combining depletion and barrier effects (Jackson and Fahrig, 2011).

4.3. Interspecific variations

Our results revealed important interspecific contrast in landscape influences. The occurrence of two species (*T. marmoratus*, *R. dalamanina*) was mainly influenced by landscape features, pointing out the importance of terrestrial habitat for these taxa. For most species (5), occurrence was explained by a combination of breeding-site attributes and landscape features. When the influences of ponds density, wood cover or hedge density were detected, the sign of the relation was predominantly positive (Fig. 3). Similarly the negative effect of crop farming and road density was most of the time negative (Fig. 4). This consistency at the species level supports conclusion drawn above on amphibian richness. One species (*P. ridibundus*) showed contrasted response (positive effect of road linear and negative effect of wood cover) but this taxa is closely associated to human activities in the area.

4.4. Amphibian conservation in farmlands

The global decline of amphibians is a major conservation issue (Alford and Richards, 1999; Beebe and Griffiths, 2005). The negative effects of agricultural intensification is well known in this group (Beebe and Griffiths, 2005). For example, it has been shown that

functional connectivity between breeding sites affects genetic diversity and population size (Crawford et al., 2016), as well as species richness and occurrence (Ribeiro et al., 2011). Habitat heterogeneity is a major driver of biodiversity and Collins and Fahrig (2017) have demonstrated that both landscape structure (i.e. crop diversity) and configuration (i.e. field size) exert a positive influence on amphibian richness within an agricultural context in Canada. Similarly, Suárez et al. (2016) demonstrated the negative impact of agriculture on species richness, and the importance of forest cover in proximity (< 500 m). Important variation among species response to practice intensification may exist (Koumaris and Fahrig, 2016).

Farming practices are not necessarily in conflict with amphibian conservation. Manenti et al. (2013) found a positive effect of traditional pastoral activity on structural heterogeneity and amphibian richness and this conclusion is in agreement with our findings. Hedgerow networks landscapes are a unique cultural heritage that offers considerable habitat heterogeneity and a diversity of breeding sites. Considering the spatial scales retained for positive landscape effects (100–400 m), the average farm size (70 ha) in the study area appears to be suitable for developing relevant landscape conservation policies (i.e., promoting pond quality and density, patches of woodland, and hedges network).

5. Conclusion

The importance of hedgerow landscape for amphibian conservation remains largely understudied. Our study extends previous findings demonstrating the dual importance of local (e.g. breeding site) and landscape attributes on amphibian populations either in agricultural (Van Buskirk, 2005) or urbanized (Hamer and Parris, 2011) contexts. The relative contribution of landscape components on species assemblage and their effective spatial scale clearly warrants further investigations. Pond creation and/or restoration (Baker and Halliday, 1999) should take into account contrasting breeding sites requirements as well as the surrounding landscape (ponds density and habitat connectivity).

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