

# Water, stream morphology and landscape: complex habitat determinants for the fire salamander *Salamandra salamandra*

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**Abstract.** Understanding the relationship between environmental features and species distribution is a key step for successful habitat conservation. In semiaquatic amphibians, the features of both breeding sites and the surrounding upland habitat can play important roles. We evaluated the relative role of (1) stream morphology, (2) biotic features of water, and (3) composition of landscape surrounding wetlands, for the distribution of the fire salamander, *Salamandra salamandra*. We determined the presence of larvae in 132 localities, and we used an information-theoretic approach to build species distribution models. We then used variance partitioning to evaluate the relative importance of environmental variables. A model including both stream and landscape features explained a large proportion of variation. Larvae were associated to heterogeneous and shallow streams, with scarce periphyton, rich macrobenthos communities characteristic of oligotrophic water, and surrounded by woodlands. Variance partitioning showed that stream morphology was the parameter with the largest independent effect, but most of variation was explained by the combined effect of multiple variables, suggesting a strong interplay among biotic and abiotic features in determining species distribution. The complementation between multiple elements, such as wetlands and landscape features, can be the key of a correct understanding of distribution of semi-aquatic amphibians.

**Keywords:** breeding habitat, landscape, microhabitat, *Salamandra salamandra*, spatial scale, wetland features.

## Introduction

In the last two decades, many studies pointed out a widespread decline of amphibians at global scale (Blaustein and Wake, 1995; Stuart et al., 2004), with hundreds of amphibian species now facing concrete extinction risk (Stuart et al., 2004; Beebee and Griffiths, 2005). Diseases, global warming, alien species and complex interactions among factors are often key causes of the decline (Blaustein and Wake, 1995; Stuart et al., 2004; Beebee and Griffiths, 2005). However, habitat changes caused by human activities probably are the most important drivers of population decline worldwide (Gardner, Barlow and Peres, 2007). An increasing number of studies evaluated the relationship between amphibian distribution and habitat across all the continents, to provide scientific information helping to set up conservation

plans. These studies improved our knowledge of mechanisms influencing the patterns of species abundance and occurrence (Van Buskirk, 2005), increased our understanding of the ecological processes that underlie the effects of habitat change (Gardner, Barlow and Peres, 2007), and helped to individuate the factors determining variation in species distribution (Skelly, Werner and Cortwright, 1999; Dalbeck, Lüscher and Ohlhoff, 2007; Werner et al., 2007). Nevertheless, our knowledge of the effect of environmental modification on amphibians is far to be complete, and more studies are required on the relationships between amphibian distribution and habitat, before generalizations can be performed (Gardner, Barlow and Peres, 2007).

Many amphibians are semi-aquatic, and require different habitats occupied at different stages of their biological cycles. This complexity increases the range of environmental factors that may influence species distribution. It is thus important to evaluate the relationship between species and the features of both terrestrial and aquatic ecosystems (Denoël and Ficetola, 2008). However, analyses including both aquatic and upland features must be performed

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at large spatial scales (Cushman, 2006). Despite many studies investigated the relationship between environmental features and species presence, only a subset had the spatial replication required to correctly investigate processes occurring at both the wetland and landscape level (Cushman, 2006; Denoël and Lehmann, 2006; Denoël and Ficetola, 2008).

In this study, we investigated the relationship between the distribution of the fire salamander *Salamandra salamandra* and environmental features of both wetland (streams) and upland environments. In part of its range, the fire salamander is usually considered a common species. However, in several areas it is currently declining and becoming rare (Carpaneto, Bologna and Scalera, 2004; Bosch and Martínez-Solano, 2006), probably also because of habitat loss. Salamanders constitute a substantial portion of the biomass in small lotic environments, and thus have a very important role in the food web and for the energy flow of these ecosystems (Davic and Welsh, 2004). The consequences of the decline of previously common species can be strong, particularly when keystone species are involved, because they can cause cascade effects influencing ecosystem dynamics. Unfortunately, “common species” are often neglected by conservation studies; it is thus necessary playing more attention to their status and habitat requirements (Gaston and Fuller, 2008). Moreover, despite the ecology of the fire salamander is well studied (e.g., Joly, 1968; Denoël, 1996; Schmidt, Feldmann and Schaub, 2005; Schmidt, Schaub and Steinfartz, 2007; Schulte, Küsters and Steinfartz, 2007) most of studies on habitat requirement focused on microhabitat (Baumgartner, Waringer and Waringer, 1999) while large scale analyses are more scarce (but see Egea-Serrano, Oliva-Paterna and Torralva, 2006). Our work uses data on a large number of potential breeding sites and an information-theoretic approach to evaluate the relative role of stream and landscape features for the distribution of the fire salamander.

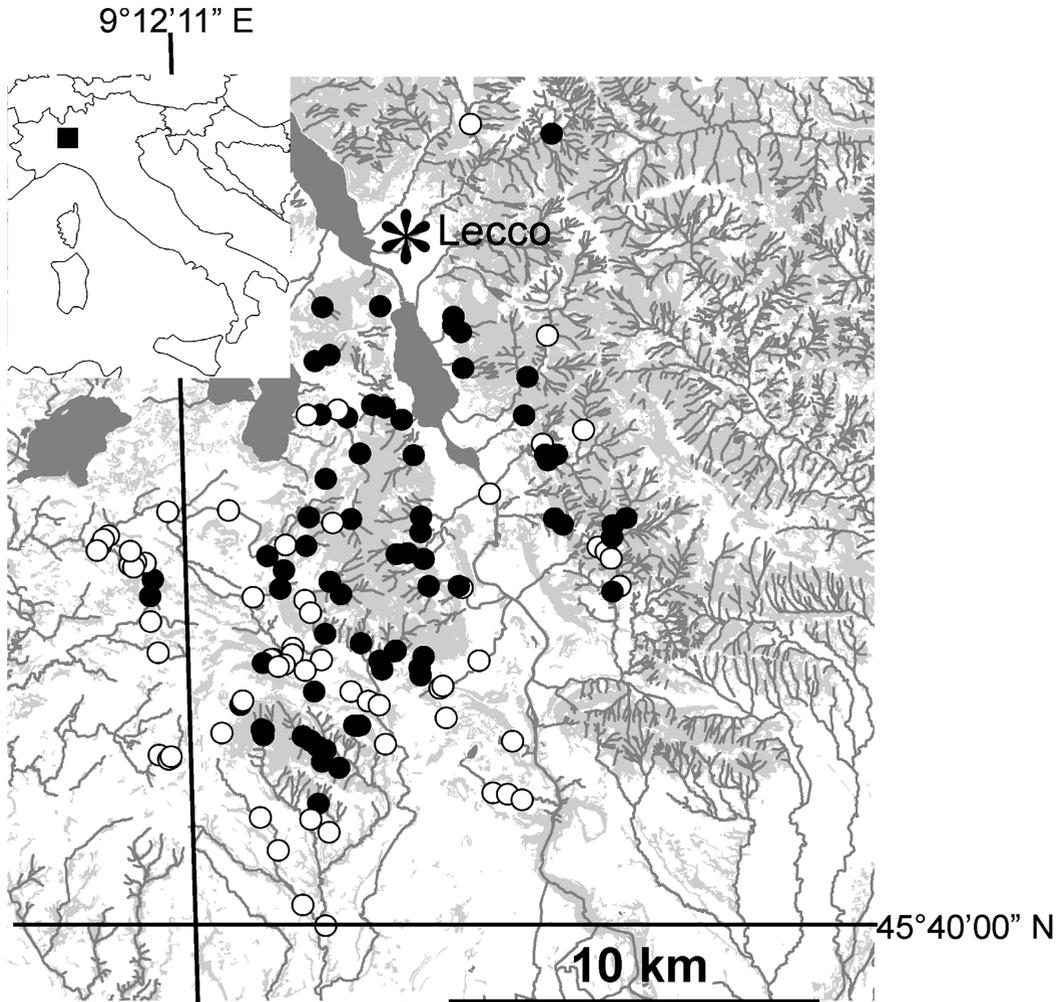
## Materials and methods

### *Study area and surveys*

For four consecutive years (2003-2006) we surveyed 132 localities on 82 watercourses in the southern part of the Lecco province, Northern Italy (fig. 1). The study area is dominated by hills and low elevation mountains, is crossed by a dense hydrographic network, and the fire salamander is widespread in this area (Di Cerbo and Razzetti, 2004). However, ongoing urban and industrial development is increasingly modifying the landscapes. We identified sampling localities on the basis of 1 : 25 000 or 1 : 10 000 topographical maps. Their elevation was 200-642 m above sea level, and was therefore within the usual range of the species in the study area (Di Cerbo and Razzetti, 2004). Each locality was surveyed in at least two consecutive years, during the most suitable period for the larval deposition and occurrence, i.e., from the end of February to the beginning of May and from September to the beginning of November. During the whole sampling period, each locality was visited 3-6 times (median: two times per year).

We used both nocturnal and diurnal visual encounter surveys to evaluate the presence/absence of larvae of the fire salamander (Crump and Scott, 1994). To maximize the homogeneity of sampling among streams, the same observer performed all surveys; for all streams, at least one visit was performed in daytime, and at least one visit was performed after dusk, using spotlights to lighten the stream. The fire salamander was considered present in a site if we observed larvae during at least one survey. All streams have clear water, therefore visual surveys allow an accurate detection of the presence of larvae. Our estimates of species occurrence are probably robust for two reasons. First, a preliminary study, performing multiple surveys and using a range of other sampling techniques (funnel traps, dip-netting, drift nets), showed that visual surveys correctly detected the presence/absence of *S. salamandra* in >95% of surveys (Maz-zoleni, 2005), and therefore allow an adequate assessment of species distribution. This preliminary analysis has been performed within the study area. Strong variation in detectability among sites may increase the experimental error and affect the comparison across habitats. Nevertheless, imperfect detection does not bias estimates of habitat distribution models unless detection differed among habitat types (Gu and Swihart, 2004). For this reason, we used a sampling protocol maximising sampling homogeneity among streams. Under these conditions, non-detection might more likely occur when abundance is low, in suboptimal habitats; in this case, species-habitat relationships are estimated correctly (Van Buskirk, 2005).

During each survey, we conducted a linear transect (100 m) along the stream, or until we recorded the presence of salamander. Most of streams were headwaters (100-300 m from the spring). In some cases, we considered multiple sampling localities in the same stream, if environmental conditions (e.g., landscape, stream morphology) markedly changed along the stream course; the average distance between nearby sampling localities was 1062 m. Therefore,



**Figure 1.** Study area, and distribution of the sampling localities. Black dots: localities where *Salamandra salamandra* is present; empty dots: localities where *S. salamandra* is absent. Pale grey: woodlands; dark grey: hydrographic network.

multiple transects within the same stream represent localities with different environmental conditions. We used Spatial Eigenvector Mapping (SEVM: Dormann et al., 2007) to evaluate whether sampling more than a single locality per stream can bias the results of our analyses (see *Statistical analyses*).

#### *Habitat characterisation*

Sites were described on the basis of rapid bioassessment protocols (Barbour et al., 1999) including features describing water quality and ecosystem functioning, and parameters that can be important for the ecology of fire salamander. We measured five different environmental features, during the second visit to each locality. We assumed that habitat variables were almost constant during the study period, since we did not observe major modifications of environmental features. Two parameters described stream morphol-

ogy: maximum stream depth (cm) within the 100 m transect, and watercourses heterogeneity. We measured watercourse heterogeneity on the basis of the percentage of alternation of fluvial elements (seeps, riffles and pools; see Petersen, 1992). Each stream transect was classified using the following rank scale: 1, absence of diversification, only a single fluvial element covering almost 100% of the transect; 2, poorly diversified, only 2 fluvial elements covering >90% of the transect; 3, quite diversified, each of the three elements present in at least 10% of the transect; 4, highly diversified, >90% of the transect presenting an alternation of the three elements.

Two parameters described the biotic features of streams: macrobenthos community and periphyton. These parameters are also often used as a measure of water quality, as polluted streams have poor macrobenthos and very abundant periphyton (Maitland, 1990; Moss, 1998). We used the Extended Biotic Index (EBI) modified for the Italian streams

**Table 1.** A-priori habitat models, and their rank, based on AIC values. The best models have the lowest AIC.  $k$ : number of parameters for each model;  $\Delta$ -AIC: Difference between the AIC of a model and the best AIC;  $w$ : Akaike's weight of the model;  $r_N^2$ : Nagelkerke's  $r^2$ .

Rank	$k$	Variables	$\Delta$ -AIC	$w$	$r_N^2$
1	5	depth, heterogeneity, EBI*, periphyton, wood cover	0	0.870	0.76
2	4	depth, heterogeneity, EBI, periphyton	3.846	0.127	0.73
3	3	depth, heterogeneity, wood cover	11.372	0.003	0.68
4	3	EBI, periphyton, wood cover	16.006	<0.001	0.66
5	2	depth, heterogeneity	22.586	<0.001	0.62
6	2	EBI, periphyton	22.706	<0.001	0.62
7	1	wood cover	54.916	<0.001	0.41

\* Extended Biotic Index.

(Woodiwiss, 1978; Ghetti, 1997) to assess macrobenthos communities. EBI is a standard method used in Europe to assess stream quality; on the basis of the number and identity of taxa found, each stream has a score ranging from 1 (lowest quality: poor communities including very tolerant species) to 13 (maximum quality: the richest communities, including stenoeccious species). EBI is also correlated to the structure of amphibian communities in streams (Lebboroni et al., 2006).

The abundance of periphyton over the stream bottom was visually assessed using a rank scale (1: periphyton absent or covering < 5% of the stream bottom; 2: 5%  $\leq$  periphyton cover < 40%; 3: 40%  $\leq$  periphyton cover < 60%; 4: 60%  $\leq$  periphyton cover < 80% and 5: periphyton covering  $\geq$  80% of stream bottom).

As a measure of landscape composition, we used the 1:10 000 vector map of Lombardy to measure wood cover percentage within 400 m from each sampling point, since woodlands are the main habitat for adult salamanders (Nollert and Nollert, 1992). We used a radius of 400 m because *S. salamandra* and other species of Salamandridae respond strongly to habitat alteration at this spatial scale (Denoël and Ficetola, 2007; Ficetola, Padoa-Schioppa and De Bernardi, in press). Wood cover was measured using the ArcView GIS 3.2 (© Esri, 1999). All woodlands within the study area are broadleaved, dominated by oak, hornbeam and chestnut.

#### Statistical analyses

We used an information-theoretic approach (Burnham and Anderson, 2002; Mazerolle, 2006) to evaluate the relative support of different a-priori models to explain species distribution. First, we formulated three simple a-priori models to explain the distribution of salamander larvae. Following the first model (thereafter, the landscape model) the distribution of the salamander is mostly determined by composition of terrestrial landscape. This model thus included a single independent variable, wood cover. Following the second model (biotic features) the distribution of salamander is mostly determined by the features of the aquatic environment. This model included two independent variables, macrobenthos community (EBI index) and abundance of periphyton. These two biotic variables are strongly influenced

by eutrophication and are commonly used indicators of water quality (Ghetti, 1997; Barbour et al., 1999; Nardi et al., 2005), but also represent the food items and the biotic community available for the salamanders. Following the third model (stream morphology), the distribution of salamander larvae is mostly determined by the morphological features of streams. This model included two independent variables, stream maximum depth and watercourse heterogeneity. We then built all the possible combinations of these three models (total: 7 a-priori models: see table 1).

We used generalized linear models assuming binomial error distribution to relate presence/absence of salamanders in each stream to the seven a-priori models. We then calculated the Akaike's Information Criterion (AIC) for each model: models explaining the highest proportion of variation using the smallest number of predictors have smallest AIC values and are considered to be the "best models". The use of the Akaike's Information Criterion corrected for small sample size (AICc) is controversial (Richards, 2005) therefore we report the results obtained using AIC. The results obtained using AICc are nearly identical. We calculated Akaike's weights  $w_i$  (AIC weights), representing the probability of the different models given the data, and the evidence ratios  $E = w_i/w_j$  to compare the relative support of the different models by the data (Lukacs et al., 2007). Subsequently, for each variable we summed the AIC weights of all the models in which the variable was included, to obtain the probability for each variable to be included in the best model (Burnham and Anderson, 2002). We also calculated Nagelkerke's  $r^2$  ( $r_N^2$ ) as a measure of predictive efficiency of the models. Finally, we used standard variance partitioning to assess the percentage of explained variation attributed to stream morphology, water features and landscape composition, on the basis of the explained deviance (Cushman and McGarigal, 2002). Variance partitioning allowed us to decompose the independent and the joint effect of variables, and to rank them according to their explanatory power.

Our data are spatially structured points, and spatial autocorrelation of observations could potentially bias the results of the analysis (Kühn, 2007). Moreover, in some cases we sampled more than a single point per stream, and this can violate the assumptions of independence. Therefore, we attempted to use Spatial Eigenvector Mapping (SEVM) to build models taking into account the spatial structure of the

data (Dormann et al., 2007). SEVM is a recently developed method, allowing the translation of the spatial arrangement of data points into explanatory variables capturing the spatial effects (Dormann et al., 2007). In SEVM, eigenvectors reducing the spatial autocorrelation of residuals are computed and then included as spatial predictors into generalized linear models. A recent analysis showed that SEVM produces results very similar to spatial mixed models. Moreover, SEVM is very appropriate for ecological analyses because, unlike other methods, its aims to remove residual spatial autocorrelation (Dormann et al., 2007). However, it was not possible to build SEVM following the procedure in Dormann et al. (2007), because in all our best models spatial autocorrelation of residuals was not significant (Monte Carlo permutation test,  $P > 0.05$ , see Lichstein et al., 2002). This analysis suggests that our dataset was not affected by nonindependence of residuals, and spatial autocorrelation did not bias the estimates of our analysis.

There were no strong correlations between independent variables (Pearson's correlation, all  $r \leq 0.60$ ) therefore multicollinearity did not bias our analyses (Berry and Feldman, 1985). We performed statistical analyses in R 2.6, using the packages spdep and car (www.r-project.org).

## Results

We recorded the presence of the fire salamander larvae in 72 sites out of the 132 surveyed. Univariate tests (Mann-Whitney  $U$  test and Student  $t$ -test) showed that *S. salamandra* was significantly associated to streams with low periphyton, high wood cover, high EBI score, high watercourse heterogeneity and low maximum depth (table 2).

The best model according to AIC assumed that stream morphology, stream communities and landscape cover are important to explain the distribution of *S. salamandra* (table 1). Based on AIC weights, the probability that this was

the best model, given the data, was 0.87. The second best model assumed that only water features and stream morphology are important (AIC weight = 0.127). Based on AIC evidence ratios, this model was about 7-times less likely to be the best model. All the other alternative models showed AIC weights below 0.003 (table 1); based on evidence ratios, all these models were much less likely than the best model (all evidence ratios < 0.004).

The averaged model clearly showed that salamanders were significantly associated to high wood cover, high EBI scores, scarce periphyton, high stream heterogeneity and low water depth (table 3). The model-averaged confidence intervals of these variables did not overlap zero, therefore all these variables had a strong relationship with the distribution of *S. salamandra* (table 3).

Following variance partitioning, stream morphology was the variable with the largest independent effect (16.6% of explained variation),

**Table 3.** Model-averaged parameters of environmental variables influencing the distribution of *Salamandra salamandra* in streams.  $w$ : cumulative AIC weight of the variable;  $B$ : averaged regression coefficient, with 95% confidence intervals.

Variables	$w$	$B$	95% C.I.
wood cover	0.873	3.78	0.69 / 7.31
heterogeneity	>0.999	1.59	0.56 / 2.84
depth	>0.999	-5.20	-9.05 / -2.11
EBI*	0.997	0.46	0.06 / 1.02
periphyton	0.997	-0.80	-1.58 / -0.10

\* Extended Biotic Index.

**Table 2.** Features of streams occupied and not occupied by *Salamandra salamandra*, and univariate tests evaluating the differences between occupied and unoccupied streams. The table reports the average  $\pm$  SE for depth and wood cover, and the median for watercourse heterogeneity, EBI score and periphyton. In parenthesis, the observed range of the variables. We performed  $t$ -test for depth and wood cover, and Mann-Whitney  $U$  test for heterogeneity, EBI and periphyton.

Variable	Occupied streams ( $n = 72$ )	Not occupied streams ( $n = 60$ )	
Watercourse heterogeneity	4 (3-4)	3 (1-4)	$U_{60,72} = 614.5, P < 0.001$
Maximum depth (cm)	$14 \pm 1.1$	$22 \pm 1.4$	$t_{130} = 4.982, P < 0.001$
EBI*	10 (7-13)	8 (2-11)	$U_{60,72} = 778.0, P < 0.001$
Periphyton	1 (1-4)	2 (1-5)	$U_{60,72} = 574.0, P < 0.001$
Wood cover (%)	$61 \pm 2.4$	$34 \pm 2.6$	$t_{130} = 7.554, P < 0.001$

\* Extended Biotic Index.

while landscape composition and water features explained a similar amount of variation (13.1% and 12.7% of explained variation, respectively). The joint effect of stream morphology and water features contributed to 22.8% of explained variation. The joint effect of stream morphology and landscape, and the joint effect of water features and landscape, contributed to less than 1% of explained variation. Most of explained variation (34.7%) was due to the joint effect of morphology, water features and landscape composition.

## Discussion

Our study clearly shows that landscape composition, biological and morphological features of watercourses act together to determine the distribution of the fire salamander. The influence of landscape and local factors on amphibian distribution is well known for lentic habitats (Van Buskirk, 2005; Werner et al., 2007) but has been less studied in running waters (Lowe and Bolger, 2002; Crawford and Semlitsch, in press). Our analysis allows an objective evaluation of the role of different environmental features for the distribution of the stream salamander, and provides key information that can be used for conservation management.

Stream morphology was the environmental feature most important to explain the distribution of the fire salamander. Salamanders were associated to shallow streams and with high heterogeneity. In natural watercourses, there is a complex sequence of riffles, pools and seeps, caused by geomorphological forces. Therefore, the presence of these elements is used as a measure of quality in watercourses (Petersen, 1992). A complex sequence of riffles and pools is often associated to diverse freshwater communities, as it constitutes the habitat of different species (Petersen, 1992). Young larvae of *S. salamandra* live in pools, where they find shelter and prey items, while larger larvae can take advantage of the heterogeneity of microhabitats, since they can also exploit areas with slightly

faster current velocity (Baumgartner, Waringer and Waringer, 1999). Therefore, heterogeneous streams with presence of different elements are extremely important for the larval development of salamanders.

The significant association with the shallowest streams probably reflects the higher probability of reproductive success due to the absence of fish (Cruz, Rebelo and Crespo, 2006). In the study area, the shallow streams are rarely colonised by fish, also because they can be separated from the major watercourses during arid periods. Fish are important predators of salamander larvae. The effect of predatory fish on amphibians density and distribution has been observed by several studies, particularly on Urodeles (Hecnar and McLoskey, 1997; Ficetola and De Bernardi, 2004; Denoël, Dzukic and Kalezic, 2005; Denoël and Ficetola, 2008) hence fish can strongly affect the suitability of potential breeding sites.

Water features have an importance comparable to stream morphology. Larvae live in streams with high EBI scores, i.e., with the rich macrobenthos communities that are characteristic of oligotrophic water. These communities are dominated by insect larvae with high sensitivity to both organic and chemical pollutants, and require high oxygen concentration (Woodiwiss, 1978). The association with the highest EBI scores can arise for two nonexclusive reasons. First, macrobenthos includes the primary preys of larvae of fire salamanders living in streams (Weitere et al., 2004). Moreover, high EBI scores can be considered an indicator of lack of pollutants. Salamanders are also associated to streams with very scarce periphyton. Periphyton is usually abundant in eutrophic waters (Moss, 1998). The relationship between *S. salamandra* and scarce periphyton provides further support for the association of *S. salamandra* with oligotrophic running waters. This relationship is well known (Zakrzewski, 1987). Nevertheless, our analysis is one of the few large-scale studies supporting this widely accepted idea with quantitative data from multiple

elements of aquatic communities, such as algae and invertebrates.

The analysis of landscape features clearly shows the association of *S. salamandra* with high wood cover around breeding sites. Even if some populations in the European range of the species are able to survive in environments without wood cover, mostly in Spain (Nollert and Nollert, 1992; Veith, 1997), woodlands are the most important habitat of adults, which usually live in the dense leaf litter of broadleaved forests (Joly, 1968). Therefore, the presence of terrestrial habitat is necessary for the survival of populations, and loss of forest cover can cause their decline (Schmidt, Feldmann and Schaub, 2005). Wetland features are extremely important to explain amphibian distribution at local scale, but landscape variables can be more important to explain large scale patterns (Resatarits, 2005). Indeed, deforestation is a major factor causing amphibian extinctions (Gardner, Barlow and Peres, 2007), and large-scale loss of forested habitat may cause the extirpation of formerly common species.

Even if stream morphology, water features and landscape explained a significant proportion of the variation, it should be noted that most of variation was explained by the combined effect of multiple variables. The complementation between multiple elements, such as wetlands and landscape, is the key of a correct understanding of distribution of semiaquatic amphibians (Pope, Fahrig and Merriam, 2000; Denoël and Lehmann, 2006). Stream features are important, and conservation actions are often focused on the preservation and management of breeding wetlands (Beebee, 1996). However, suitable wetlands are not enough for population survival if the terrestrial habitat of adults is lacking (Gibbons, 2003; Cushman, 2006; Denoël and Ficetola, 2008). Elements acting at multiple spatial scales and that are important for different life history traits should be integrated for a correct understanding of requirement of semiaquatic species (Ficetola et al., 2004; Fischer, Lindenmayer and Cowling, 2004; Price et al.,

2004; Gagné and Fahrig, 2007), and to set up conservation plans.

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