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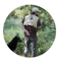

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Effects of habitat and fragmented-landscape parameters on amphibian distribution at a large spatial scale

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Amphibians generally have low dispersal abilities and are often habitat specialised, which makes them particularly sensitive to landscape changes, such as habitat destruction and fragmentation. Because they depend on wetlands for breeding, many conservation studies focus on aquatic habitat degradation and destruction. Additionally, few studies showed that changes in terrestrial habitats could be another threat that may cause the decline of amphibian populations. However, little is known about the terrestrial habitat preferences of most species. Although the proximity of forests and wetlands was expected to be positively related to amphibian presence, while human-modified habitats were expected to be avoided by these species, we still have little information on how these responses are species-specific. Based on an ecological niche factor analysis completed by partial least squares path modelling, we tested whether or not relationships between terrestrial and aquatic habitat parameters and occurrences are congruent across a metacommunity of seven amphibian species co-occurring at the regional spatial scale. We highlight that habitat type could strongly affect amphibian presence at large spatial scales, but in different ways. Agricultural landscapes, semi-natural areas and fragmented-landscape parameters showed expected negative correlations with the presence of some species. However, these habitats were also positively associated to the presence of other species. Indeed, because they could offer some benefits, some species could show a preference for these landscapes. Our results should have implications in conservation programmes, and could help predict future distribution and responses of these species to global change, which could be different among species.

Key words: agricultural landscapes, amphibian presence, ecological niche factor analysis, habitat preference, landscape parameters, partial least squares path modeling

INTRODUCTION

Amphibians are one of the most threatened taxonomic groups worldwide (Temple & Cox, 2009). Their decline is the product of multiple and complex factors such as habitat destruction, disease exposure and/or climate change (Houlahan et al., 2000; Blaustein & Kiesecker, 2002; Stuart et al., 2004; Beebee & Griffiths, 2005). Habitat destruction and fragmentation are considered major threats to amphibian populations (Marsh & Trenham, 2001; Chanson et al., 2008). In particular, habitat fragmentation can reduce connectivity among local populations (Reh & Seitz, 1990; Fahrig, 2003; Cushman, 2006), which can affect long-term population persistence by increasing inbreeding (Sjögren-Gulve, 1994).

Aquatic environments are critical habitats for amphibian reproduction, so amphibian conservation studies often focus on aquatic habitat degradation and destruction. There has been an overall reduction in wetland areas by 40 to 90% in different northern European countries since the beginning of the twentieth century (Hull, 1997), which has severely and negatively impacted amphibian occurrence and distributions (Barnaudet al., 1996; Wood et al., 2003). Organic and inorganic pollution of ponds exacerbated these negative trends through different consequences on amphibians (Relyea, 2005; Hayes et al., 2006; Gendron et al., 2003). In the meantime, other studies showed that changes in the structure of terrestrial habitats could be another factor that may increase the decline of amphibian populations. Due to their semi-aquatic lifestyle, amphibians are sensitive to changes in both aquatic and terrestrial habitats (Boissinot, 2009). For instance, the modification of terrestrial habitats with road or train infrastructure has proven to be detrimental by functioning as dispersal

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barriers for amphibian populations (roads: Gibbs, 1998; De Maynadier & Hunter, 2000; Cushman, 2006; railways: Clauzel et al., 2013; Vos et al., 2001). By limiting dispersal between ponds, principally in the breeding season during which individuals move to mate, roads increase the risk of inbreeding and reduce genetic diversity (Reh & Seitz, 1990).

Amphibians are often considered as species with low dispersal ability (Smith & Green, 2005; Boissinot, 2009) and are frequently specialised to a particular habitat, which makes them particularly sensitive to landscape changes. Nevertheless, habitat preferences, and particularly terrestrial habitats, of amphibian species require further investigation. Little is known about the terrestrial habitat preferences of most amphibian species, even if these landscapes should explain a significant part of species distribution, especially given recent changes induced by habitat fragmentation and habitat destruction. Consequently, better understanding relationships between species occurrences and habitat distribution should help setting conservation plans that adequately protect these species. Notably, given the high habitat specialisation of amphibians, we expect that not all species will respond similarly to habitat modification such as the development of road infrastructure/urban areas and the destruction of forest fragments. Hence, although it is expected that amphibian presence will be generally positively correlated (i.e. across species) to pristine forest and wetland areas (Knutson et al., 1999; Houlahan et al., 2000; Trenham & Shaffer, 2005), and negatively correlated to human-modified habitats and road densities (Fahrig et al., 1995; Delis et al., 1996; Carr et al., 2002), we still have little information on how these responses differ across species (Kolozsvary & Swihart, 1999).

The primary objective of this study was to test whether or not relationships between terrestrial and aquatic habitat parameters and amphibian occurrences are congruent across a meta-community of seven amphibian species co-occurring at the regional spatial scale. From our knowledge, a few studies have focused on the relative importance of both aquatic vs. terrestrial habitat features at such large spatial scale for multiple amphibian species. This information is a prerequisite for improving our knowledge on species-specific responses to habitat modification, which could have significant implications in conservation programmes, and could help predict the future distribution and response of these species to global change. Statistical models focusing on distribution patterns have been developed to understand the processes and the landscape parameters affecting spatial distribution of species (Vetaas, 2002; Thuiller, 2003). Specifically, Geographical Information Systems (GIS) coupled with ecological niche factor analysis (ENFA) provides a useful tool in conservation biology and evolutionary ecology (Epps et al., 2005; De Knegt et al., 2011) but as yet has rarely been applied to amphibians (but see Chen, 2013; Dolgener et al., 2014; Sillero et al., 2009; Soares & Brito, 2007). Another major contribution of our work was to complete this approach using partial least squares path modelling (PLS-PM; Esposito-Vinzi et al., 2010) for inter-specific comparison within a meta-community. This statistical approach aims to isolate the specific landscape parameters driving the distribution of the seven amphibian species and to identify direct and indirect relationships between each landscape parameter and the distribution of each amphibian species, and hence the underlying processes.

MATERIALS AND METHODS

Study area, biological models and sampling design

Our study compiled long-term data from 773 ponds scattered across a 4890 km² area in the south of France (Fig. 1). This studied area was chosen because it displays a strong environmental variability and includes several habitat types such as plains, forests, mountains and agricultural landscapes. The total length of the road network was 5813 km in 2011, including 16 km of highways, 91 km of national roads, 2639 km of departmental roads and 3067 km of communal roads. Since 2002, the highway network length did not vary, while the length of communal roads increased (MEDDE, 2012).

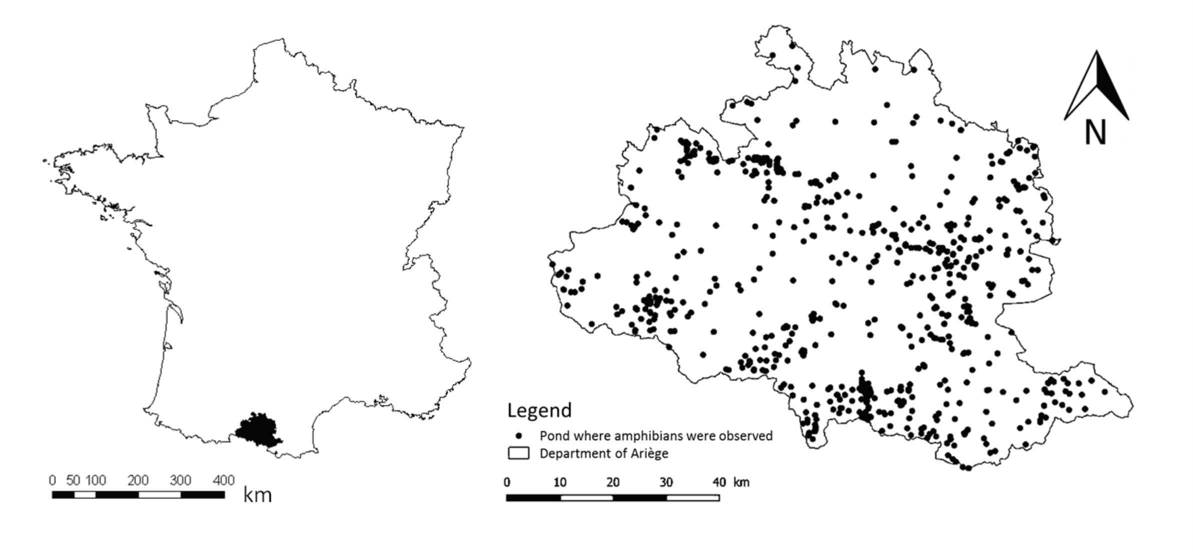

Fig. 1. Study site (France) showing the 773 ponds where at least one amphibian species was identified.

Table 1. Habitat and fragmented-landscape parameters used in the ENFA and PLS-PM analyses to study habitat selection by 7 amphibian species.

	Environmental variables		Surface (in ha), length (in km), range (min-max), or number	Percent of departmental territory	CLC habitat classes compiled	Mean	Range (min-max)	Description
	Latent variables ('LV')	Manifested variables ('MV')						
Landscape parameters	Topography	Slope	0-74.53%	-	-	13.19	0-51.36	Slope
		Altitude	198-3108 m	-	-	1061.94	223-2736	Altitude
	Hydrography	Water bodies	n=2 217	-	-	1211.22	0-9931.35	Shortest distance between each sampled site and the nearest water body (pond, lake, pool)
		Water system	9 071.2 km	-	-	253.65	0.60-1069.31	Shortest distance between each sampled site and the nearest water system
		Wetlands	1045.2 ha	0.29%	411-512	8816.15	0-28619.43	Shortest distance between sampled site and the nearest wetland (marsh, swamp)
	Forest	Deciduous forest	153 753.7 ha	31,24 %	311	906.82	0-9501.15	Shortest distance between each sampled site and the nearest deciduous forest
		Mixed forest	23787 ha	4,83 %	313	2563.18	0-12915.41	Shortest distance between each sampled site and the nearest mixed forest
		Coniferous forest	25 675.5 ha	5,22 %	312	2875.96	0-11507.59	Shortest distance between each sampled site and the nearest coniferous forest
	Semi-natural areas	Open areas	46 682.4 ha	9,49 %	332 + 333	8995.26	0-47555.35	Shortest distance between each sampled site and the nearest open area
		Shrub vegetation	79 093 ha	16,07 %	321 + 322 + 324	1161.03	0-16811.39	Shortest distance between each sampled site and the nearest shrub vegetation (lawn, natural pasture, moorland, brush or scrubland changing)
	Agriculture lands	Arable lands	35 259.6 ha	7,16 %	211	15083.82	0-43605.09	Shortest distance between each sampled site and the nearest arable land outside irrigation
		Permanent crops	67 190.5 ha	13,65 %	222 + 242 + 243	2439.29	0-13302.08	Shortest distance between each sampled site and the nearest permanent crop (orchard or complex plot)
		Grassland	51 956.8 ha	10,56 %	231	2630.73	0-12624.37	Shortest distance between each sampled site and the nearest grassland (bare rock or sparsely vegetated areas)
Fragmented-landscape parameters		Urbanized areas	7 340.3 ha	1,49 %	111 + 112 + 121 + 122 + 124 + 131 + 142	5236.92	0-21604.61	Shortest distance between each sampled site and the closest artificialized or urbanized area (commercial areas, buildings, etc)
		Railway	108.5 km	-	-	19311.41	103.58-62514.79	Shortest distance between each sampled site and the nearest railway
		Primary roads	394.1 km	-	-	8950.05	5.32-28764.72	Shortest distance between each sampled site and the nearest primary road (including highways, national and departmental roads)
		Secondary roads	8 399.5 km	-	-	985.39	0.1861-8536.94	Shortest distance between each sampled site and the nearest secondary road (including communal and unpaved roads)

The occurrence of twelve amphibian species was recorded annually in this area by the Association of the Naturalistes d'Ariège (http://www.ariegenature.fr) and by the Nature Midi-Pyrénées association (http://www.naturemp.org). Occurrences were determined by two standardised surveys per sampling site and per year during 1992–2014. At each pond, one-hour surveys were conducted, which involved active searches for amphibian species. Species occurrences were detected by calls, by visual search adults in water and/or by visual search of clutches or larvae in water in each sampled site. All observers were naturalists used to identifying amphibian species. We obtained 1910 observations for twelve amphibian species, however we limited our study to species for which presence was recorded for at least 10% of the sampled ponds (around 70 observations within the 773 ponds; Online Appendix 1), i.e. seven species including four anurans and three urodela species totalling 1350 observations. We obtained presence data for 4 anurans: *Alytes obstetricans, Bufo spinosus, Hyla meridionalis, Rana temporaria*; and 3 urodela: *Lissotriton helveticus, Salamandra salamandra, Triturus marmoratus*. Outside their breeding season, these species live in a variety of terrestrial landscapes, such as agricultural (open areas such as fields, flat lands, moors and meadows) or urbanized (parks, gardens, buildings, ruins) areas, but can also be found in forest zones (woodlands, glades and forest edges, rocky slopes, dense bush and herbaceous vegetation; Online Appendix 1). We used a GPS (Garmin®) to record the geographical coordinates of each sampled pond. All data were geo-referenced (Lambert-93 projection) using geographic information systems (GIS; QGIS v. 2.2 Valmiera and ArcGIS v. 10.0 software).

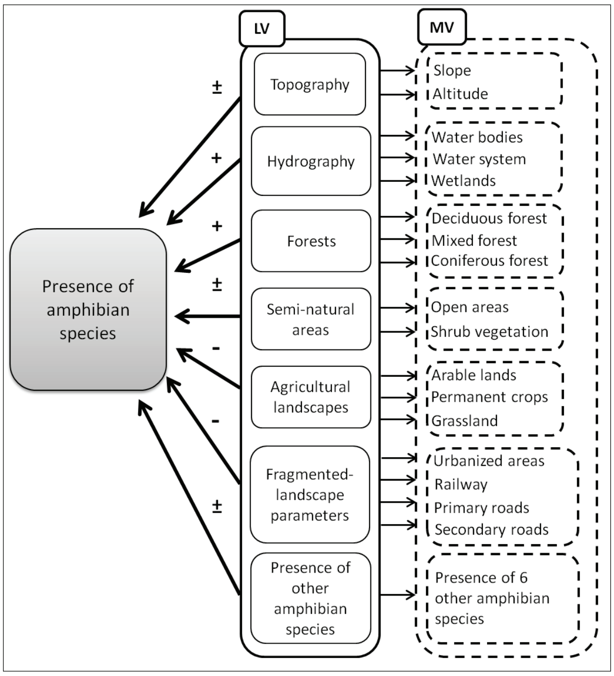

Fig. 2. A conceptual model of the presence of amphibian species associated with proximity of environmental variables. We considered 7 latent variables (LV) in this hypothetical scheme including each manifested variable (MV) (see Table 1 for details). Negative signs stand for hypothetical negative impacts and positive signs stand for potential positive effects. Some hypothetical relationships are expected to be positive or negative

Landscape parameters

Habitat and landscape parameters were obtained using Corine Land Cover classes (CLC; available from http://www.stats.environnement.developpement-durable.gouv.fr) clipped to the extent of the study area. The CLC classes vary from 1 (artificial surfaces), 2 (agricultural areas), 3 (forests and urbanized areas), 4 (wetlands) to 5 (marine waters). Each of these five codes were separated into several sub-categories, resulting in 22 different habitat types. Based on our knowledge of the ecological requirements of each target species, some CLC habitat classes were merged to obtain 10 distinct habitat classes: 3 forest habitats, 3 agricultural habitats, 2 semi-natural habitats, artificial areas and wetlands (Table 1). We then added other landscape features that may impact amphibian distribution: road and railway networks, water systems (rivers and isolated water points such as ponds and lakes) and topography data (altitude in metres and slope in percentage; all available from http://www.ign.fr, resolution 25x25 m) calculated in GIS from the digital elevation model of the study site. All these data were then rasterised using GIS and converted into an ASCII file to be used in R. We then calculated Euclidean distances between each sampled site and each nearest environmental variable using GIS tools (Table 1). We chose to work on distances between habitats to test how and whether the terrestrial landscapes around ponds could affect species presence, which in return might structure population distributions, and hence the genetic structure of populations.

Ecological niche factor analysis (ENFA)

We used ENFA analysis (a correlative presence-only model) to develop and validate a realised niche model (Sillero, 2011) for the seven amphibian species. Spatial analysis methods such as ENFA are based on a multivariate comparison between resource units (RU) used by species (RU with at least one presence observation) and RU availability throughout the studied area (Hirzel et al., 2002). These methods assume that individuals select locations with particular environmental conditions (Dolgener et al., 2014). By creating habitat suitability maps, the ENFA approach allows analysis and visualisation of the environmental niche of species (Grinnell, 1917; Hutchinson, 1957), and the creation of potential species distribution maps (Hausser, 1995; Hirzel et al., 2002).

For our analysis, the studied area was divided into a 100x100 m grid, corresponding to 495,587 cells. Each cell of 100x100 m represents an RU potentially exploitable by amphibian species. For each environmental parameter (see Table 1), we calculated the distance between the centroid of each RU and the nearest environmental variable. For each RU, we also attributed a value of altitude and slope, by averaging values in each 100x100 m cell. Consequently, each RU was defined by a single value for each environmental variable, which was hence used to describe the landscape context within each RU. To standardise the distance values obtained for each RU and each environmental variable, we applied a square root transformation on each variable. As in Principal Component Analysis, ENFA summarises environmental variables into two main axes. The first axis called "marginality" maximises the difference between the average environmental conditions used by species and environmental conditions available in the studied area, hence summarising information on habitat preference of each species. The second axis called "tolerance" is orthogonal to the axis of marginality and maximises the ratio of the RU variance of the available environmental space on the RU variance of the environmental space used by species. This axis provides information on the habitat specialist-generalist gradient of each species (Fonderflick et al., 2015). We tested the significance of each value obtained for the marginality and tolerance axes using a Monte-Carlo procedure. The number of presence observations (1350) was randomly distributed 1000 times and an ENFA analysis was performed at each step. The principle of the Monte-Carlo test is to compare the distribution of simulated RU (from the 1000 random draws) on both marginality and tolerance axes with the actual scores of RU used (Fonderflick et al., 2015). This tested whether or not the distribution of species is randomly distributed, and whether or not a species selects particular environmental conditions.

From this analysis, we mapped the habitat suitability for each amphibian species in the studied area, using the Mahalanobis distances method (Knick & Dyer, 1997; Cayuela, 2005). In multidimensional environmental space, the Mahalanobis distance assigns to each available RU a distance to the optimum habitat of the species in the environmental conditions of the studied area (Calenge et al., 2008). When this distance is low for a given RU, the probability to be a favourable habitat for the species concerned is high. Based on this probability, it is possible to calculate for each RU an index of habitat quality (Habitat Suitability Index, HSI) ranging from 0 to 1. The HSI is equal to 1 when RU is at the core of the environmental space used and is equal to 0 when the position of RU is outside of the environmental space used by the species (Fonderflick et al., 2015). Potential habitat maps were built on 70% of the observed locations while the remaining 30% were used to test the predictive performance of the model. The predictive performance was evaluated according to the Receiver Operating Characteristic (ROC) method widely used in the context of the potential spatial distribution of species (Lobo et al., 2010). The ROC method is based on the construction of a graph representing the true positive rate (presence observed and predicted by the model) relative to the false positive rate (presence predicted by the model but not verified in the observed data). Area under the curve (AUC) gave the measure of the quality prediction and varied from 0 to 1 (0.5 is the value for a random model). We considered that the predictive performance of the model was robust when the AUC was greater than 0.7 (Baldwin, 2009).

Partial least squares path modelling (PLS-PM)

We used PLS-PM to determine the strength of each significant environmental variable selected by the ENFA analysis on species occurrence. This approach is relatively novel and is used to analyse complex multivariate systems (Tenenhaus et al., 2005). PLS-PM allowed explaining and predicting relationships between amphibian presence and a set of environmental variables. This relevant and robust method was used to identify the most relevant variables that might affect each species distribution across the study area. Additionally, we used this analysis to simultaneously test the relationships between the occurrences of each species so as to explore whether or not positive or negative interactions may occur among species. PLS-PM, is a type of path analysis (Esposito-Vinzi et al., 2010) allowing direct and indirect relationships between observed variables (named manifested variables: 'MV'; i.e. our environmental variables) and latent variables ('LV'). For example, three manifested variables 'MV' as "wetlands", "water systems" and "water bodies" were compiled in only one latent variable ('LV') named 'Hydrographic' (see Fig. 2 and Table 1). PLS-PM assumes that LV, estimated through PLS approaches (Esposito-Vinzi et al., 2010), are multivariate constructs used to condense information summarised into the MV. This approach is particularly appropriate when patterns and processes are not well-known (Chin, 2010), and when MV are strongly inter-correlated (see Online Appendix 2 for the inter-correlation matrix). Rather than emphasising causal relationships between variables, PLS approaches focus on optimal predictive relationships. This approach is oriented to test predictive causal hypotheses. Thus, instead of validating a model in terms of quality adjustment, as in other path analyses (e.g., structural equation models), predictive quality indices are used, such as the goodness-to-fit-index (GOF; Chin, 1998; Tenenhaus et al., 2005; Esposito-Vinzi et al., 2010). Based on *a priori* knowledge, we hypothesised theoretic relationships between environmental variables and species occurrence (Fig. 2). Latent variables were constructed in a reflective way based on the path scheme. Path coefficients, estimated through PLS regression, were used to assess the strength and direction of expected causal effects of MV on species distribution. Loadings were then used to assess the contribution of each MV on LV. Finally, we also tested a "per group" PLS-PM analysis to test whether or not habitat parameters affect differentially the spatial distribution of species (i.e. a test for species-specific responses).

All statistical analyses were performed using R (R. Development Core Team, 2011) and the 'adehabitat' (Calenge, 2006) and 'plspm' (Sanchez & Trinchera, 2012) R-packages for ENFA and Habitat Suitability Mapping and PLS-PM, respectively.

RESULTS

Monte-Carlo tests were all highly significant (all $p<0.009$, Online Appendix 3), indicating that all seven species had non-random distributions relative to resource availability, and that species actively select specific habitat at this

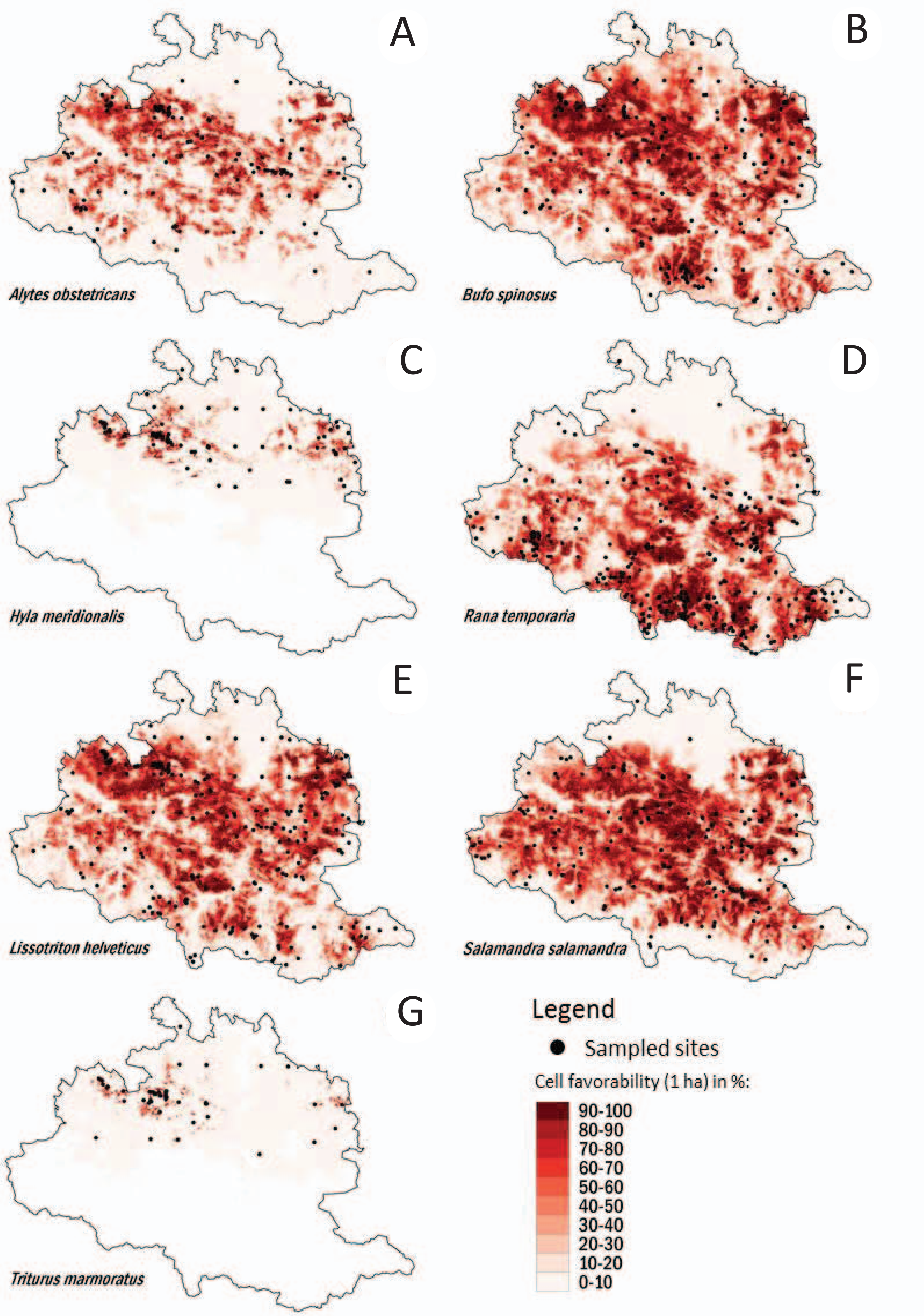

Fig. 3. Predictive maps of potential suitable habitats in 7 amphibian species at the large spatial scale. Black points represent all sampled sites. For each 100 x 100 m RU, a presence probability (i.e. suitability) was attributed and varied from 0 (light red: low presence probability) to 1 (dark red: high presence probability).

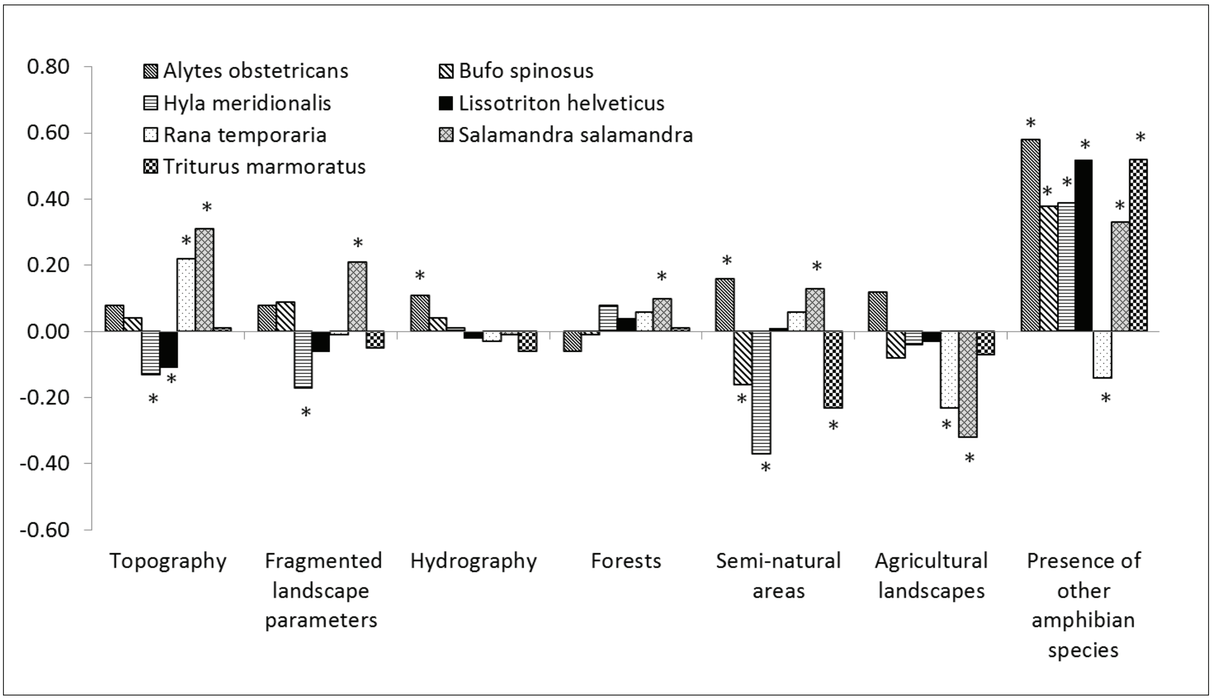

Fig. 4. Path coefficients from PLS path modeling analysis of each latent variables. Stars represent significant path coefficients. Positive values mean a positive effect of these variables on the presence of amphibians species (habitat preferred). Negative values mean that species avoided the habitat parameter concerned.

large spatial scale. We obtained AUC values for all seven species (Fig. 3 and Table 2), indicating good predictive performance of the habitat suitability maps..

Amphibian species showed high and low habitat suitability (Real et al., 2006) at the studied scale (Fig. 3). Two species (*H. meridionalis and T. marmoratus*) were relatively rare in the studied area, with both of them restricted to some localities in the northern part of the studied area (more agricultural zones). Conversely, *B. spinosus* was predicted to occur all over the studied area, indicating a widespread and weakly specialised species. *R. temporaria, L. helveticus and S. salamandra* were mainly distributed to the south of the studied area (more forest and mountainous zones), whereas the last species *A. obstetricans* occurred in the central part of the studied area (Fig. 3). Given these heterogeneities in the distribution of these seven species, we can expect that each responded to specific habitat characteristics.

Inter-specific effects of habitats on amphibian distribution

The cross-species comparison showed that landscape parameters differentially seem to influence the occurrence of species (Fig. 4 and Online Appendix 4). Indeed, the strength, the sign and the significance of the relationships between latent variables and the occurrence of species strongly varied among species (Fig. 4). This was particularly the case for the relationships between topography, fragmented-landscape parameters, semi-natural areas, agricultural land proximity and the occurrence of each species (Fig. 4). The occurrence of two species (*R. temporaria and S. salamandra*) was positively associated with topography, whereas the relationship was negative and/or neutral for all other species. The among-species contrast was even stronger for semi-natural areas, with the occurrence of some species (*A. obstetricans* and *S. salamandra*) being positively and strongly associated with the presence of semi-natural areas, whereas the effects tended to be negative and/or much weaker for all other species (in particular for *H. meridionalis*, Fig. 4). Surprisingly, the influence of fragmented-landscape parameters (roads, railway and urbanized areas) on the occurrence of species was relatively high for most species, and also demonstrated differences in the sign of the relationship. The proximity of fragmented-landscape parameters was positively associated with the presence of *S. salamandra*, whereas the same relationship was significantly negative for *H. meridionalis*. Agricultural landscapes were also correlated with the occurrence of species with negative relationships for *R. temporaria* and *S. salamandra*, (Fig. 4). Finally, forest proximity and hydrography were only weakly related to the occurrence of amphibian species (significant relationship only with *S. salamandra* and *A. obstetricans* respectively) which is surprising given their importance for amphibian life-cycles), while the occurrence of each species tended to co-vary positively with the occurrence of each other species, except for *R.*

Table 2. Values of AUC from the ROC method showing the performance of predictable habitat distribution of 7 amphibian species.

	Species	AUC value
Anurans	*A. obstetricans*	0.734
	B. spinosus	0.828
	H. meridionalis	0.722
	R. temporaria	0.859
Urodela	*L. helveticus*	0.683
	S. salamandra	0.820
	T. marmoratus	0.838

temporaria for which the occurrence tended to be higher when other species were absent (Fig. 4).

To summarise, although the distribution of some species tended to co-vary in the studied area (see Fig. 3), the distribution of each species seemed to be affected by a very specific set of habitat and landscape characteristics (Fig. 4). Interestingly, the effects of variables resulting from the influence of humans on the landscape (e.g., agricultural landscapes or fragmentation) strongly varied from one species to another (Fig. 4). Beyond the influence of other species presence, agricultural landscapes and semi-natural areas were latent variables for which path coefficient from PLS path modelling were high and significant (Fig. 3).

DISCUSSION

We tested whether or not the occurrence of seven amphibian species correlated with the distances from different habitat types. We combined two innovative statistical approaches (ENFA and PLS-PM) to show (i) that the seven species were not randomly distributed over the studied area, and (ii) that landscape features did not uniformly affect the distribution of these amphibian species. For instance, the distribution of some species was positively correlated with semi-natural area proximity, whereas two other species were affected negatively by these variables. We further showed that roads, railways and urbanized areas (fragmented-landscape parameters) also affected amphibian distribution, both positively and negatively. Contrary to expectation, the distances to forests patches (except for *A. obstetricans* and *S. salamandra* respectively) and to hydrographic variables seemed to be a non-significant parameter affecting amphibian distribution. These findings improve our understanding of habitat-species interactions (Guisan & Zimmermann, 2000) and are pertinent for conservation management (Dolgener et al., 2012), especially in fragmented landscapes.

Effects of agricultural lands and semi-natural areas on amphibian presence

Agricultural landscapes were expected to strongly and negatively affect amphibian occurrence, due to water body disappearance, disturbance and pollutants in ponds, habitat fragmentation, desiccation risk (Bishop et al., 1999; Kolozsvary & Swihart, 1999; Zampella & Bunnell, 2000; Joly et al., 2001; Benton et al., 2003; Hayes et al., 2006; Gendron et al., 2003; Relyea, 2005). Our results corroborated this hypothesis by showing a negative correlation between the proximity of agricultural landscapes and the presence of *R. temporaria and S. salamandra* (Fig. 4), species that seem to avoid high-intensity agricultural lands (Nöllert & Nöllert, 2003). Indeed, agricultural practices may have strong negative effects on amphibian populations, such as reducing the survival rate (Porej et al., 2004). As such, agricultural lands should create less permeable landscapes for amphibian movements, and consequently increase population the risk of extinction (Porej et al., 2004). This hypothesis was corroborated by a tracking study showing that some amphibian species tended to avoid grasslands through orientation changes in adults and juveniles migratory behaviour (Rittenhouse & Semlitsch, 2006).

Two species (*A. obstetricans* and *S. salamandra*) showed a preference for a proximity to semi-natural areas (open areas and shrub vegetation) whereas a negative impact of these landscapes was showed in *B. spinosus, H. meridionalis* and *T. marmoratus* (Fig. 4). Semi-natural areas were composed of two specific habitats: open areas (partially vegetated and often associated to mountain habitats and high altitudinal levels, where roads and urbanized areas were very rare) and shrub vegetation (dominated by bushes, shrubs and herbaceous plants, and more vegetated than open areas). Contrary to agricultural landscapes described here, semi-natural areas can offer an increasing abundance of ligneous vegetation. *Alytes obstetricans* showed a preference for proximity to open areas, and is a pioneer species (Nöllert & Nöllert, 2003), which seems to be consistent with its presence in habitats that are often unstable and subject to structural changes. Contrarily, the presence of *S. salamandra* was mainly influenced by shrub vegetation (Online Appendix 4). Amphibians can benefit from vegetation because of the maintenance of humidity (desiccation avoidance), food resources or protection against predators. Moreover, shrub vegetation was generally located throughout the study area, and present between disturbed areas, in contrast to open areas that are mainly constrained to mountain habitats and within forests. This habitat type can be likened to an ecological corridor by improving habitat connectivity and leading to dispersal events between habitat patches for species that live in disturbed landscapes. However, three studied species showed avoidance to these landscapes, which can also be associated with predation and desiccation risks or low wetland density.

Effects of fragmented-landscape parameters on amphibian presence

Fragmented-landscape parameters are believed to strongly fragment the distribution of amphibian populations, irrespective of the targeted species. Our findings showed that these landscape parameters (especially roads and urbanized areas) can affect amphibian presence, although not all species were affected the same. At an extreme, the occurrence of *S. salamandra* was positively related to the proximity of roads, which was not expected. Despite the high risk of mortality on roads shown in many studies (Fahrig et al., 1995; Forman & Alexander, 1998; Hels & Buchwald, 2001; Andrews et al., 2008), the use of such fragmented-landscape parameters was found in some species however (in *Bufo marinus*: Brown et al., 2006; in *Vulpes vulpes*: MacDonald, 1979; in *Chlamydosaurus kingie*: Griffiths, 1999; in *Lithobates sylvaticus*: Trenham et al., 2003; see also Eigenbrod et al., 2008). Although paradoxical, it is possible that amphibians use the linear infrastructure related to roads (i.e. dispersal in ditches). Moreover, settling basins present at the periphery of roads are sometimes used as breeding sites, explaining why amphibians might be closely associated with roads. Furthermore, *S. salamandra* is a woodland associated species, which moves to water bodies only for a very short breeding period, and lives most of the time out of water. Nevertheless, surveys performed in this analysis could be biased toward roads, which might also explain why one species seems to prefer roads proximity. For *H. meridionalis* however, the relationship with occurrences on this fragmented-landscape parameter was negative, which suggests that some species avoided these landscapes parameters (roads and urbanized areas) and that habitat fragmentation could also have a strong and negative impact on amphibian distribution in this region. This last result was in accordance with other studies (Vos & Chardon, 1998; Porej et al., 2004; Cushman, 2006; Fahrig & Rytwinski, 2009), which demonstrated that roads might be associated to dispersal barriers in many species. Moreover, urbanized areas were already identified to be a factor reducing genetic structuring in amphibians, and increasing their mortality risk due to lack of favourable habitats and population isolation within (Hitchings & Beebee, 1997). Furthermore, *H. meridionalis* might be a long-distance disperser (12.6 km recorded in a sister-species *Hyla arborea* in Vos et al., 2000). Compared with the effect of road proximity on *S. salamandra*, which is a low-distance disperser (503 m in Schulte et al, 2007; Gibbs, 1998), this finding corroborated the hypothesis proposed by Fahrig & Rytwinski (2009) that stipulates that species with large range movements should be more affected by habitat fragmentation than others. This suggests that species will experience pressures of habitat change differently, and that conservation plans should take this into account.

Effects of other landscape parameters on amphibian presence

Contrary to expectations, neither hydrographic parameters nor forest proximity (except for *A. obstetricans* and *S. salamandra*) showed significant effects on the occurrence of the amphibian species tested here (Fig. 4 and Online Appendix 4). The only positive relationship found between the proximity of forests with the presence of *S. salamandra* was in accordance with its ecological requirements (Online Appendix 1). Indeed, *S. salamandra* is an urodela species typically living in deciduous and mixed forest areas (Nöllert & Nöllert, 2003). As with the hydrographic variables, forest habitat seemed to be not strongly significant for the presence of other species, which appeared to be more affected by disturbed landscapes (agricultural and semi-natural areas). This result does not support many studies suggesting that both forest cover and hydrographic parameters proximity might be strong landscape predictors of amphibian occurrence (Laan & Verboom, 1986; Houlahan & Findlay, 2003; Herrmann et al., 2005). However, because amphibian detection methods were performed within ponds, we suggested that if an amphibian is within a pond, the distance to another pond is probably less important than the distance to feeding or wintering areas. We suggest that forest cover might be highly negatively related to roads and agricultural areas (Houlahan & Findlay, 2003) and that the use of the PLS-PM method allowed us to highlight the most important landscape parameter affecting amphibian presence, which could explain the non-significance of hydrographic and forest variables, that might be used by amphibian species as feeding or wintering areas. Topography was identified as a significant parameter affecting the distribution of four amphibian species. These relationships were certainly linked with the ecological niche of each species. Generally, *R. temporaria* inhabits forested or wet areas (Cogalniceanu et al., 2000; Covaciu-Marcov et al., 2008, 2009) and is usually found in higher altitudes up to 200 m (Cogalniceanu et al., 2000). Our results also show that *L. helveticus* presence depends on topography. Indeed, the palmate newt has a large altitudinal range (from sea level up to at least 2,400m) but is however most common between 500 and 1500m (Gasc, 1997). This species was related to this habitat parameter and the presence of other amphibian species only. Both methods used did not allow us to identify environmental variables specifically sought by *L. helveticus* (GoF value=0.4011 and r^2=0.2911). We also supposed that the study extent (specifically the RU size) may not have been appropriate to discerning the environmental drivers of *L. helveticus* distribution. Moreover, this newt is a ubiquitous species (Nöllert & Nöllert, 2003), covering a wide range of habitats (i.e. forests, wetlands, farmland, etc.), explaining why the models did not allow us to identify any strong environmental constraints on its distribution.

Technical bias of analyses

We demonstrated strong relationships between the occurrence of amphibian species and the proximity of certain habitat types. However, our analysis depended on the environmental variables that were chosen, and we suppose that some other habitat types could be related to amphibian presence. The predictive values of our statistical models were highly depending on selected environmental variables and on the number/density of observation sites by species in the study area. By consequence, our results have to be taken with care as point aggregation can affect predictive maps. Also, pollutants were here neglected whereas they have been showed to impact amphibian populations (Hayes et al., 2006; Gendron et al., 2003; Relyea, 2005). In this study, we did not have information about the presence of contaminants on different sampling sites, so our results should be interpreted with care. It would be interesting to compare the predictive values obtained with other types of analysis, such as Factor Analysis in Mahalanobis distance (MADIFA: MAhalanobis DIstances Factor Analysis; Calenge et al., 2008) or the method of Maximum Entropy (MaxEnt; Baldwin, 2009). It would be also pertinent to repeat this study by increasing the number of species per location, and supplemented by abundance data, homogenising zone surveys (i.e. north and west of the department) and refining the mapping used.

Conclusions

We highlighted that habitat type could strongly affect amphibian presence at large spatial scales. Notably, the effects of different habitat types were highly significant on the presence of several amphibian species, but by different ways. Agricultural landscapes, semi-natural areas and fragmented-landscape parameters were the most important habitat parameters that determined amphibian presence, and were negatively correlated with the presence of certain amphibian species. However, these habitats were also positively associated to the presence of other species, which should be taken into account in conservation plans. Indeed, because fragmented-landscape parameters and semi-natural areas could offer some benefits, some species could show a preference for these landscapes. Our results should have implications in conservation programmes, and could help predict future distribution and responses of these species to global change, which could be different among species.

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