



Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability

NICOLAS RAY^{1,*}, ANTHONY LEHMANN¹ and PIERRE JOLY²

¹Laboratoire d'Ecologie et de Biologie Aquatique (LEBA), Anthropology and Ecology Department, University of Geneva, Switzerland; ²UMR CNRS 5023, Ecologie des Hydrosystèmes Fluviaux, Université Claude Bernard Lyon 1, France; *Author for correspondence (e-mail: nicolas.ray@anthro.unige.ch; fax: +41-22-300 0351)

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Abstract. Predictions of occurrence of two amphibian species, the common toad and the alpine newt, were made using information on land use surrounding breeding ponds. A geographical information system (GIS) was used to compile a landuse map, from which permeability estimates (friction) were derived. Potential migration zones based on friction and maximum migration distance were then modeled. Contacts between several migration zones suggest the potential for migration between ponds by adult individuals. The ability of the migration zones to enhance predictions of species occurrence was tested using generalized additive models (GAMs), and several landscape variables were selected as determinants of amphibian presence. The area of a migration zone and the number of ponds within that zone were positively related to both toad and newt presence, suggesting the importance of buffer habitats around each pond in amphibian conservation. Toad presence declined with cultivated field area and newt presence declined with vineyard area, suggesting the negative effect of agricultural activity on amphibians. The friction-based modeling approach improved the prediction of toad presence when compared to a more classical analysis of habitat composition within a circular zone centered on the focal pond. Prediction of newt presence was, however, less accurate than prediction of toad presence. Despite its exploratory nature and the subjectivity of permeability estimates, this study shows the usefulness of GIS in the functional analysis of a landscape, with potential applications in biological conservation. It also highlights the need for improving our knowledge of habitat use by animals.

Key words: Amphibian, *Bufo bufo*, Dispersal model, Generalized additive model, Geographical information system, Least-cost path, Migration modeling, Permeability, Switzerland, *Triturus alpestris*

Abbreviations: GAM – generalized additive model; GIS – geographic information system; GRASP – generalized regression analysis and spatial predictions; LEBA – Laboratoire d'Ecologie et de Biologie Aquatique; MCM – Maximum cost of migration; MDM – Maximum distance of migration; SITG – Système d'Information du Territoire Genevois.

Introduction

Habitat fragmentation is considered to be one of the major causes of contemporary loss of biodiversity (Soulé 1987; Blaustein et al. 1994). Fragmentation acts to increase local extinction risks by reducing local population size (Shaffer 1987),

which may in turn reduce a species geographical distribution. However, rescue effects due to dispersal between local populations (Brown and Kodric-Brown 1977; Hanski et al. 1996) may ameliorate extinction risks. This process depends on the availability of propagules for dispersal (individuals which leave a donor population to join a receptor population), the geographical distance between donor and receptor populations and the permeability of the habitat matrix to movement by these migrating propagules (Dunning et al. 1992; Taylor et al. 1993; Wiens 1997; Villalba et al. 1998; Brooker et al. 1999; Wiens 2001). Dispersal distance can be increased by habitat destruction whereas matrix permeability can become altered by changes in land uses.

The impact of matrix permeability on a species distribution may be evaluated by relating species presence or abundance to the composition or the structure of the matrix (Joly et al. 2001). In this respect, small habitat patches and linear habitats can enhance dispersal as they act as stepping-stones or corridors for dispersing individuals (DeMaynadier and Hunter 1998; Gibbs 1998; Lehtinen et al. 1999). Conversely, matrix elements such as built areas or roads can act as more or less impassable barriers (Hitchings and Beebee 1997; Wederkinch 1988).

While the quality of the matrix influences dispersal (the one way movement of an individual from its natal territory to a new potential breeding site), it also influences other movements such as breeding migrations. The biological cycles of many animal species involve migrations between different habitats, such as hibernation migrations in birds and breeding migrations in species with complex life cycles (e.g., insects, fish, amphibians).

In amphibians, the growth habitat of the larvae markedly differs from the habitat of adult individuals. Ponds or land/water ecotones are used as larval habitats, while terrestrial habitats (e.g. forests) are utilized for juvenile and adult stages. Such complex cycles imply annual go-and-return migrations between terrestrial and breeding aquatic habitats in the adults, and a landward migration in the postmetamorphic juveniles. Population dynamics depend on the success of such migrations, and extinctions are likely to occur in landscapes where habitat matrix permeability has been altered by modifications in land use (Sinsch 1989; Semlitsch 1998; Joly et al. 2001). Agriculture practices, for instance, can modify the permeability of the matrix. Areas under intensive cropping are less favorable to the movements of many amphibian species than meadows, due to scarce refugia, low water availability, low food resources, and toxicity from pesticide use.

Due to the peculiarities of the amphibian biological cycle, each breeding site is surrounded by an area in which migration is possible (a potential migration zone), which may be composed of a network of suitable terrestrial habitat patches and unsuitable habitat patches that have to be crossed. The area of this migration zone would primarily depend on the potential migration distance of the species under consideration, and the success of migration would then depend on the presence of other suitable breeding ponds within this zone. However, simple distance mea-

asures may not adequately reflect the true cost of crossing patches through which movement is difficult. As an alternative, distance measures can be weighted by species-specific costs related to the permeability of the habitat patches that have to be crossed.

Permeability models are grid-based models that consider both energy expenses and mortality risks that an individual experiences when it moves across the matrix. The principle of such modeling is to assign a value to each cell that represents its permeability to the crossing by an organism. Random walk or least-cost movements of individuals are then simulated. They are governed by local rules depending on neighboring cells. Although these modeling techniques have been used in several studies of animal migrations (e.g. Schippers et al. 1996; Walker and Craighead 1997; Villalba et al. 1998; Purves and Doering 1999), they remain exploratory as the knowledge of habitat use by animals is often too fragmentary for accurate modeling.

Permeability models take advantage of geographical information systems (GIS) that have been used extensively during the last decade for population biology in a wide range of applications (Johnston 1998). GIS is a powerful tool when dealing with permeability and dispersal, and most GIS packages offer built-in simple dispersal and so-called 'cost distance' functions that allow migration zone modeling.

The aim of this work was to model the migration zones of two amphibian species with contrasting dispersal capabilities, in order to assess the likelihood of successful migration between ponds. The permeability of each habitat patch was established by using the empirical knowledge of habitat use and ease of dispersal through habitat types by each of the two species. Land uses and number of breeding sites within the migration zones were used in turn to predict the presence of the species among sites. Predictions of this model were compared to predictions of presence by a classical analysis of habitat composition.

Region studied

The study region was the State of Geneva (western Switzerland; Figure 1). This 246 km² area is densely inhabited and developed. It is crossed by the western end of Lake Geneva and River Rhone. In the middle of the state, Geneva City and suburbs stretch around the southern end of the lake. The other parts of the area are mainly devoted to agriculture (crops, vineyards and pastures). Forested lands are mainly small wood lots, except two relatively large forests in the northern and the south-eastern part of the area. The heavy building program of the last 10 years together with an intensification of agriculture has led to the multiplication of barriers for the movements of wild fauna. However, several water-bodies have been preserved, and most of them are suitable for amphibian breeding.

The ponds of Geneva State (127 ponds exceeding 10 m²) were sampled by the LEBA in 1992 (Auderset et al. 1992). Ponds of this size are readily utilized for

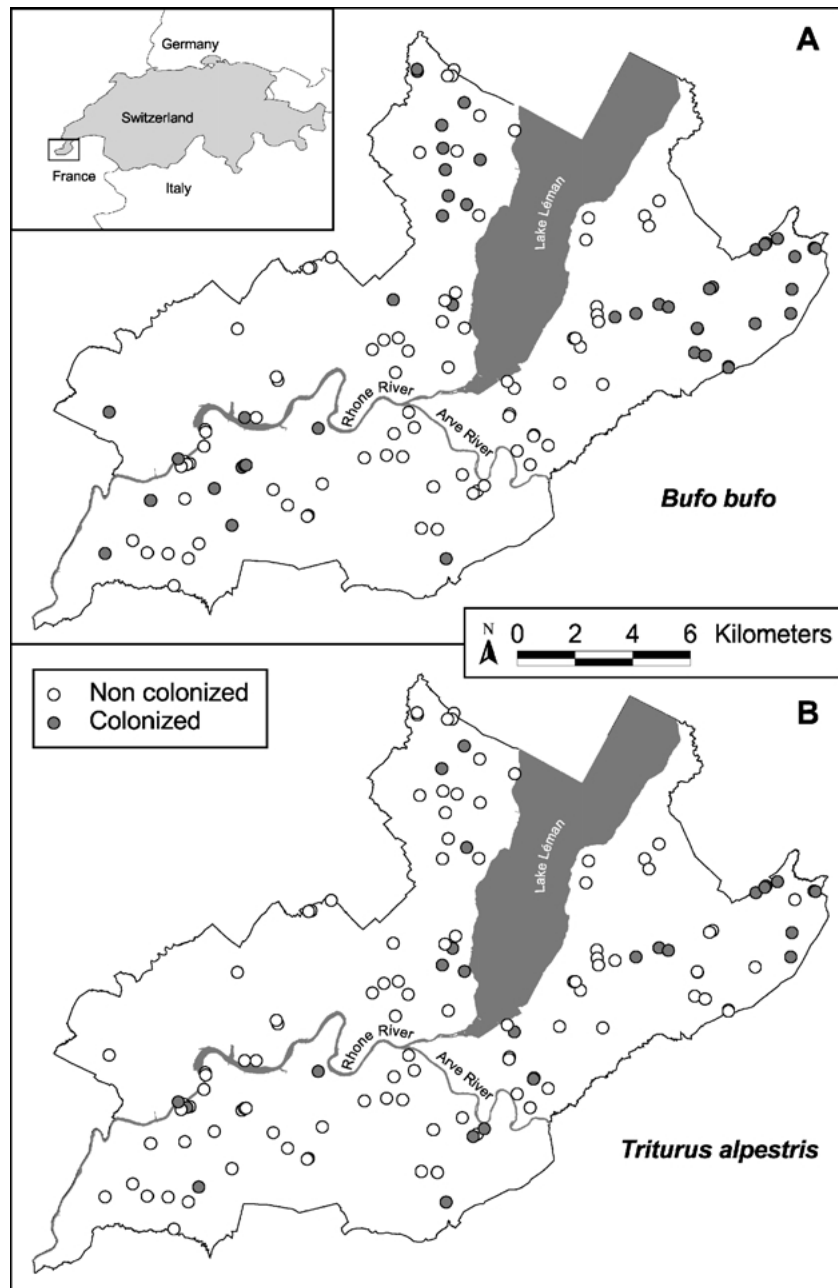


Figure 1. Pond location and amphibian presence in the State of Geneva.

breeding by the species under consideration. This database was imported into GIS, allowing the mapping of the ponds (see Figure 1). Due to the scale of the study area and the relatively small areas of the ponds, the shapes of each pond were not considered in GIS, where only the coordinates of their geographic centers were registered.

Species studied

The common toad (*Bufo bufo*) and the Alpine newt (*Triturus alpestris*) were chosen because of their terrestrial habits, differing dispersal capacities and occurrence in the studied area. Data on presence/absence of these two species in each pond were available from a survey made by the Museum of Natural History of the Geneva State (P. Maunoir (1999) unpublished) performed during the period 1998–1999. Figure 1 presents the distributions of both species in the ponds of the studied area. Although no standardized routine was used to assess amphibian presence in each pond, the survey of species occurrences is likely to be reliable due to the relatively small study area, the low number of breeding sites, and the plurality of herpetological knowledge in identifying species at each location. Species abundance, which would have required standardized sampling, was therefore not considered.

The common toad is one of the best-known amphibian species, and literature relating to this species is widely available. Forested areas are its preferred habitat, but it occasionally occurs in grass fields and backyards. High mortality has been observed in sandy and open environments (Denton and Beebee 1991), and it is therefore reasonable to consider that the species avoids these kinds of environments when migrating. The common toad uses forested habitats during both active summer periods and hibernation winter periods. Adults are usually sedentary (Sinsch 1988) and faithful to a breeding place (Heusser 1969). However, some juveniles (up to 20%) disperse from their native pond to breed in other ponds, such as newly created ponds (Reading et al. 1991; Schlupp and Podlousky 1994; Cooke and Oldham 1995). The distance between the breeding pond and the hunting areas has been estimated to range from a few meters up to 3 km (Heusser 1968; Sinsch 1989). For the migration zone computation, we tested maximum distances of migration (MDM) of 1500 and 3000 m.

The newt *Triturus alpestris* uses habitats similar to those of the common toad but habitat patches can be smaller, such as woodlots, groves and hedgerows. Breeding ponds can also be smaller than those used by the common toad, such as farm ponds and ditches. Whereas site fidelity has been shown in adult newts (Joly and Miaud 1989, 1993), dispersal from one pond to another is also frequent (N. Perret et al., submitted). Migration distances are less precisely known than in the common toad, and are considered to range from a few meters to 1 km (Joly et al. 2001). For the computation of migration zones, we tested MDMs of 400 and 800 m.

Methods

Overview

Initially, land use patterns were incorporated into a landuse map. By assigning permeability values (migration cost) to each landuse type, we obtained species-specific permeability maps (friction maps). These friction maps were used to calculate migration zones. The area encompassed by these migration zones and circular zones centered on ponds (used in classical analyses) were used to extract the values of the landscape variables derived from the landuse map. Prediction of occurrence of each species was then performed using the explanatory landscape variables. These methodological steps are explained in details in the following sections.

Landuse map

Since no satisfactory landuse map existed for our study area, we gathered the required information to build a suitable map. The environmental data of the Geneva area is managed by the Information System of Geneva's Territory (SITG = Système d'Information du Territoire Genevois). All the required environmental data sets were obtained from SITG, except the vegetation data set that was made available by the Geneva Botanical Garden (Werdenberg and Hainard 2000). The selected landuse patterns are presented in Table 1.

We used the GIS package *ArcView* (Environmental Systems Research Institute, USA) to store and manage the data sets. Each data set was rasterized at a resolution of 10 m in *ArcView* using the module *Spatial Analyst*. As well as their relevance to amphibian ecology, the data sets were chosen in order to minimize information gaps when merged. The landuse map was obtained by merging all data sets, using the Merge function of the Spatial Tools extension to *ArcView* (Hooge 1999). Because least-cost path procedures unrealistically consider information gaps (pixels with no value) as migration barriers, we used the Nibble function of the Spatial Tools extension to *ArcView* (Hooge 1999) to fill these gaps with the spatially closest landuse type.

Friction maps

A friction map is a matrix of cells defining the energy cost for crossing each cell. In this study, the landuse map was used to obtain the friction matrix. A conversion table was used to assign a migration cost to each landuse type, according to the assumed permeability of landuse types for each species. Using the conversion table, the friction map is then obtained by reclassification of the landuse values. We considered the migration costs to be linked to both energy expense and mortality risks of an individual moving across the matrix. Each time an individual crosses a cell, it loses the corresponding amount of energy assigned to this cell through the friction map.

Table 1. Description of the 11 landscape variables.

Variable	Description	Friction cost	
		<i>Bufo bufo</i>	<i>Triturus alpestris</i>
Dense vegetation	Area of forests and dense bushes	5	5
Sparse vegetation	Area of sparse bushes and pioneer vegetation	25	25
Green grounds	Area of grass fields, gardens, and groves	45	80
Vineyards	Area of vineyards	80	80
Cultivated fields	Area of cultivated fields	45	80
Densely constructed zones	Area of zones surrounding densely inhabited surfaces	80	80
Second order roads	Area of roads, except highways	80	80
Migration barriers	Area of elements that are impermeable to migration by amphibians: Lake Geneva Main rivers (Rhône, Arve) Buildings Airport Ravines and embankments Low walls Railways Highways	Infinite	Infinite
Number of ponds	Sum of colonized and non-colonized ponds within the migration zone		
Number of colonized ponds	Number of colonized ponds within the migration zone		
Area of the migration zone	Area of the computed migration zone		

The first eight variables have an associated friction cost for both species.

Very few data exist on energy costs of amphibian migrations. For each habitat type, movement costs were estimated both from literature on habitat use by each of the species (where available), together with advice from herpetologists (P. Fallot, P. Joly, P. Maunoir, personal communication). The range of cost values varied from 5 to 80. This range was arbitrary, but is reasonable in comparison to other migration studies (e.g. Schippers et al. 1996). The least cost was attributed to forest habitat that is the most favorable for the movements of the two studied species. Any other matrix habitat was attributed a higher migration cost (see Table 1 for cost values).

Apart from distinctive weights attributed to land uses, migration barriers were also defined as any physical element that could not be crossed by migrating individuals (infinite friction). Care is required when assigning migration barriers, since there are few observations which explicitly demonstrate that a landscape feature completely blocks migration rather than increasing the difficulty of migration. Barriers affecting migration were chosen on the basis of literature and empirical observations.

Lake Geneva and the two main rivers (Rhône and Arve) were considered impenetrable to migration by the common toad and *Triturus alpestris* due to their widths

and high rates of flow. While it is indeed very unlikely that individuals cross them frequently, the possibility exists that they act to enhance migration in specific directions by acting as riparian corridors.

Buildings and associated human activity around them may influence amphibian migrations. Even if migrating common toads have been observed very close to isolated farmhouses (Van Gelder et al. 1986), it is probable that built areas negatively influence migration because of the presence of small walls, fences, or open playgrounds, that can act as migration barriers.

To account for this potential barrier effect, every building of the state was recorded and the ArcView buffer tool was used to add a 10 m buffer around each building. Although no data were available, it is reasonable to consider that the Geneva airport also has the potential to adversely affect toad and newt migration due to large areas of inhospitable terrain, and it was therefore considered a barrier (see Figure 2).

Studies have shown that railway tracks in some areas strongly affected amphibian populations by disrupting movements of individuals among breeding sites (Berthoud and Antoniazza 1998) which may ultimately affect gene flow among breeding sites (Reh 1989). Similarly, it is well established that roads are potentially destructive for amphibian populations (Ashley and Robinson 1996), and a negative correlation has been established between traffic intensity and mortality in several amphibian species (Fahrig et al. 1995; Hitchings and Beebee 1997; Berthoud and Antoniazza 1998; Vos and Chardon 1998). Railway tracks and highways were therefore considered to be migration barriers, (although due to lower traffic intensity, second order roads were not considered as migration barriers, but were attributed a high friction cost). Landscape features that are likely to interrupt amphibian migration routes such as ravines, embankments and low walls were also considered to be barriers.

The individual barrier data sets were standardized with a 10-m resolution, merged together to obtain a global barrier map, and finally merged with the landuse map in order to obtain the complete landuse map shown in Figure 2. During this last merging process, the decision to categorize a cell as a barrier was given priority over any other present landuse type. A list of migration barriers can be found in Table 1.

Migration zones and landscape variables

Ponds were considered as focal points around which migration zones were modeled. A migration zone represents the potential area within which adults can roam between the breeding period and the hibernation period. Juveniles were not considered since there were too few biological data to incorporate this parameter. Migration zones are delimited by an edge, which can be seen as a theoretical threshold of energy cost that is not possible to exceed. Once a migration zone, or a more classical circular zone, is defined, it is then possible to extract values of landscape variables such as areas of each landuse type.

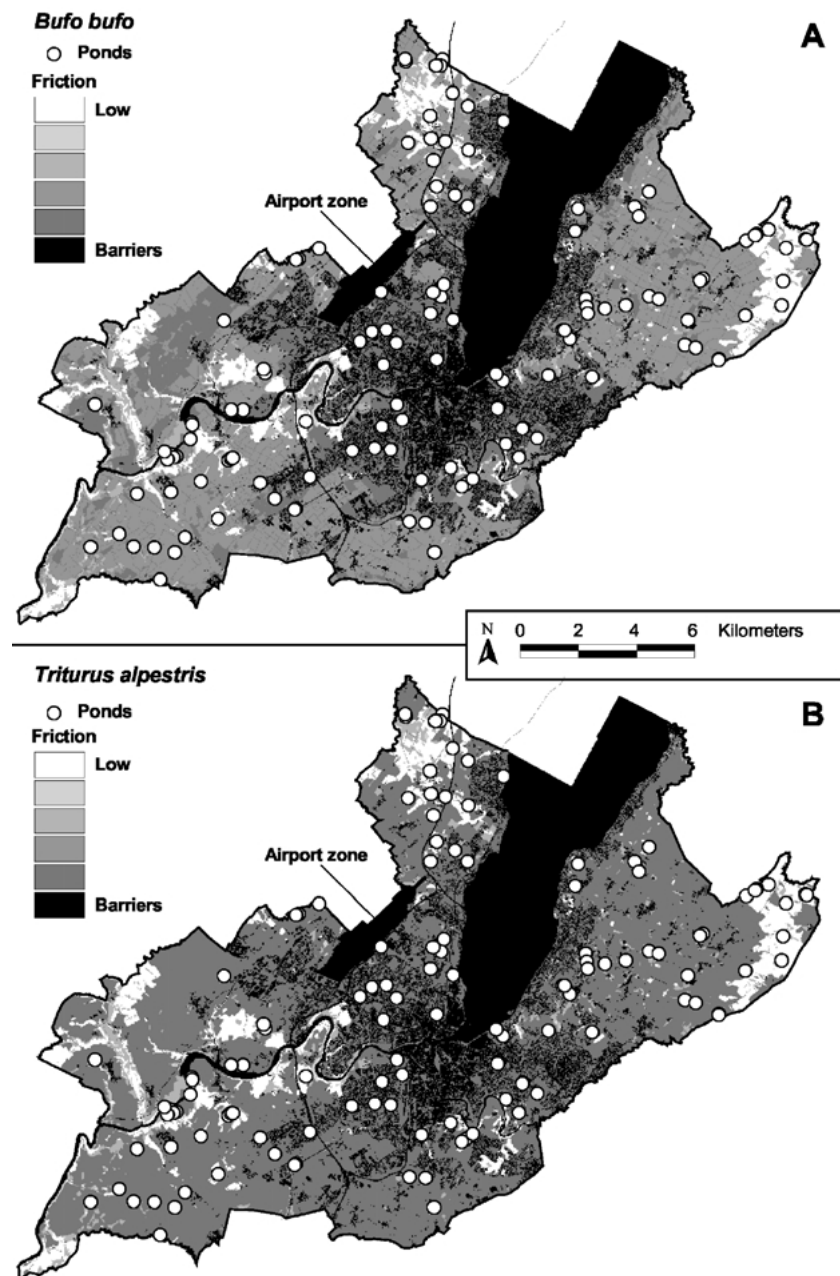


Figure 2. Friction maps for *Bufo bufo* and *Triturus alpestris*.

The migration zone was delimited by the maximum cost of migration (MCM, expressed in cost units). Under the assumption that the maximum distance of migration

(MDM, determined from the literature and expressed in distance units) was realized in favorable habitats, MCM was obtained by multiplying the MDM by the friction cost of the most favorable habitat (expressed in cost units per distance unit). It is possible that the migration movements of adults occur over two breeding seasons (Reading et al. 1991; Schlupp and Podlousky 1994). When individuals return from their hibernation site towards a breeding site, we can realistically assume that the same constraints on energy expense apply to their movements. The MCM from the hibernation site towards a breeding site can thus be considered equal to the MCM from the breeding site towards a hibernation site. The matrix separating two ponds separated by a maximum of two MCMs can thus be regarded as permeable enough to allow the potential exchange of individuals between these two ponds. In order to encompass this 'connectivity' (the exchange that takes place between two successive breeding seasons) the analyses were made with doubled MCM. Result maps (Figures 3 and 4) are, however, presented with a migration zone extent of one MCM, which ensures that observation of contact between two migration zones expresses potential connectivity between ponds.

We used the standard ArcView Cost Distance function to compute the migration zones for the whole set of ponds. This spreading function is based on a least-cost path algorithm (Douglas 1994; ESRI 1996; Collischonn and Pilar 2000), and computes the accumulated cost of moving from a focal point (the pond) towards the surrounding cells based on an underlying friction map. The spreading function can be seen as the movement of virtual individuals in every direction from the pond. The crossing of a cell implies energy loss equal to the friction of that cell. When the virtual individuals have lost an amount of energy equal to the MCM, they stop, defining the edge of the migration zone. An advantage of this method is the underlying (realistic) assumption that individuals can disperse in all directions from a pond with the same probability.

We used an in-house script written in Avenue that automatically computed the migration zone of each pond, and that extracted within each migration zone (i) the area of each landuse type, (ii) the number of colonized and non-colonized ponds, and (iii) the total area of the migration zone. For comparison, the same landscape variables were extracted within a circular zone centered on each pond, the radius of which was equal to twice the MDM. We used standard ArcView Buffer tools to generate these circular zones. The two methods (friction-based and circular) were applied to both migrating distances, resulting in four different scenarios established for each species.

We produced a total of 11 landscape variables which included: eight landuse areas (dense vegetation, sparse vegetation, green grounds, vineyards, cultivated fields, densely constructed zones, second order roads, and migration barriers), the number of ponds (colonized and non-colonized), the number of colonized ponds, and the area of the migration zone. A short description of each variable may be found in Table 1. Migration barriers are avoided by the cost distance algorithm, which applies an infinite cost to them. Their areas were therefore not recorded when using the friction-based computation. When using the circular zones, friction was not taken into account, and

area of migration barriers was recorded as a habitat variable. However, all the areas of a circular zone were by definition equal (unless for the ponds near the borders of the State, for which migration zones are truncated), and this area was therefore removed from the explanatory variables.

Data analysis

We used generalized additive models (GAMs) (Yee and Mitchell 1991) to relate occurrence of each species to the landscape characteristics of the migration zones as in Joly et al. (2001). GAMs are preferred in general to other regression methods (classical linear models or generalized regression models) because of their ability to handle non-linear relationships between responses and predictive variables. Binomial models were selected to fit this presence-absence data, using S-Plus (Mathsoft Inc., Seattle) and the GRASP library developed by Lehmann et al. (2002). GRASP uses a stepwise procedure to select a model with significant explanatory variables based on the change of deviance associated to adding or removing them from the model (χ^2 test, $P = 0.05$) (Hastie and Tibshirani 1990; Chambers and Hastie 1993). The selected model belongs to a group of equally significant models that can be sorted by their goodness of fit using the ratio between explained deviance and total deviance (D^2).

To select the most satisfactory model, we computed every possible model with four variables using GRASP and an in-house script. D^2 values were computed for each model, which was retained if significant. The choice of a maximum of four variables was subjective, but preliminary analyses of our data showed a good fit with four explanatory variables and that overfitting was likely to occur with more variables. A final model was selected for each scenario on the basis of a trade-off between goodness of fit, ecological interpretability of selected variables, and the shape of response curves. Standard ANOVA was used to analyze D^2 variance within and among scenarios using all significant models.

Results

Migration zones for *B. bufo* are shown in Figure 3. Overlapping migration zones of two adjacent ponds reflect potential connectivity between them. The MDM was set at 1500 m (Figure 3A) and 3000 m (Figure 3B). The gray scale shows the extent of the cumulative cost. Similar maps for *T. alpestris* are shown in Figure 4. For this species, the MDM was set at 400 (Figure 4A) and 800 m (Figure 4B). In order not to overload the maps, land uses are not shown. The density of migration barriers in the center of the studied area resulted in smaller migration zones than in the less inhabited environments where friction is lower (see Figure 2). As a consequence, most of the ponds in this central area were not connected to another pond. Some ponds were

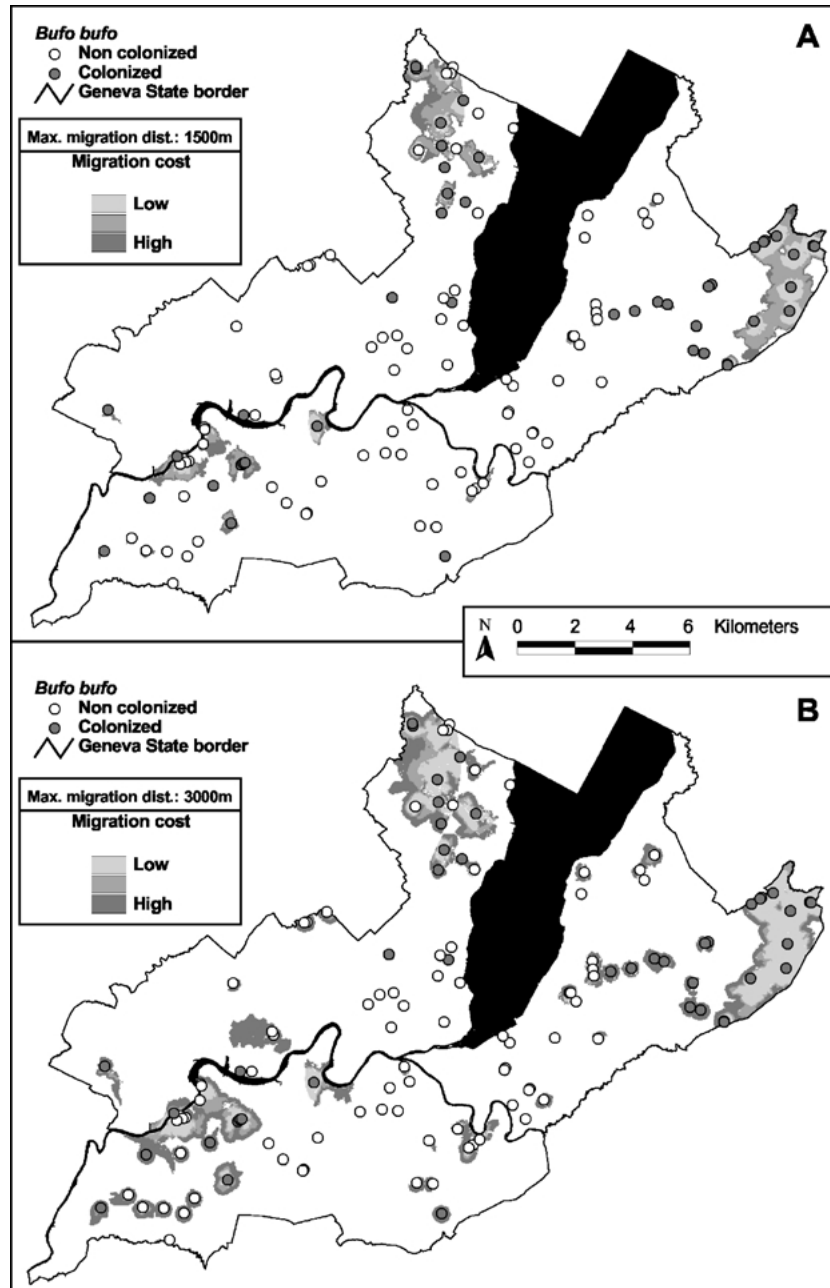


Figure 3. Migration zones for *Bufo bufo*, modeled with an MDM of 1500 m (A) and 3000 m (B).

surrounded by a barrier network such that migration zones were too small to appear on the map.

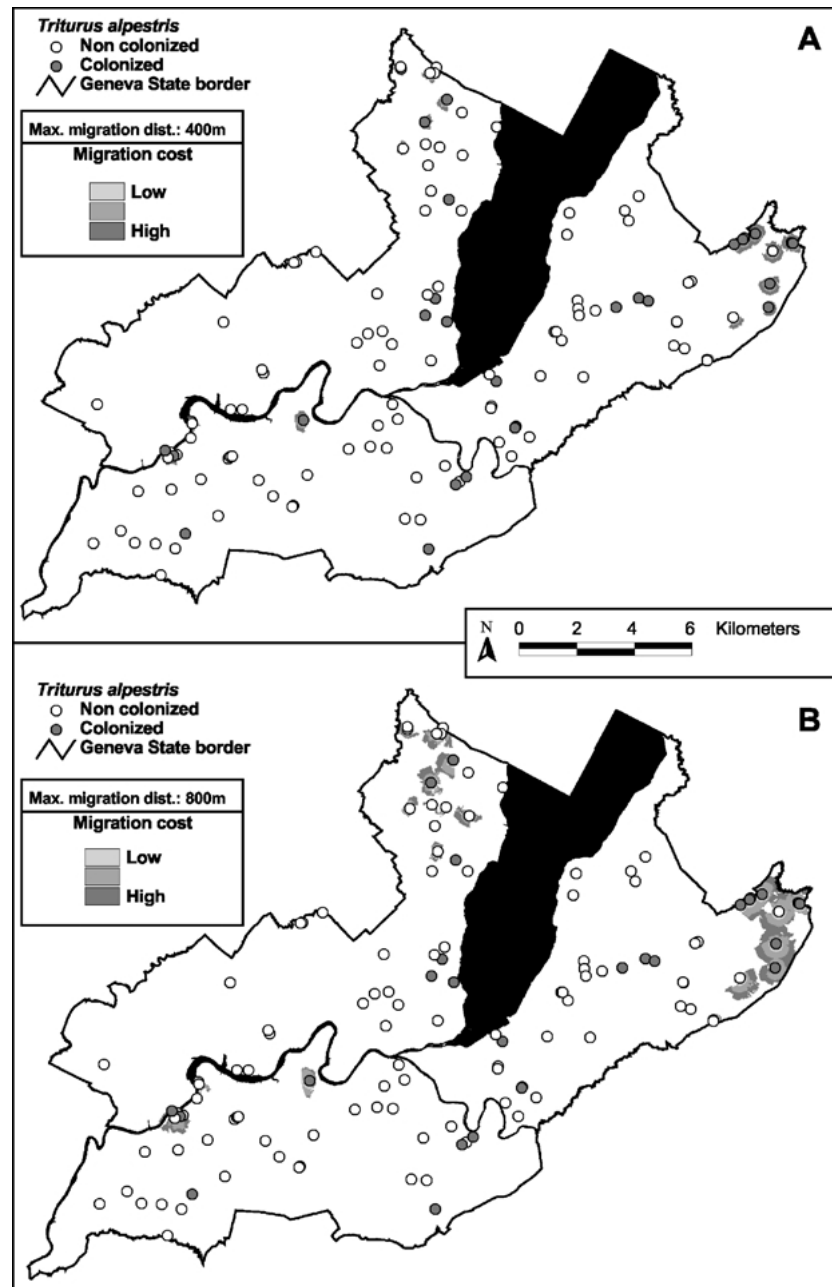


Figure 4. Migration zones for *Triturus alpestris*, modeled with an MCM of 400 m (A) and 800 m (B).

With an MDM of 1500 m (Figure 3A), the largest migration zones for *B. bufo* were situated exclusively in the most forested landscapes. In the western part of the

Table 2. Number of significant ($P < 0.05$) four-variable GAM models for each species and each scenario.

	Number of four-variable GAM models			
	Migration zone		Circular zone	
	MDM of 1500 m (400 m)	MDM of 3000 m (800 m)	MDM of 1500 m (400 m)	MDM of 3000 m (800 m)
<i>Bufo bufo</i>	22	5	8	24
<i>Triturus alpestris</i>	0	1	0	7

Parenthesized MDM are for *T. alpestris*.

studied area, all colonized ponds appeared connected to each other by permeable habitat matrices. However, in the northern part of the studied area, several ponds appeared isolated despite a forested environment. When setting the MDM to 3000 m (Figure 3B), the number of connected ponds strongly increased in this zone.

MDM used for *T. alpestris* (400 and 800 m) resulted in smaller migration zones than in *B. bufo*. As for *B. bufo*, the connections were more frequent in forested landscapes. When the MDM was set at 400 m (Figure 4A), few ponds were connected. With an MDM of 800 m (Figure 4B), only the ponds in the forested environment had a migration zone of sufficient area and shape to allow interconnections.

Table 2 gives the number of significant four-variable GAM models for the different scenarios out of the 330 possible models. Figure 5 shows graphical outputs as box plots (A and C) for all significant scenarios, and interaction curves (B and D). Models for *B. bufo* had significantly ($P < 0.001$) higher D^2 values when friction-based migration zones were used (mean $D^2 = 0.52$) instead of circular zones (mean $D^2 = 0.40$). When MCM was set at 3000 m, D^2 values were also significantly higher ($P < 0.001$) when friction-based migration zones were used (mean $D^2 = 0.57$) instead of circular zones (mean $D^2 = 0.50$). For a given type of area computation, a higher MCM gave a significantly higher ($P < 0.001$) mean D^2 value.

For *T. alpestris*, no significant models were found for both types of area computation, when MDM was set at the lowest value (400 m). Only one significant model ($D^2 = 0.39$) was found for the highest MDM (800 m) of the friction-based computation, and it was not significantly higher than the models based on circular zones (mean $D^2 = 0.37$) (Figure 5C, D).

For each species, we selected a GAM model with the better trade-off between goodness of fit and ecological interpretation of the variables. For *B. bufo*, this model ($D^2 = 0.55$; friction based; MDM = 3000 m) was:

$$s(\text{number of colonized ponds}) + s(\text{sparse vegetation area}) \\ + s(\text{migration zone area}) + s(\text{cultivated fields area})$$

where $s(x)$ is a smoothed variable.

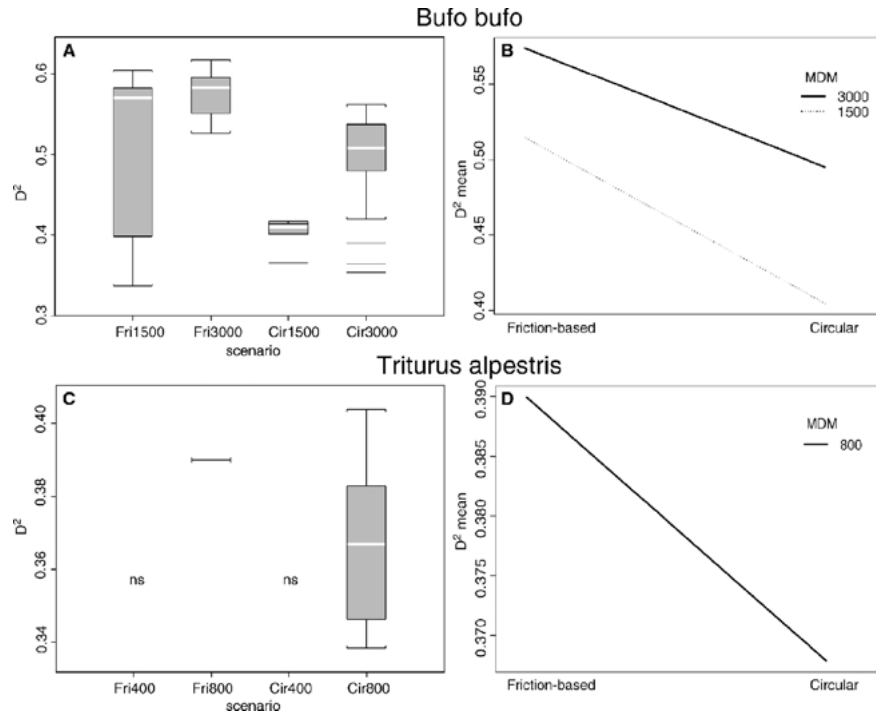


Figure 5. Box-plot summary of D^2 values for significant four-variable GAM models (A and C). White lines are median, gray boxes limit the 50% quartile, horizontal squared parentheses limit the 75% quartile, and isolated plain lines depict outliers. 'Fri' represents a friction-based scenario, and 'Cir' represents a circular zone, while attached numbers are MDM. Interaction curves (B and D) show mean D^2 values for friction-based or circular migration areas. Non-significance is indicated by 'NS'.

For *T. alpestris*, the model ($D^2 = 0.39$; friction based; MDM = 800 m) was:

$$s(\text{number of colonized ponds}) + s(\text{number of ponds}) \\ + s(\text{migration zone area}) + s(\text{vineyards area})$$

where $s(x)$ is a smoothed variable.

Response curves of the two species to the landscape variables varied from one species to the other and were not always linear (Figure 6). All the significant friction-based models (MDM of 3000 m) for *B. bufo* selected the number of colonized ponds.

Discussion

The relationship between the functioning of population systems and dispersal of individuals has long been recognized (Andrewartha and Birch 1954; den Boer 1968;

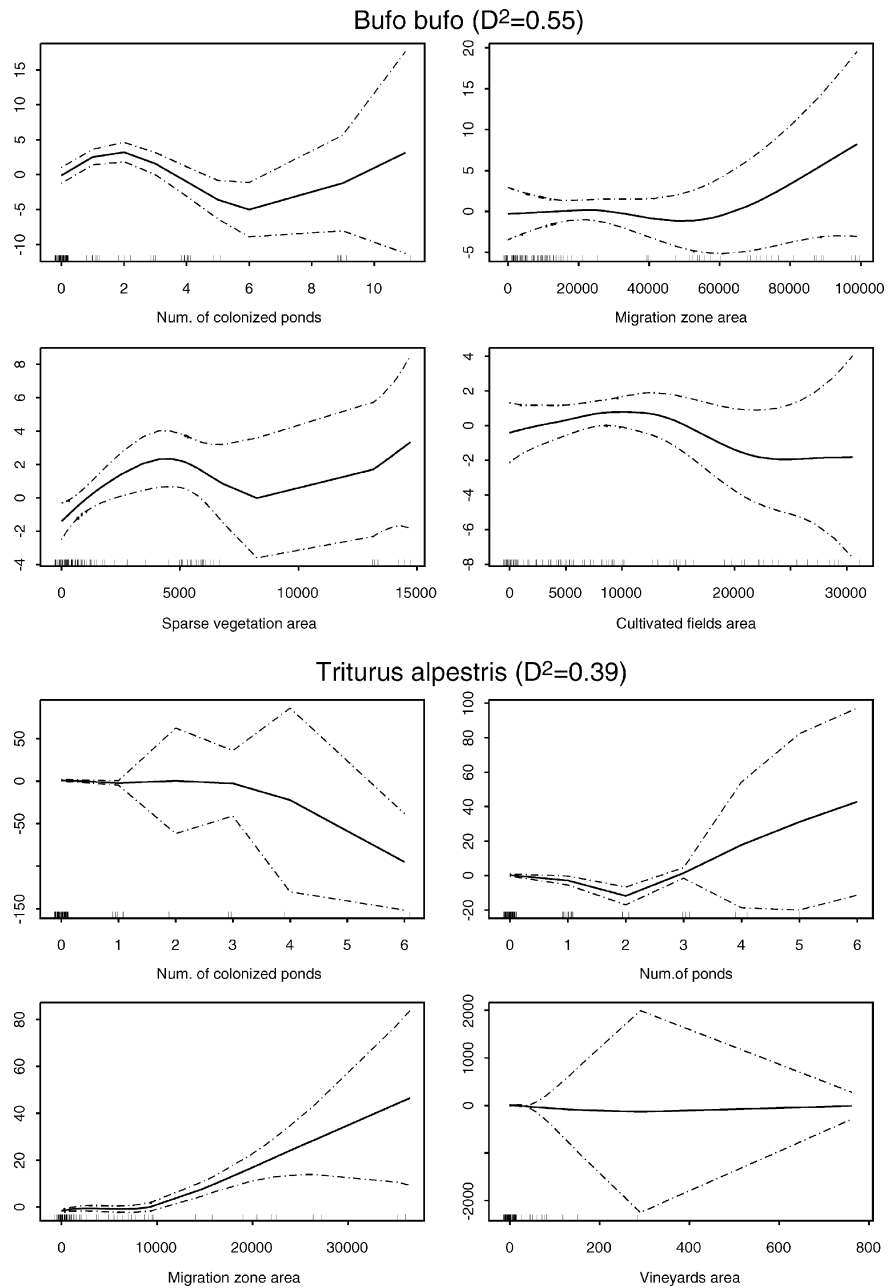


Figure 6. Response curves of the presence/absence of both species to the landscape variables kept in the GAM analysis (center lines). The y-axes are based on partial residuals, and indicate the relative influence of each explanatory variable on the prediction. Distances between the upper and lower curves indicate two times the pointwise standard errors for each curve. Areas are expressed in map units (100 m^2).

Levins, 1969, 1970). Increasing urbanization and habitat alteration make it particularly important to find ways to assess the impact of these changes on the distribution of natural populations. Presence–absence models, together with an appropriate dispersal model, provide the advantage of allowing for predictions of species occurrence either within an existing landuse framework, or under differing scenarios of landscape change. Presence–absence models have previously been used to predict the effect of landscape variables on metapopulation function in amphibians (e.g. Joly et al. 2001). However, these analyses use a simplistic method of assessing the capacity for movement through a heterogeneous landscape without considering the energy costs associated with movement through particular habitat types.

In the current study, prediction of species occurrence was made through the analysis of landscape variables drawn from a friction-based migration zone and compared with a classic circular zone. Under reasonable assumptions of habitat matrix impact on migration movements, our results clearly show the consequences of habitat variability on the shape of the migration zones for both species. In *Bufo bufo*, the best model is composed of landscape variables that were expected to influence population functioning, such as the area of the migration zone and the number of colonized ponds within the migration zone. Toad presence increased with migration zone area, which was expected because this area is directly linked to the amount of suitable habitats in the terrestrial neighborhood of a pond. Toad presence decreased with cultivated-field area. This result was also expected as several studies have shown the avoidance of agriculture land by this species (e.g. Sinsch 1989). The migration model shows that contacts between migration zones of neighboring ponds occur, which should result in higher toad presence under the assumption of rescue effect or extinction–recolonization dynamics (Hanski and Simberloff 1997). However, this assumption is only partly validated, as the response curve of toad presence to the number of colonized ponds does not increase monotonously. This unexpected result should be treated cautiously since ponds may be clumped in forested zones, resulting in spatial autocorrelation.

In *Triturus alpestris*, the area of the migration zone also influenced newt presence positively. However, the area occupied by cultivated fields was not selected by the GAM analysis. Only vineyards seemed to influence newt presence negatively, but high confidence intervals make the interpretation of the response curve to this variable difficult. The output of the migration model shows small migration zones due to a relatively small MDM. As a result, most populations do not appear to be connected with others by adult short-distance migrations. The GAM analysis nevertheless selected the number of colonized ponds within the migration zone as a determining variable, but with a rather negative influence. By contrast, a positive influence of the number of ponds (whether colonized or not) on newt occurrence was detected. These conflicting results may be the result of newt detection failures in the original survey, which are more likely in these animals than in toads because of underwater habits that imply lower detection probability.

Moreover, lack of significant models observed for *T. alpestris* with the small MDM, and the unexpected shape of most of the GAM response curves of the significant models might be due to specific features of the breeding site such as fish presence or vegetation type. Indeed, Joly et al. (2001) have shown that half of the variables predicting newt occurrence were intrinsic to the pond, which could explain some discrepancies in the present results. Newts are more sensitive to fish than toads because toad tadpoles are preserved from fish predation by skin secretions (Griffiths and Denton 1992). The better matching of expected and observed distributions in *B. bufo* than in *T. alpestris* could thus express a lower sensitivity of the former species to pond intrinsic factors such as vegetation type and bank slope (Morand 1996; Joly et al. 2001).

Presence/absence models for *B. bufo* showed higher prediction power when using friction-based migration zones rather than circular zones suggesting the utility of the friction-based approach. Results for *T. alpestris* suggest the importance of connectivity between ponds, but the friction-based approach did not provide higher predictive power than the circular zone approach.

In both species, the quality of the connections between aquatic and terrestrial habitats appeared as a decisive predictor of presence, as shown by previous analyses of landscape influence on amphibian distribution (Joly et al. 2001). The present results agree with these previous findings by using a friction-based approach, and highlight the importance of buffer zones of favorable habitats around ponds for the maintenance of amphibian diversity (Semlitsch 1998).

Direct visualization of migration zones around each breeding site after the application of this technique will show the contacts among actual or potential breeding sites and is thus in itself a way of assessing potential connections among local populations. Although theoretical and empirical efforts remain to be made in building connectivity indices based on this approach, we can foresee practical conservation actions based on the visualization of these potential migration zones. Such an approach could potentially help evaluating the impact of pond destruction on the functioning of a connected network of populations. Similarly, the ecological value of created ponds could be optimized, if the spatial structure of the surrounding pond network is known. The impact of removing or building migration barriers could also be accurately assessed by using such permeability models. The identification of suitable habitat networks could therefore better ensure success of a population reintroduction.

In the same way, this approach would help to identify the ponds that are most isolated, and around which restorations could potentially be undertaken to enhance biological connections with other ponds.

While the utility of a friction-based approach has been demonstrated in this study, the techniques employed here could be further strengthened by the use of empirical data to accurately delineate migration barriers and estimate permeability coefficients. Migration barriers can only be unambiguously detected on such a scale via field-based

studies (e.g. through radio tracking), and this was not possible within the context of the present study. Additionally, while efforts were made to ensure that the permeability estimates employed in this study were reasonable, they were inherently subjective. Few studies have been performed to gauge energy loss during migration, and apparently none have been performed using amphibians. This lack of data could be addressed by using artificial matrices, through which energy loss could be quantified. Such data could greatly enhance the realism of the extent of migration zones through more reliable friction maps, therefore potentially increasing the predictive power of regression models. The high importance of the area of the migration zone in the GAM analysis reinforces the need for reliable data on species migration behavior and on friction costs assigned to the matrix habitat variables.

Due to metapopulation functioning, the distributions of many amphibian species may change frequently even in undisturbed environments (Skelly et al. 1999; Hecnar and M'Closkey 1997). It is probable that the recent increase in urbanization within the State of Geneva may have accentuated such changes by higher fragmentation of suitable habitats. Therefore, the predictive power of our models could be improved with a more consistent survey of potential breeding sites over a larger number of breeding periods.

The small number of studied sites and the low diversity of landscape configurations led the values of the landscape variables to be non-uniformly distributed along their range of variation (e.g. sparse vegetation area for the GAM model of *B. bufo*). Pointwise standard errors were indeed often relatively large in comparison with studies where the number of observations is much higher (e.g. Lehmann et al., this issue). We believe that a similar study with a higher number of breeding sites would increase the predictive power of the friction-based approach.

The scale and the resolution at which this study was made depended on data availability, and on the assumption that matrix permeability in the metapopulation context was relevant within that landscape context. However, it has been recently shown by Johnson et al. (2001) that the predictive power of landscape variables on amphibian occurrence varies according to the spatial scale examined (site-specific, local-scale and broad-scale landscape), and according to the species considered. In this respect, it would be interesting to also take into account site-specific variables and to weigh their respective influence through GAM analysis.

This study was mainly based on the current knowledge of migrations by adult individuals. It ignored the possibility of long-distance migrations or nomadism, the consequences of which are less precisely defined even if they are known to occur. Natal dispersal was also ignored, and remains a 'black box' in the modeling of spatial functioning of amphibian populations because of the inability of marking juvenile individuals and monitoring their movements. The better knowledge of gene flows between populations by more and improved analyses of molecular data will partly compensate such a deficiency and will improve distribution modeling from habitat structures.

Conclusions

This study represents a first attempt at using friction-based computation of potential migration zones as a tool for assessing habitat suitability for viable amphibian population management. This approach proved valuable when combined with GAM for presence/absence prediction. Overall, this study shows the potential of the GIS approach for amphibian conservation strategies. It is important to note that friction values assigned to the landscape variables are key components of the resulting migration zones. Consequently more data on amphibian migration behavior, and especially on juvenile dispersal, are needed to more efficiently assess the factors responsible for the spatial distributions of amphibians. Validation of this approach with other amphibian species would be necessary before they could be confidently used as part of a conservation strategy. Gathering data is a necessary and often time consuming first step in any scientific study, and this is particularly apparent in studies utilizing GIS as an analytical tool. While this study benefited greatly from a state-administered environmental database (most information layers that were required were readily available) lack of adequate spatial data sets (e.g. low resolution) is the key factor limiting further investigations of spatial components affecting amphibian populations in most study regions. However, the increasing availability of such environmental data sets at local and regional scales should trigger further projects with similar approaches. This will allow comparisons between species, regions, and scales, which will ultimately help to build more comprehensive and appropriate amphibian conservation strategies.

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