AMPHIBIAN CONSERVATION IN HUMAN SHAPED ENVIRONMENTS: LANDSCAPE DYNAMICS, HABITAT MODELING AND METAPOPULATION ANALYSES

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ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Suisse
2006

À mes parents

À Elodie

Table of contents

Preface

"A world where people understand, value, and conserve the diversity of life on Earth"

Vision for the future of the international Society for Conservation Biology (www.conbio.org/)

This research is a contribution of the WSL Research Focus "Land Resources Management in Peri-Urban Environments" (www.wsl.ch/programme/periurban). Amphibian data used in this work were for the most part furnished by the Swiss Amphibian and Reptile Conservation Program (www.karch.ch). We also benefited from habitat data collected in summer 2004 during a Master's thesis, which I had the chance to supervise in the laboratory of Ecosystem Management at the EFPL. A second Master's thesis in the context of landscape dynamics, and the collaboration (2003-2005) with the Forest and Landscape Service (Canton Valais, Switzerland) also enlarged the data-set and provided enriching discussions. Data on land cover in the Rhone plain for the years 1850, 1900, 1950 and 2003 were collected in collaboration with the Swiss Federal Institute for Aquatic Science and Technology (www.eawag.ch). The issue of spatial autocorrelation in data was approached and developed in 2004 during a visit to the Spatial Ecology Laboratory at the University of Queensland, Australia (www.uq.edu.au/spatialecology). Metapopulation analyses would have been impossible without the close collaboration with the department of Ecology and Evolution at the University of Lausanne, Switzerland, (http://www.unil.ch/dee).

This thesis comprises a general introduction and conclusion, and five research manuscripts. Manuscripts in **Chapter 3, 4, 6** and **7** are reproduced here in their current state as submitted to the relevant journals, whereas the manuscript presented in **Chapter 5** is in preparation for submission.

Abstract

Global biodiversity is experiencing a worrying decline. Habitats destruction, associated to their degradation and fragmentation are among the greatest causes. Amphibians are particularly interesting because they are more threatened and decline more rapidly than either birds or mammals. In this context, the objective of our research is to improve some methodological approaches and offer practical scientific bases for decision making in landscape management and amphibian conservation. Our study focuses on fragmented Swiss landscapes.

We developed a method that uses land-cover data and expert knowledge to enable a spatially explicit assessment of 1) the temporal changes in the nature conservation value of the landscape and 2) the rehabilitation potential of the landscape. We applied this Geographical Information Systems (GIS) based approach in the Swiss Rhone plain and we used the years 1900 as the reference state. The method constitutes a helpful tool for communication, decision-making and biological conservation management in landscape planning.

Effective and optimal species management strategies can only be formulated after relationships between species distribution and environmental factors have been identified. Concerning amphibians, several approaches exist but they generally suffer from two limitations: 1) the spatial autocorrelation (i.e. the dependency between two observations) in data is rarely explicitly analyzed, even if it may affect the accuracy of species-habitat relationships models. We showed how this spatial autocorrelation can be measured and included in logistic models with the example of the agile frog (*Rana dalmatina*) in north-eastern Switzerland. We used the *Moran's I* and the autologistic model (i.e. a logistic model including a measure of the spatial arrangement of the response variables). We found that if spatial autocorrelation is not considered, then conclusions on species-habitat relationships can be incorrect. 2) The effect of landscape on amphibian occurrence in ponds is often assumed to be equal in every direction (isotropic). However, barriers and inhospitable surfaces may reduce movement patterns and the area around ponds accessible to species. This implies that the ideal circular area has in reality a shape depending on the surrounding landscape. We developed a method to determine the effect of habitat variables on amphibian species distribution, considering physical barriers in their movement around ponds. We studied two amphibian species: the common toad (*Bufo bufo*) and the common frog (*Rana temporaria*) in the Rhone plain. We demonstrated that reducing the boundaries of circular area following barriers, allowed to compute landscape predictors which better explained species distribution. These results suggested that the proposed approach is more pertinent than the traditional circular buffers analysis. Our results stress the necessity to consider barriers and ecological corridors in species distribution models in order to avoid incorrect inferences.

Species distribution models are usually established for a single region. It is generally unknown whether the identified relationships between species distribution and environmental variables can be directly transferred to another geographical area. We examined landscape-level habitat relationships for six amphibian species by measuring correlations with their presence in 655 ponds of five different regions. We analyzed several models by using the information-theoretic approach and the Akaike Information criterion (AIC). For five out of six species, the best models predict that site occupation probability depends on region. Our results suggest that caution is needed when predictions of species occurrence and species management strategies are done using models built in other geographic regions. We also observed that connectivity was generally more explicative than landscape variables. In addition, we found that the spatial scale at which habitat affected species occurrence varied from pond to several km around ponds. Management strategies for amphibian conservation should be conducted taking into account the geographic context, connectivity of ponds and habitat characteristics at multiple spatial scales.

Finally, we demonstrated that the landscape, separating patches in metapopulation models, has to be considered in order to avoid incorrect conclusions on population viability analyses. We explored how patch occupancy is sensitive to Euclidean (shortest) versus a landscape-based distance (least-cost). We found: 1) from a theoretical standpoint, that inter-patch landscape affects patch occupancy; 2) from a practical and conservation standpoints, which patches should be considered in priority for landscape management. The approach was illustrated in the case of two metapopulations of the Yellow-bellied Toad in the Rhone plain.

We applied successfully the developed practical approaches to the case of several amphibian species, but they can doubtlessly be extended to any species functioning on a spatially defined patch basis (e.g. pond, nesting place, den …), structured as a metapopulation and affected by landscape structure during movement. By improving and combining spatially explicit approaches, we are more likely to provide wildlife managers with tools for valuable decision making.

Key words

Conservation planning, landscape dynamics, landscape ecology, amphibians, spatial autocorrelation, generalization of species distribution models, dispersal barriers, patch occupancy metapopulations models, inter-patch ecological distance, least-cost algorithms, Geographic Information Systems.

Résumé

La biodiversité à l'échelle mondiale subit un déclin préoccupant. La destruction des habitats, leur dégradation et fragmentation en sont les principales causes. Les amphibiens méritent une attention particulière puisqu'ils sont plus menacés d'extinction que d'autres taxons tels les oiseaux ou les mammifères. Dans ce contexte, l'objectif de notre recherche est d'améliorer certaines approches méthodologiques et de fournir des bases scientifiques utiles pour la prise de décision dans le domaine de l'aménagement du territoire et de la conservation des amphibiens. Notre étude se concentre sur des paysages fragmentés de Suisse.

Nous avons développé une méthode basée sur l'occupation du sol et sur l'avis d'experts, permettant une évaluation spatiale 1) des changements dans le temps de la valeur du paysage pour la conservation de la nature et 2) du potentiel de réhabilitation du paysage. Nous avons appliqué cette approche au paysage de la Plaine du Rhône et utilisé la situation dans les années 1900 comme état de référence. La méthode constitue un outil de communication et de prise de décision pertinent dans la planification territoriale.

Une gestion efficace des espèces peut être atteinte uniquement si les relations entre la distribution des espèces et les facteurs environnementaux ont été identifiées. Plusieurs approches existent pour les amphibiens, mais elles possèdent deux limites majeures: 1) l'autocorrélation spatiale (i.e. la dépendance entre deux observations) est rarement explicitement analysée, même si elle peut affecter l'exactitude des modèles espèce-habitat. Nous avons montré comment cette autocorrélation spatiale peut être mesurée et intégrée dans un modèle logistique avec l'exemple de la grenouille agile (*Rana dalmatina*) au nord-est de la Suisse. Pour cela nous avons utilisé le *I de Moran* et le modèle autologistique (i.e. un modèle logistique intégrant une mesure de l'arrangement spatial de la variable réponse). Nos résultats confirment que si l'autocorrélation spatiale n'est pas considérée, alors les conclusions sur les relations espèces-habitat peuvent être erronées. 2) L'effet du paysage sur la présence des amphibiens dans leur site de ponte est souvent supposé identique dans toutes les directions (isotrope). Cependant, des barrières ou des surfaces défavorables peuvent réduire l'aire accessible à l'espèce autour du site. Ceci implique que cette aire, idéalement circulaire, est en réalité d'une forme dépendante du paysage qui entoure le site. Nous avons donc développé une méthode pour déterminer l'effet du paysage sur la distribution des amphibiens en considérant les barrières physiques limitant leurs déplacements autour des sites. Nous avons étudié deux espèces d'amphibiens: le crapaud commun (*Bufo bufo*) et la grenouille rousse (*Rana temporaria*) dans la plaine du Rhône. Nos résultats confirment l'hypothèse que d'étudier uniquement le paysage potentiellement accessible aux espèces, permet de calculer des variables paysagères qui expliquent mieux

la distribution des espèces. Ce résultat suggère que la méthode proposée dans cette recherche est plus pertinente que la pratique traditionnelle. Nos résultats mettent l’accent sur la nécessité de considérer les barrières et les corridors écologiques des espèces dans les modèles prédictifs de distribution.

Les modèles de distribution des espèces sont en général établis pour une seule région. Il est donc peu connu, dans quelle mesure la relation entre une espèce et des variables environnementales peut être directement appliquée dans d’autres régions géographiques. Nous avons ainsi analysé les relations espèce-habitat pour six espèces d’amphibiens dans 655 sites de reproduction et dans cinq régions différentes. Nous avons évalué plusieurs modèles en utilisant la théorie de l’information et le Critère d’Information de Akaike (AIC). Pour cinq des six espèces, les meilleurs modèles prédisent des probabilités d’occupation des sites qui sont différentes selon les régions. Ces résultats suggèrent une certaine prudence lorsque les prédictions de distribution et la mise en place de mesure de gestion d’une espèce sont réalisées dans d’autres régions géographiques que celles utilisées pour construire les modèles. Nous avons également observé que la connectivité est généralement un meilleur déterminant de l’occurrence d’une espèce que les variables paysagères. De plus, nous avons montré que l’échelle spatiale à laquelle l’habitat affecte la distribution des espèces varie entre celles du site de reproduction et jusqu’à quelques kilomètres de distance. Les stratégies de gestion des amphibiens devraient donc considérer le contexte géographique, la connectivité des populations et les caractéristiques de l’habitat à plusieurs échelles spatiales.

Enfin, nous avons démontré que le paysage qui sépare les patches dans des modèles de métapopulation doit être considéré afin d’éviter des erreurs dans les analyses de viabilité des populations. Nous avons analysé si la probabilité qu’un patch soit occupé est sensible à la distance Euclidienne (la plus courte) qui le sépare des autres, versus une distance basée sur les caractéristiques du paysage (distance de moindre coût). Nous avons trouvé que 1) d’un point de vue théorique, le paysage entre patches affecte la probabilité d’occupation et que 2) d’un point de vue pratique pour la conservation, notre approche permet d’identifier les patches prioritaires pour des mesures d’aménagement. L’approche a été illustrée avec l’exemple de deux métapopulations du sonneur à ventre jaune (*Bombina variegata*) dans la plaine du Rhône.

Nous avons appliqué les méthodes développées à des espèces d’amphibiens. Il est cependant évident que nos approches peuvent s’appliquer à d’autres espèces qui utilisent des patches spatialement définis tels que des étangs, des nids ou des tanières, qui sont structurés en metapopulation et affectés par la structure du paysage durant leurs déplacements. L’amélioration et combinaison de différentes approches spatiales fournissent des outils essentiels de prises de décision aux gestionnaires de la faune.

Riassunto

La biodiversità a livello mondiale mostra un declino preoccupante. La distruzione degli habitat, il loro degrado e riduzione in frammenti sempre più piccoli e isolati ne sono le cause principali. Gli anfibi meritano un’attenzione particolare visto che rappresentano un gruppo faunistico particolarmente minacciato di estinzione, ancor più di uccelli e mammiferi. In questo contesto, l’obiettivo della nostra ricerca è di migliorare alcuni approcci metodologici e fornire delle basi scientifiche utili alla presa di decisioni nell’ambito della pianificazione territoriale e della conservazione degli anfibi. Il nostro studio si concentra sui paesaggi frammentati in Svizzera.

La metodologia sviluppata nella prima parte della nostra ricerca si fonda sulle informazioni inerenti la copertura del suolo e sul parere di specialisti, e permette una valutazione spaziale 1) dei cambiamenti temporali del valore del paesaggio per la conservazione della natura; e 2) del potenziale di rinaturazione del paesaggio. Questo approccio è stato applicato ai paesaggi della pianura del Rodano, in Vallese, utilizzando la situazione nel 1900 come stato di referenza. La metodologia adottata costituisce un mezzo di comunicazione valido, e fornisce utili elementi nell’ambito dei processi decisionali di pianificazione territoriale.

Una gestione efficace delle specie può essere raggiunta unicamente se le relazioni tra la loro distribuzione sul territorio e i fattori ambientali che la determinano sono stati identificati. Esistono diversi approcci per gli anfibi, ma tutti presentano due importanti limiti: 1) l’autocorrelazione spaziale (la dipendenza tra due osservazioni) è raramente testata in modo esplicito, sebbene possa influenzare l’esattezza dei modelli specie-habitat. In questo studio, abbiamo mostrato come l’autocorrelazione spaziale può essere misurata e integrata in un modello logistico, usando, come esempio, la rana agile (*Rana dalmatina*) al nord-est della Svizzera. Per fare ciò, abbiamo utilizzato l’*I di Moran* e un modello autologistico (un modello logistico che integra una misura della disposizione spaziale della variabile risposta). I nostri risultati confermano che se l’autocorrelazione spaziale non viene considerata, allora le conclusioni sulle relazioni specie-habitat possono essere errate. 2) L’effetto del paesaggio sulla presenza degli anfibi nel loro sito di riproduzione è spesso ipotizzato identico in tutte le direzioni (isotropo). Tuttavia, ostacoli o superfici inospitali situati nei pressi del sito di riproduzione possono ridurre l’area realmente accessibile alla specie. Ciò implica che questa area, normalmente considerata come circolare, possiede in realtà una forma che dipende dal paesaggio circostante il sito. Durante la nostra ricerca, abbiamo quindi sviluppato un metodo per determinare l’effetto del paesaggio sulla distribuzione degli anfibi considerando le strutture che ostacolano il loro movimento attorno ai siti di riproduzione. Abbiamo studiato due specie nella pianura del Rodano: il rospo comune (*Bufo bufo*) e la rana temporaria

(*Rana temporaria*). I nostri risultati confermano l'ipotesi che studiare unicamente il paesaggio realmente accessibile alle specie, permette di calcolare delle variabili paesaggistiche che spiegano meglio la distribuzione delle specie. Questi risultati suggeriscono che la metodologia proposta in questa ricerca è più pertinente dell'approccio tradizionale e mettono l'accento sulla necessità di considerare le barriere e i corridoi ecologici nei modelli predittivi di distribuzione delle specie.

I modelli predittivi di distribuzione delle specie sono generalmente elaborati analizzando una sola regione geografica. È quindi relativamente poco conosciuto se le relazioni tra specie e variabili ambientali possono essere direttamente applicate in altre regioni. Abbiamo pertanto studiato le relazioni specie-habitat per sei specie d'anfibi in 655 siti di riproduzione e 5 diverse regioni in Svizzera. Abbiamo valutato diversi modelli utilizzando la teoria dell'informazione e il Criterio d'Informazione di Akaike (AIC). Per cinque delle sei specie, il migliore modello prevede delle probabilità di occupazione dei siti che sono differenti secondo la regione geografica. Ciò significa che è necessaria una certa prudenza, quando si fanno previsioni sulla distribuzione di una specie e si definiscono misure di gestione basandosi su modelli realizzati in altre regioni rispetto a quella di studio. Abbiamo pure messo in evidenza che, per quanto riguarda la distribuzione delle specie, la connessione tra popolazioni è generalmente un fattore più importante rispetto alle variabili paesaggistiche. Inoltre, abbiamo dimostrato che la scala spaziale per la quale l'habitat esercita un'influenza sulla distribuzione delle specie, è compresa tra il sito di riproduzione fino ad alcuni chilometri di distanza. La strategia di gestione degli anfibi dovrebbe quindi considerare il contesto geografico, la connessione delle popolazioni e le caratteristiche dell'habitat a differenti scale spaziali.

Inoltre, abbiamo dimostrato che il paesaggio che separa due siti di riduzione (patch) nei modelli di metapopolazione deve essere considerato per evitare errori nelle analisi di vitalità delle popolazioni. Abbiamo verificato se la probabilità di occupazione di un sito fosse sensibile alla distanza Euclidea (lineare) che lo separa dagli altri, *versus* una distanza fondata sulle caratteristiche del paesaggio (distanza di minor costo). Abbiamo messo in evidenza che: 1) da un punto di vista teorico, il paesaggio presente tra due siti di riproduzione ne influenza la probabilità di occupazione e che 2) da un punto di vista pratico ai fini della conservazione, il nostro metodo permette di identificare i siti prioritari per delle misure di gestione. L'approccio è stato illustrato con l'esempio di due metapopolazioni di ululone dal ventre giallo (*Bombina variegata*) nella pianura del Rodano.

Sebbene le metodologie sviluppate nella presente ricerca siano state applicate unicamente agli anfibi, i nostri approcci possono essere estesi ad altre specie che utilizzano dei siti spazialmente definiti (come stagni, nidi o tane), che sono strutturate in metapopolazioni e i cui spostamenti sono influenzati dalla struttura del paesaggio. Il miglioramento e l'impiego combinato di diversi approcci spaziali fornisce ai gestori della fauna, e del territorio in genere, strumenti essenziali per la presa di decisioni.

Chapter 1

Introduction

Biodiversity decline

Global biodiversity is experiencing a worrying decline. The 2004 update of the IUCN Red List (Baillie et al. 2004) assessed the threat of extinction for 38047 species including vertebrates, invertebrates, plants, and fungi. The results were clear: **15589 species (41.0%) are threatened with extinction (listed as Critically Endangered, Endangered or Vulnerable)**, 844 (2.2%) are Extinct or Extinct in the Wild, 3700 (9.7%) are listed as Near Threatened, 3580 (9.4%) are Data Deficient, and 14334 (37.7%) are in the Least Concern category[1]. Only a very small proportion (2.5%) of the world's described species has been evaluated, which in addition indicates that the current list underestimates the real number of threatened species. In Switzerland, 14 (70%) out of the 20 native amphibian species are listed as threatened on the Red List (Schmidt and Zumbach 2005).

Worldwide, the 15589 species threatened with extinction included 12% of all bird species, 23% of all mammal species and 32% of all amphibian species (i.e. one in every eight birds, one in every four mammals, and one in every three amphibians) (Baillie et al. 2004). Moreover, the world’s list of extinctions continues to increase. The 2004 IUCN Red List contains 844 documented extinctions since 1500 AD. Over the past 20 years (1984-2004), 27 documented extinctions or extinctions in the wild have occurred. But these numbers certainly underestimate the true number of extinctions due to very incomplete and uneven sampling, both geographically and

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[1] A taxon is 1) Extinct when there is no reasonable doubt that the last individual has died; 2) Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range; 3) Critically Endangered when it facing an extremely high risk of extinction in the wild; 4) Endangered when it facing a very high risk of extinction in the wild; 5) Vulnerable when it facing a high risk of extinction in the wild. 6) Near Threatened when it is likely to qualify for a threatened category in the near future; 7) Data Deficient when there is inadequate information to make a direct, or indirect, assessment. The criteria used in these evaluations are presented by IUCN (2001).

taxonomically, and due to the fact that proving that a species has become extinct can take years to decades (Baillie et al. 2004).

Habitat destruction and associated degradation and fragmentation are the greatest threats to assessed terrestrial species (Baillie et al. 2004)**.** Habitat loss appears to be by far the most pervasive threat, impacting 86% of threatened birds, 86% of threatened mammals and 88% of threatened amphibians. Over-exploitation, invasive alien species, pollution and disease are other threats. Incidental mortality, human disturbance and persecution have so far had less impact in terms of the total numbers of species affected, but they can be serious for some susceptible groups. The impact and expected consequences of climate change have only recently been analyzed and remain uncertain. A recent work investigating the potential consequences of climate change across a range of global habitats suggested the extinction of 15-37% of the species in their sample (Thomas et al. 2004). However, it appears certain that habitat loss will remain a dominant threat, as there is no sign that human transformation of the landscape is slowing (Balmford and Bond 2005). Reversing this tendency is a worldwide priority challenge if we want to preserve the biodiversity of our planet (Dobson et al. 1997, Knop et al. 2006, Robinson 2006).

A changing landscape due to human actions

The context

Habitat destruction, degradation and fragmentation is often the result of human activities and it appears more and more evident that natural former ecosystems are undergoing changes which are mostly negative, ominously large in scale and accelerating (Balmford and Bond 2005). This is not a surprising statement if we look at the amount of human made landscapes in the world. **Urbanization, agriculture rationalization and deforestation are among the main drivers of this worrying situation** (Pimm and Raven 2000, Tilman et al. 1994, Stuart et al. 2004).

In this context, the research field of landscape dynamics has gained increasing interest. A landscape (i.e. *the area that is spatially heterogeneous in at least one factor of interest"*, Turner et al. (2001, p. 3)) can be described by its composition (the number or abundance of factors of interest) and its configuration (the spatial arrangement of factors of interest), which determine the structure of the landscape

(Forman and Godron 1986). The “factor of interest” can be for example land occupation classes. **In addition to spatial heterogeneities at time *t*, a landscape has also to be characterized by its temporal dynamics** (Forman and Godron 1986). These temporal dynamics are driven by natural (e.g. volcanic eruption, river dynamics) or anthropogenic factors (e.g. deforestation, urbanization) called driving forces. Driving forces are the forces that cause observed landscape changes (Burgi et al. 2004). Driving forces determine landscape dynamics.

In recent years, numerous case studies have focused on several aspects of landscape dynamics: methodological (Kienast 1993, Cousins 2001, Petit and Lambin. 2002a), description of changes of landscape structure (Olsson et al. 2000, Lu et al. 2003, Bender et al. 2005, Soini 2005), consequences of these changes on biodiversity (Black et al. 1998, Parody et al. 2001, Turner et al 2003) and on fire occurrence (Moreira et al. 2001). Some works investigated the dynamics of specific ecosystems like grassland (Partel et al. 1999, Cousins et al. 2002), alluvial (Jungwirth et al. 2002, Hohensinner et al. 2004) and forest (Bürgi and Turner 2002, Bürgi and Schuler 2003). Other works investigated driving factors of changes (Poudevigne et al. 1997, Pan et al. 1999, Petit and Lambin. 2002b, Hietel et al. 2004, Bürgi et al. 2004). The large number of studies in various contexts testifies to the interest and the large potential applications of such research. **In particular, the utilization of historical data in restoration or rehabilitation ecology has become increasingly interesting in recent years** (Egan and Howell 2005, **this thesis: Chapter 3**).

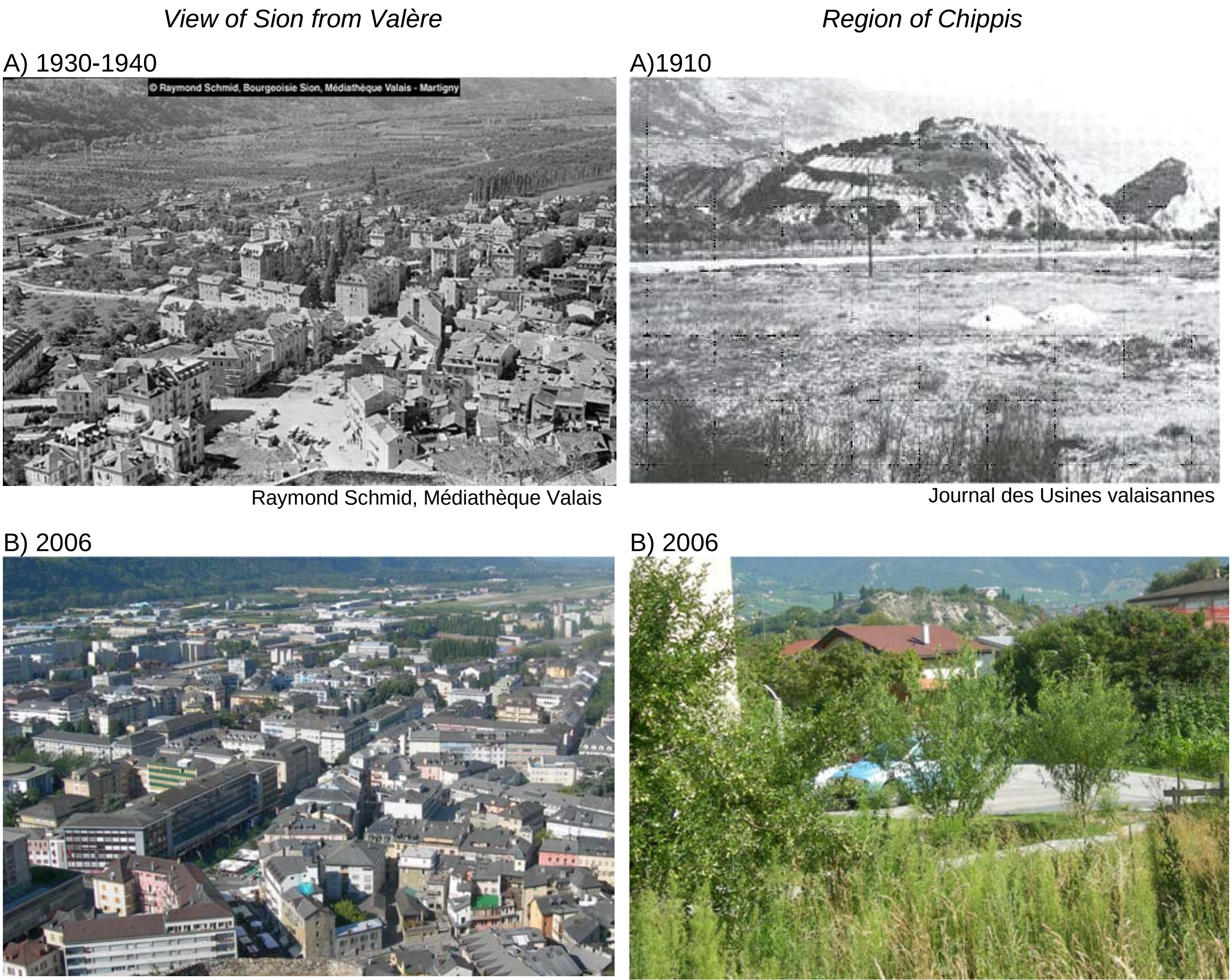
In the next section, we present the landscape changes in a Swiss fragmented landscape (The Rhone plain) as an introductive example of the ecologically negative effects of anthropogenic landscape changes and to familiarize the reader with some commonly used methodological approaches in landscape dynamic studies. This section is based on Paulmier (2004a,b), Zanini (2005) and Zanini et al. (submitted).

Habitat loss and degradation: the example of the Rhone plain in Switzerland

In Switzerland, as in other industrialized countries, the landscape has experienced important changes during last decades, which have negatively affected biodiversity (Broggi and Schlegel 1990, 1998). In the plain regions, the most evident transformation is the increase of the urban area to the detriment of agricultural fields. Recent studies of land cover changes between the periods 1979/85 and 1992/97 revealed that the urban area has increased by 327 km^2 (+13.3%) and in 1992/97 covered 6.8% of the surface area of Switzerland (http://www.bfs.admin.ch/). This is equivalent to the construction of 0.9 m^2 of urban area per second.

The Swiss Rhone plain, in Valais, is a clear and emblematic example of this landscape transformation and natural habitat destruction due to human activity. In this region (240 km^2: between Brig and the Lake Geneva, see Figure 1, § 3), we described the landscape dynamics, in term of land cover changes, between 1850 and 2003, in order to present an objective picture of the evolution of the landscape from a near-natural state to a highly anthropogenic state (Paulmier 2004a,b, Zanini 2005, Zanini et al. submitted). The land cover data were digitalized on the basis of topographic maps (for a comprehensive description of data used in this study see § 3 and Zanini et al. submitted).

Landscape changes are already evident after a simple visual comparison of pictures and topographic maps (Figure 1 and Figure 2).



View of Sion from Valère

Region of Chippis

A) 1930-1940

A)1910

Raymond Schmid, Médiathèque Valais

Journal des Usines valaisannes

B) 2006

B) 2006

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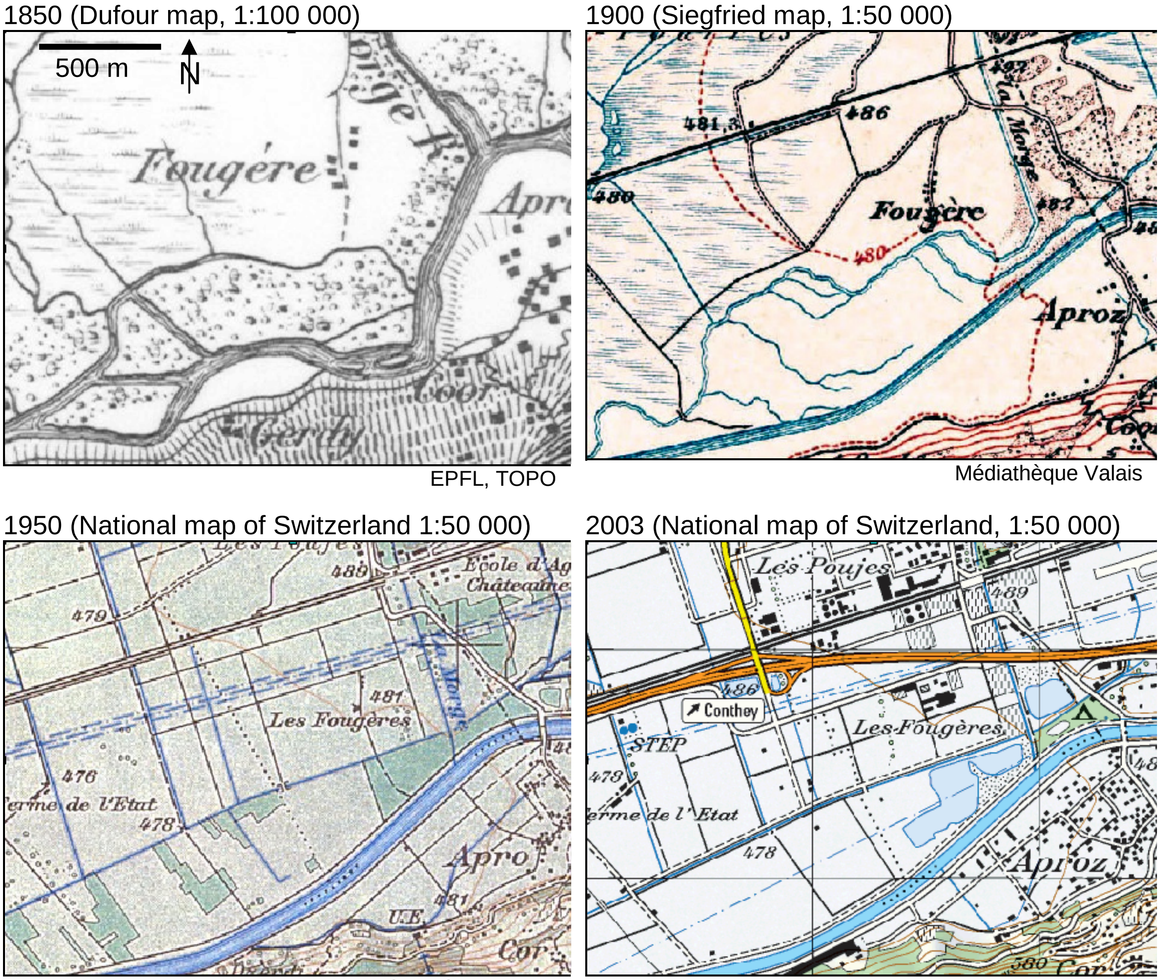
***Figure 1**. Pictures showing some of the landscape changes in the Rhone plain (Valais, Switzerland) during the 20th century.*


1850 (Dufour map, 1:100 000)

1900 (Siegfried map, 1:50 000)

EPFL, TOPO

Médiathèque Valais

1950 (National map of Switzerland 1:50 000)

2003 (National map of Switzerland, 1:50 000)

Médiathèque Valais

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***Figure 2**. Topographic maps illustrating landscape changes between 1850 and 2003 in the region of Aproz (Rhône plain, Switzerland). The former alluvial area and river dynamics have been completely destroyed. Fragmentation increases, for example due to the construction of the highway (in orange) and the development of urbanization.*

This visual examination is a simple and only qualitative estimation of land cover changes. It is possible to present a more accurate and quantitative descriptions of the changes by digitalize topographic maps and using GIS-based analyses (Figure 3 and Table 1). This allows assessing clearly that formerly extensive natural habitats (forest, wetland and alluvial areas) have suffered from a fundamental reduction of their surface and an important fragmentation during the last 150 years. In the region of Martigny, most of these changes took place before the years 1950 (Figure 3). This period was characterized by the Rhone river canalization and important draining work (Wallis 2000). The first systematic river correction, which was carried out in the late 19th century, almost completely destroyed the alluvial river-floodplain system, which covered 10.9% of the plain in 1850 and only 1.6% in 1900 (Table 1). Wetlands covered 8.2% of the plain in 1850 and only 1.3% in 2003, while forested areas were reduced by almost half (Table 1). Furthermore, we observed a significant increase in urban area, in particular in the second half of the 20th century (3.6% in 1950 and 13.8% in 2003). The agricultural zone continuously increased in its area until the middle of the 20th century, before losing a part of its surface during the last 50 years. As a result, the Rhone plain is today a human-shaped landscape dominated by intensively exploited agricultural land (76.6%) and significant urbanization, in which the former natural ecosystems have almost completely disappeared (Table 1).

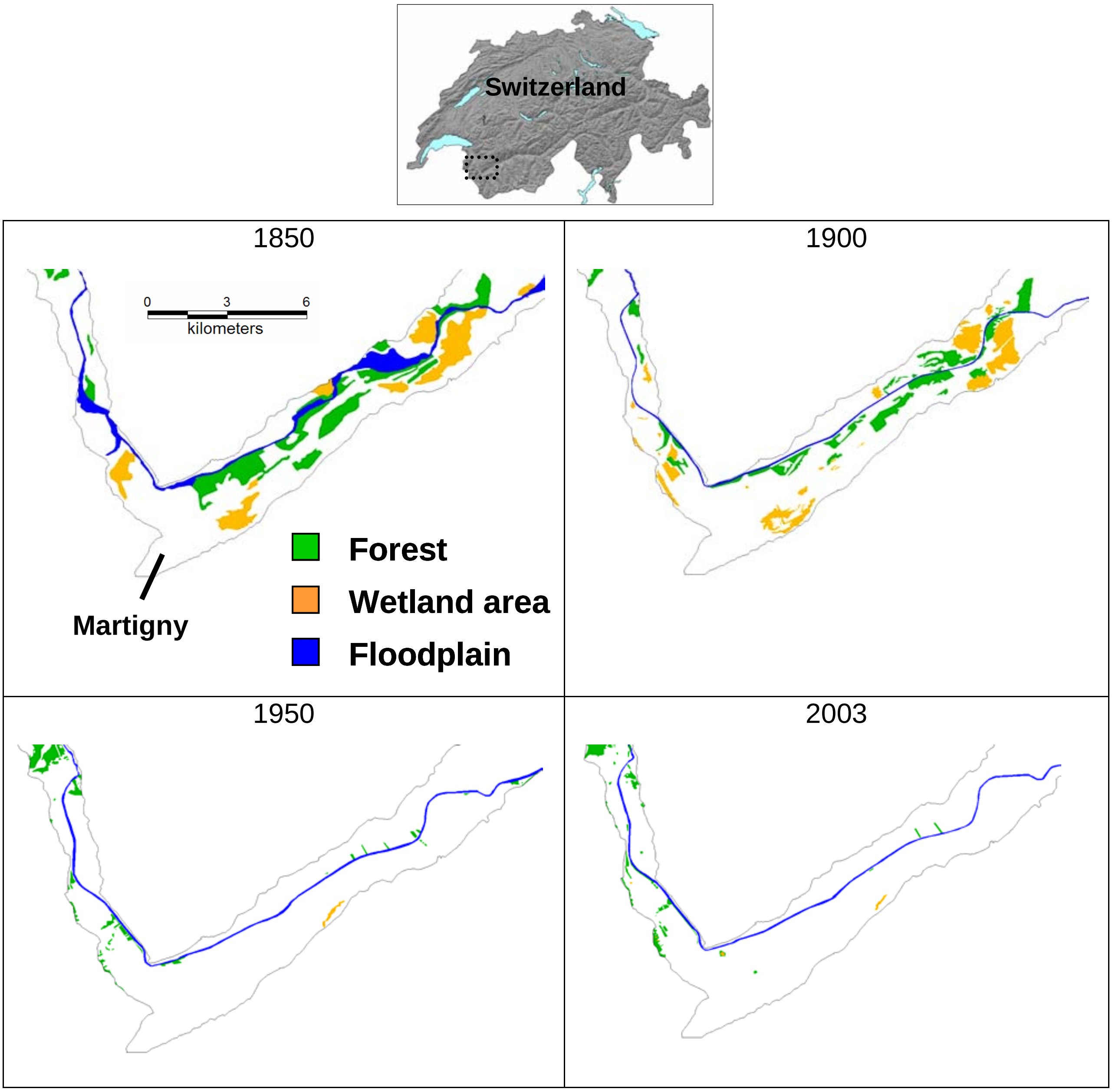


Figure 3. *Maps of temporal evolution of natural areas (forest, wetland and floodplain) in the region of Martigny (Rhone Plain, Switzerland). Since 1900, the Rhone River has been canalized and the floodplain area completely destroyed (blue line).*

***Table 1**. Changes in landscape composition in the Rhone plain (Switzerland) since 1850.*

Land cover		**Composition for years**				**Changes since 1850 (%)**
		1850	**1900**	**1950**	**2003**	
Forest	ha	2391	2081	1100	1248	- 48
	%	9.9	8.7	4.6	5.2	
Wetland	ha	1971	1472	354	305	- 85
	%	8.2	6.1	1.5	1.3	
Floodplain, river Rhone	ha	2614	396	365	133	- 95
	%	10.9	1.6	1.5	0.6	
Rhone, canalized	ha	0	577	718	578	-
	%	0.0	2.4	3.0	2.4	
Floodplain tributary	ha	15	32	1	0	- 100
	%	0.1	0.1	0.0	0.0	
Hill	ha	44	40	27	26	- 41
	%	0.2	0.2	0.1	0.1	
Dune	ha	15	8	1	0	- 100
	%	15	8	1	0	
Urban area	ha	443	327	866	3320	+ 649
	%	1.8	1.4	3.6	13.8	
Agricultural zone	ha	16541	19101	20602	18424	+ 11
	%	68.8	79.5	85.7	76.6	

Important structural changes in the landscape of the Rhone plain were also observed (Table 2). During the past 100 years, the number of forest patches has increased by approximately 2.6 times (175%) and their average surface has been reduced by 78% (Table 2). This means that patches of forest are increasingly isolated and small. The number of wetland patches and their average surface have both decreased (66% and 40%, respectively). Inversely, the number of urban area patches increased by 2.2 times (122%) and their average surface by 4.4 times (344%). This confirms an expansion of urbanization; agglomerations have become bigger and new urban areas have appeared. From Table 2, we can also see a change in the trends of wetland transformation. In the first part of the last century, both the number and the mean area of patches decreased. However, between 1950 and 2003, only the number of patch continued to decrease, while the mean area increased. This may be explained by the gravel mining exploitation in the Rhone plain, which created large pools in recent decades.

***Table 2**. Changes in the number of patches (NP) and their mean size (ha) in the Rhone plain (Switzerland) since 1900.*

Land cover	**1900**		**1950**		**2003**		**Changes since 1900 (%)**	
	NP	**ha**	**NP**	**ha**	**NP**	**ha**	**NP**	**ha**
Forest	127	16.4	266	4.1	348	3.6	+175	-78
Wetland	88	16.7	38	9.3	30	10.2	-66	-40
Floodplain, river Rhone	10	39.6	2	182.3	3	44.3	-70	+12
Rhone, canalized	4	144.2	3	239.4	3	192.5	-25	+34
Floodplain tributary	5	6.5	3	0.2	0	0.0	-100	-100
Hill	41	1.0	18	1.5	19	1.3	-54	+30
Dune	19	0.4	2	0.5	0	0.0	-100	-100
Urban area	210	1.6	168	5.2	466	7.1	+122	+344
Agricultural zone	121	157.9	88	233.4	171	107.7	+41	-32
Total	625	38.5	588	40.9	1040	23.1	+60	- 40

Transition matrices (Cousins 2001, Moreira et al. 2001, Lu et al. 2003) explain the nature of the observed changes. In other words, the amount of land cover class *i* that has been converted into land cover class *j* between two temporal states. In the Rhone Plain, the extension and intensification of the agriculture and urbanization processes account for most changes since 1900 (Table 3). Most of the wetland area (86%) was converted into agricultural fields between 1900 and 1950. Then, between 1950 and 2003, 12.1% of wetland turned into forest areas, indicating the banking of water ponds due to a natural succession of vegetation. The forested area has been converted into agricultural fields (65.2%), essentially between 1900 and 1950 (Table 3). Finally, agricultural areas have lost 15% of their surface in the last 50 years, due to urban development. We note that in 1900 the floodplain area had already been destroyed and thus this important landscape transformation is not presented in Table 3.

The description of landscape dynamics can objectively quantify the evolution over time of human action on the landscape. This **allows decision makers, landscape planners, conservation biologists and the local population to evaluate landscape changes and thus become aware of the potential consequences for biodiversity and human life quality** (Luyet 2005).

***Table 3**. Matrix of land cover transitions (%) in the Rhone Plain (Switzerland) since 1900 (in bold proportion >10%).*

Land cover

1900 to 1950

	F	**w**	**FR**	**CR**	**FT**	**H**	**D**	**U**	**AZ**
Forest (F)	**26.5**	1.8	0.6	4.4	0	0	0	0.2	**65.2**
Wetland (w)	2.0	9.7	0	0	0	0	0	0.4	**86.8**
Floodplain, river Rhone (FR)	**13.4**	0.5	**64.5**	0.4	0	0	0	0.6	**20.5**
Rhone, canalized (CR)	1.4	0.2	0	**53.2**	0	0	0	0.1	**45.0**
Floodplain tributary (FT)	**23.2**	0	0	7.6	2.1	0	0	0	**67.1**
Hill (H)	2.3	0.4	4.2	0.2	0	**29.8**	0	1.0	**62.1**
Dune (D)	0	**20.4**	0	3.2	0	0	1.7	0	**74.7**
Urban area (U)	0	0	0	0	0	0	0	**73.3**	**26.7**
Agricultural zone (AZ)	2.4	0.9	0.5	1.6	0	0.1	0	3.2	**91.2**

1950 to 2003

	F	**w**	**FR**	**CR**	**FT**	**H**	**D**	**U**	**AZ**
Forest (F)	**59.0**	5.0	0.3	0.5	0	0.1	0	1.8	**35.9**
Wetland (w)	**12.1**	**48.7**	0	0.2	0	0	0	0.7	**42.8**
Floodplain, river Rhone (FR)	**31.9**	0	**32.1**	0.1	0	1.0	0	1.9	**33.0**
Rhone, canalized (CR)	5.1	0	0.1	**60.0**	0	0	0	0.8	**34.0**
Floodplain tributary (FT)	0	0	0	0	0	0	0	0	**100.0**
Hill (H)	1.9	0	0	0	0	**37.6**	0	6.1	**54.4**
Dune (D)	0	0	0	0	0	0	0	0	**100.0**
Urban area (U)	0.1	0	0	0.1	0	0	0	**87.2**	**12.6**
Agricultural zone (AZ)	2.0	0.4	0.1	0.7	0	0.1	0	**12.3**	**84.7**

1900 to 2003

	F	**w**	**FR**	**CR**	**FT**	**H**	**D**	**U**	**AZ**
Forest (F)	**22.4**	2.6	0	2.7	0	0	0	2.7	**69.5**
Wetland (w)	4.6	6.9	0	0	0	0	0	6.6	**81.8**
Floodplain, river Rhone (FR)	**36.5**	0.1	**24.5**	0.2	0	0.1	0	1.2	**37.4**
Rhone, canalized (CR)	2.6	0.1	0	**59.1**	0	0	0	0.7	**37.5**
Floodplain tributary (FT)	**10.8**	0.8	0	6.5	0	0	0	0	**81.9**
Hill (H)	1.8	0	0	0	0	**29.3**	0	9.1	**59.7**
Dune (D)	0	9.5	0	0	0	0	0	3.5	**87.0**
Urban area (U)	0.2	0	0	0	0	0	0	**86.4**	**13.4**
Agricultural zone (AZ)	2.9	0.8	0.2	0.9	0	0.1	0	**15.0**	**80.1**

Why are amphibians so threatened with extinction?

In the context of global biodiversity decline, amphibians are of particular interest because they are more threatened and are declining more rapidly than either birds or mammals (Baillie et al. 2004, Stuart et al. 2004). Even considering that sensitivity may be different among species, a global negative response and worrying worldwide decline has recently been reported (Alford and Richards 1999, Houlahan et al. 2000). At least 2468 amphibian species (43.2%) are experiencing some form of population decrease, whereas only 28 (0.5%) are increasing and 1552 (27.2%) are stable; 1661 (29.1%) species have an unknown trend (Stuart et al. 2004). These statistics have triggered large-scale concern about amphibian conservation (Beebee 1996, Semlitsch 2003).

Amphibians are extremely sensitive to environmental stressors due to their permeable skin and their dual life cycle (aquatic and terrestrial). Hence, a large set of factors affecting the amphibian population have been identified on a global scale (such as climate change or increased UV-B exposure) and also on a more local scale, involving factors such as habitat destruction, agrochemicals and chemical pollution, introduced species, human exploitation and disease (reviewed by Alford and Richards 1999, Blaustein and Kiesecker 2002, Collins and Storfer 2003, Beebee and Griffiths 2005).

However, habitat destruction and the associated degradation and fragmentation seem to be the primary cause of amphibian decline and extinction (Dodd and Smith 2003, Stuart et al. 2004, Cushman 2006). Although several studies have investigated amphibian autecology (i.e. the biological relationship between an individual organism or an individual species and its environment) and the effect of habitat loss and fragmentation on amphibian distribution (e.g. Fahrig et al. 1995, Vos and Chardon 1998, Pope et al. 2000, Joly et al. 2001, Houlahan and Findlay 2003, Pellet et al. 2004b, Van Buskirk 2005, Appendix 1) we still lack the knowledge necessary for effective conservation strategies (Cushman 2006).

For this thesis (Chapters 4, 5 and 6) we studied amphibian autoecology and improved some methodological and statistical approaches in order to better understand the determinants of amphibian distribution and persistence in a given landscape.

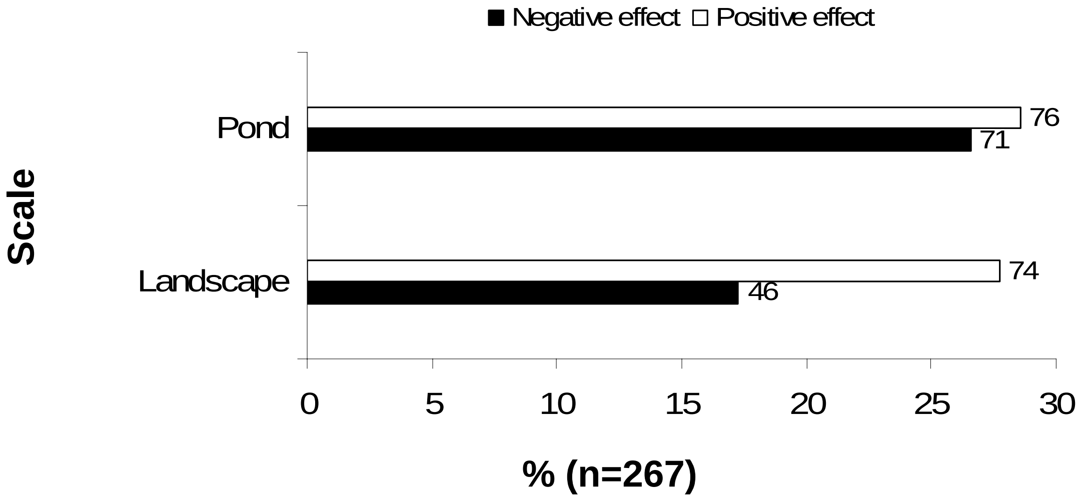
The effect of ponds and landscape characteristics on amphibian distribution

Amphibians often use aquatic and terrestrial habitats. The first provides the habitat for both breeding and larval development, and the second for juvenile and adult foraging, hibernation and estivation. The quality of breeding sites has long been identified as central for the preservation of local populations. Nevertheless, restricting habitat selection studies to pond-scale determinants has been shown to be insufficient because there is evidence that landscape-scale determinants (up to several km from breeding sites) can also influence the distribution of amphibian species (e.g. Vos and Stumpel 1995, Mazerolle and Villard 1999, Pope et al. 2000, Johnson et al. 2002, Houlahan and Findlay 2003, Van Buskirk 2005). For example, Houlahan and Findlay (2003), Gibbs et al. (2005) and Price et al. (2005) reported that land-use effects peaked at distances of several kilometers from breeding ponds. This suggests a regional effect on species distribution. Others reported that far smaller distances were important (less than 1000 m; e.g. Porej et al. 2004, Herrmann et al. 2005, Mazerolle et al. 2005). Recently, Loman and Lardner (2006), found that in experimental conditions the water quality of farmland ponds in Southern Sweden have no effect on the reproductive success of two frog species. Their results indicate that other factors (i.e. the terrestrial habitat quality and the metapopulation structure) have to be considered in order to understand the drivers of distributional patters.

Based on a review of 27 recent papers (for more details see Appendix 1) dealing with the issue of amphibian habitat selection, we found that approximately half of the significant effects on species distribution concerns landscape scale factors (i.e. variables computed in a radius >30 m from ponds, Figure 4, A). At this scale, factors more frequently studied and having a significant effect on species distribution are those related with four land uses (forest, urban, road and agricultural cover) and connectivity of populations (i.e. the number and occupancy of surrounding ponds) (Figure 4, B). Clear prevalence of positive association has been found for forest and connectivity, while urban and road factors had essentially a negative effect.

The multi-scale effect of habitat variables on amphibian distribution has a central importance in conservation. Species have to be managed at the appropriate large spatial scale (Semlitsch 2000, Van Buskirk 2005) in order to avoid inappropriate conservation measures.

A) Scale of predictor effects



B) Type of predictors used to describe the landscape scale

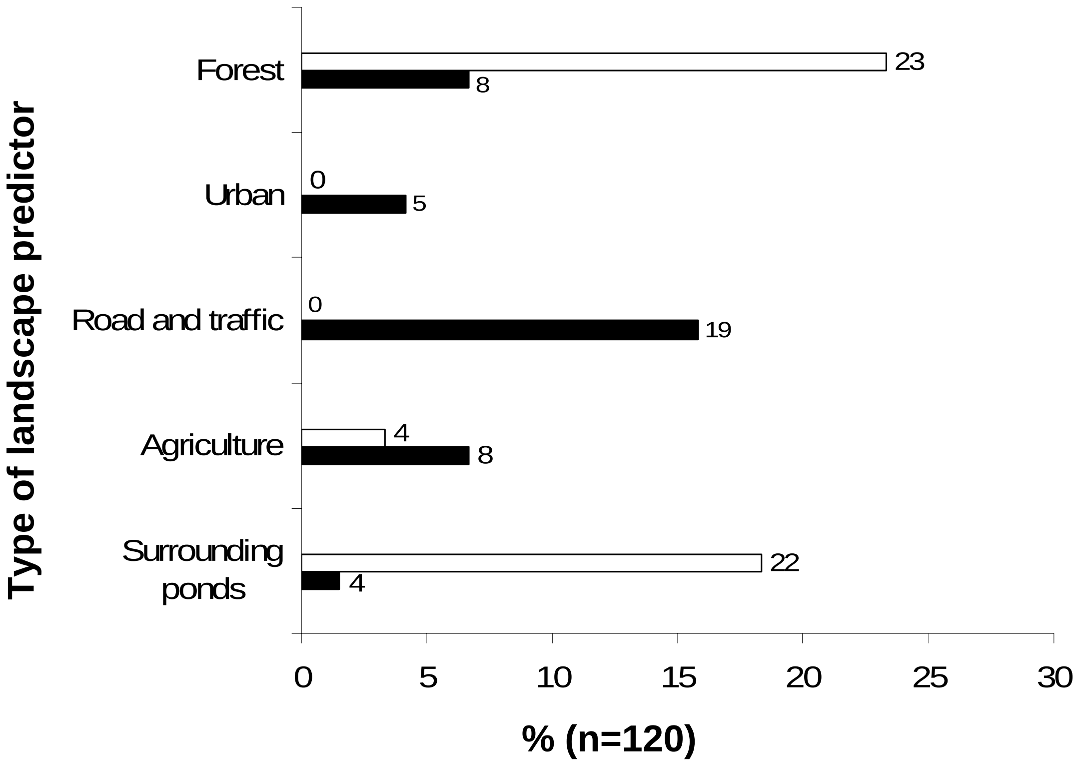


Figure 4. *Proportion and number of positive and negative predictor effects based on a review 27 recent articles (Appendix 1). The review considers 46 species and 267 predictor effects (n): 147 at pond scale and 120 and landscape scale. A) Scale at which predictors have an effect; "landscape scale" refers to the area at >30m from the focal pond. B) Type of predictors used to describe the landscape scale; "surrounding ponds" refers to the amount and occupancy of ponds in the area surrounding the focal pond. For more details see Appendix 1.*

In addition to the increasing and recognized importance of landscape scale determinants of amphibian distribution (Cushman 2006), we identify three additional issues in this research which have received scarce attention in herpetological research (Table 4). The first issue (**Chapter 4**) focus on **statistical models of**

species–habitat relationship. When data are not independent, then regression residuals may be autocorrelated, which violates the assumption of independence of errors for classical statistical tests (i.e. ANOVA). Thus, incorrect inference can result from models because of the incorrect estimation of the number of degree of freedom (Legendre 1993). Computed statistical tests with dependent variables are generally too often declared significant under the null hypothesis (Type I error), the magnitude of habitat effects tends to be overestimated and the relative importance of different habitat variables can shift (Legendre and Fortin 1989, Legendre 1993, Borcard et al. 1992, Gumpertz et al. 1997, Lennon 2000, Lichstein et al. 2002, Legendre et al. 2002). Although it is frequently observed in data, spatial autocorrelation is still rarely assessed and considered in models of amphibian habitat relationships (Klute et al. 2002, Knapp et al. 2003). In the case of amphibians, we found that 18 (69.2%) out of 26 recent studies did not test or measure autocorrelation in data (Table 4 A).

The second issue (**Chapter 5**) is the **spatial generalization of the amphibian-habitat relationship.** Usually, these statistical relationships are used to make recommendations about habitat management for threatened species in the region studied (e.g. Pellet et al. 2004b). However, one desirable feature of such statistical models is their applicability in other, separate regions. The important question is whether the results of one study on one species in one region can be transferred to the same species in a different region. This question has only rarely been addressed (Graf et al 2006, Menendez and Thomas 2006), but the implications for effective species conservation are important. In the case of amphibians we found that only three studies (Knutson et al (1999), Lehtinen et al. (1999), Johansson et al. (2005)) analyzed the autoecology of species in different regions. These studies detected a regional effect of local and landscape factors suggesting a region-by-factor interaction. Nevertheless, most of the reviewed articles (24 out of 27, 88.9%) only investigate one single region (Table 4 B).

The third issue (**Chapter 6**) concerns the **shape of the sampling area around ponds within which landscape variables are extracted**. The common practice is to use concentric disks (Table 4 C) and assumes that the landscape has an isotropic effect on the species' presence, so that species are supposed to be affected by a particular landscape element equally in every direction from a given pond. However, it is likely that frictions in the landscape, such as barriers or inhospitable surfaces, reduce movement patterns (e.g. Marsh et al. 2005, Gibbs 1998) and reshape the ideal circular surface into a non-circular form reflecting the actual use of the terrestrial landscape by amphibians (Ray et al. 2002). In **Chapter 6**, we consider non-circular buffers shaped by barriers to amphibian movement.

***Table 4**. Synthesis of the review of 27 recent articles (Appendix 1) analyzing predictors of amphibian distribution and regarding the issue developed in **Chapter 4** (A), **Chapter 5** (B) and **Chapter 6** (C) of this thesis.*

Issue	**References**	**Number of articles**	**%**
A) Autocorrelation in data			
Not tested	Vos and Stumpel (1995), Vos and Chardon (1998), Knutson et al (1999), Kolozsvary and Swihart (1999), Pope et al. (2000), Carr and Fahrig (2001), Findlay et al. (2001), Hazell et al. (2001), Joly et al. (2001), Guerry and Hunter (2002), Hamer et al. (2002), Ray et al. (2002), Beja and Alcazer (2003), Bradford et al. (2003), Jansen and Healey (2003), Martin and McComb (2003), Knutson et al. (2004), Pellet et al (2004a), Weyrauch and Grubb (2004)	18	69.2
Correlogram analyses (Moran's I)	Scribner et al. (2001), Houlahan and Findlay (2003), Johansson et al. (2005), Denoel and Lehmann (2006)	4	15.4
Mantel test!	Mazerolle et al. (2005)	1	3.8
Durbin-Watson test	Lehtinen et al. (1999)	1	3.8
Occupied ponds in neighborhood§	Pellet et al (2004b)	1	3.8
Autologistic model	Knapp et al. (2003)	1	3.8
B) Geographic variation of landscape effect			
Not assessed	Vos and Stumpel (1995), Vos and Chardon (1998), Kolozsvary and Swihart (1999), Pope et al. (2000), Carr and Fahrig (2001), Findlay et al. (2001), Hazell et al. (2001), Joly et al. (2001), Scribner et al. (2001), Guerry and Hunter (2002), Hamer et al. (2002), Ray et al. (2002), Beja and Alcazer (2003), Bradford et al. (2003), Houlahan and Findlay (2003), Jansen and Healey (2003), Knapp et al. (2003), Martin and McComb (2003), Knutson et al. (2004), Pellet et al (2004a,b), Weyrauch and Grubb (2004), Mazerolle et al. (2005), Denoel and Lehmann (2006)	24	88.9
Assessed and found!	Knutson et al (1999), Lehtinen et al. (1999), Johansson et al. (2005)	3	11.1
Assessed and not found	-	0	0.0
C) Area around focal pond within the landscape is studied			
Concentric disks	Vos and Stumpel (1995), Vos and Chardon (1998), Kolozsvary and Swihart (1999), Knutson et al (1999), Lehtinen et al. (1999), Pope et al. (2000), Carr and Fahrig (2001), Findlay et al. (2001), Hazell et al. (2001), Joly et al. (2001), Scribner et al. (2001), Guerry and Hunter (2002), Hamer et al. (2002), Beja and Alcazer (2003), Bradford et al. (2003), Houlahan and Findlay (2003), Jansen and Healey (2003), Knapp et al. (2003), Martin and McComb (2003), Knutson et al. (2004), Pellet et al (2004a,b), Weyrauch and Grubb (2004), Mazerolle et al. (2005), Denoel and Lehmann (2006)	24	92.3
Squared buffer	Johansson et al. (2005)	1	3.8
Friction-based buffer	Ray et al. (2002)	1	3.8

! Mantel test on the geographic distance between occupied ponds
§ Effect on occupancy of the number and the density of occupied ponds in various concentric disks from focal pond
! If the effect of at least one of the variables studied showed a geographic variation

Metapopulation structure and inter-patch distance

In simple terms, a metapopulation is a collection of partially isolated populations connected by occasionally dispersing individuals, whereby each population exists with a substantial extinction probability (Hanski 1999). Thus, long-term persistence of the species in a given landscape occurs only at the level of the metapopulation. Amphibians are suitable models for metapopulation studies because populations are generally organized in spatially discrete breeding sites which are straightforwardly considered as a pond-as-patch based framework (Sjogre-Gulve 1994, Marsh and Trenham 2001, but see Smith and Green 2005).

Ecologists and conservation biologists have developed metapopulation theories to predict populations' responses to fragmentation (e.g. Hanski and Simberloff 1997, Hanski 1999) and metapopulation modeling is increasingly being used for the design of species conservation strategies (McCullough 1996, Akçakaya and Sjogren-Gulve 2000, Hanski 2004). **In the context of metapopulation models one central issue is the calculation of inter-patch distance considering the behavioral response of species to landscape structure, for which no published example has been found** (Guisan and Thuiller 2005). Measuring this real inter-patch distance is far from obvious because it depends on how much the landscape features occurring between patches facilitate or impede the movement of organisms (Taylor et al. 1993; Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001). **Inter-patch distance should take into account the resistance of landscape features to movement, as with the least-cost algorithms implemented in Geographic Information Systems (GIS). In Chapter 7, we explore how patch occupancy is sensitive to Euclidean versus landscape-based distance (least-cost algorithm). We also used the results to propose conservation strategies for one threatened amphibian species**. The value of our results is notable because, when metapopulation models are used, there is a risk of devising incorrect conservation strategies if the landscape structure among patches is neglected (Wiens 1997).

Statistical tools

General framework

Recently, powerful statistical techniques and Geographic Information System (GIS) tools have allowed the development of a range of approaches to species-environment relationships and predictive habitat distribution models (Guisan and Zimmermann 2000). Such models relate the geographical distribution of species or communities to their present environment. The methodological approach to be used depends on the objective of the study and the quality of the data (for an exhaustive review see Guisan and Zimmermann (2000)). **In this research we essentially used GLMs (Generalized Linear Models), which are extensions of classical multiple regression models, allowing non-normal response variables to be modeled. Because we have presence/absence data (binomial response variables) a special case of GLM can be used: logistic regression**. A mathematical basis for these models can be found in statistical textbooks (Hosmer and Lemeshow 1989). We describe these models briefly in the next section.

GLMs and logistic regression

Widely known and used, the basic linear regression model has the form:

$$\mathrm{Y} = \alpha + X\beta + \varepsilon$$

where Y denotes the response variable, α is a constant called the intercept, $X = (X_1,...,X_p)$ is a vector of p predictor variables, $\beta = (\beta_1,...\beta_p)$ the vector of p regression coefficients (one for each predictor), and ε is the error term.

However, this classical linear regression cannot be used when the response variable is binary (e.g. presence/absence). The first reason is that the predicted values will become greater than 1 and less than 0 when moving far enough on the x-axis (X ranges between $-\infty$ and $+\infty$) and such values are theoretically inadmissible. Then the error is not normally distributed because Y takes on only two values. Finally, another assumption of linear regression is that the variance of Y is constant across values of X, which cannot be the case with a binary variable (heteroskedasticity).

In GLMs, the predictor variables X are combined to produce a linear predictor LP which is related to the expected value $\mu = E(Y)$ of the response variable Y through a link function $g()$, such as:

$$g(E(Y)) = LP = \alpha + X\beta + \varepsilon$$

To carry out a logistic regression, the *logit* link function is used. The *logit* function is defined as:

$$g(p) = logit(p) = \ln \frac{p}{1-p} = LP$$

where p is the probability that the event (e.g. presence or absence of species) occurs. $p/(1-p)$ is the odds ratio. To get from *logits* to probabilities, it is necessary to extract *p* from the previous equation:

$$p = \frac{\exp(LP)}{1+\exp(LP)}$$

If the natural logarithm of odds $(\ln(p/(1-p)))$ is linearly related to X, then the relation between X and p is not linear, and has the form of a sigmoid curve. Logistic regressions are used to assess the association with amphibian occurrence and various environmental variables in **Chapters 4, 5** and **6**.

Model selection

In this research **we also used a recently developed and increasingly used statistical approach in ecology: the model selection** (Burnham and Anderson 2002). In Appendix 2 we give some details of the theoretical and mathematical aspects of this approach, which is based on information theory and constitutes an alternative to classical null hypothesis testing (Anderson et al. 2000). **It allows models to be ranked and their relative weight to be estimated considering the principle of parsimony** (Box and Jenkins 1970). The model selection approach is used in **Chapters 5** and **6**.

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Chapter 2

Aims of the study

Conceptual design and structure of the thesis

A general overview of the structure and the relationships addressed in this thesis is presented in Figure 5. **Chapter 3** focuses on the temporal evolution of landscape conservation value. In this chapter we propose a methodology allowing the localization of hot spots with the most negative ecological alteration over time and hot spots of rehabilitation potential. **Chapters 4, 5, 6** and **7** concentrate on the problems associated with the conservation of one of the most threatened taxonomic groups in the world: amphibians. We studied several aspects of amphibian distribution modeling in order to improve the methodological approaches traditionally used and the ecological knowledge of the autoecology of this threatened species.

In **Chapter 4** we use logistic and autologistic models in order to assess the potential bias when spatial autocorrelation is not considered in regression analyses.
Our study also emphasizes the importance of incorporating spatial autocorrelation in statistical models of species distributions in order to avoid potential misinterpretation of species-habitat relationships.

In **Chapter 5** the focus is on the geographic variation of the effect of landscape factors on species distribution. Indeed, in the context of predictive distribution models and applied ecology, the important question is whether the results of one study on one species in one region can be transferred to the same species in a different region. To suggest answers to this question, we studied amphibian distribution in five separate regions and tested the interaction of region-by-landscape variables. In this chapter we also assess the spatial scale (i.e. the distance from breeding pond) of the landscape variable effect.

In **Chapter 6** we analyze the effect of pond scale and landscape scale factors on species occurrence by considering the area around a breeding pond which is really accessible to moving individuals. This area is not circular as commonly assumed, but shaped by the barriers surrounding ponds. The landscape variables were computed within these barrier-based migration areas. In order to assess the validity of the proposed methods we compare the results with the commonly used circular radius.

Finally, in **Chapter 7** we develop an approach allowing the identification of patches most sensitive to inter-patch landscape structure. The method is applied to two metapopulations of one threatened amphibian species and is based on patch occupancy metapopulation models. The approach allows a manager to identify those patches where improving connectivity would be a valuable and realistic conservation option.

We believe that the results of this thesis constitute valuable support for decision making in the planning of biodiversity conservation.

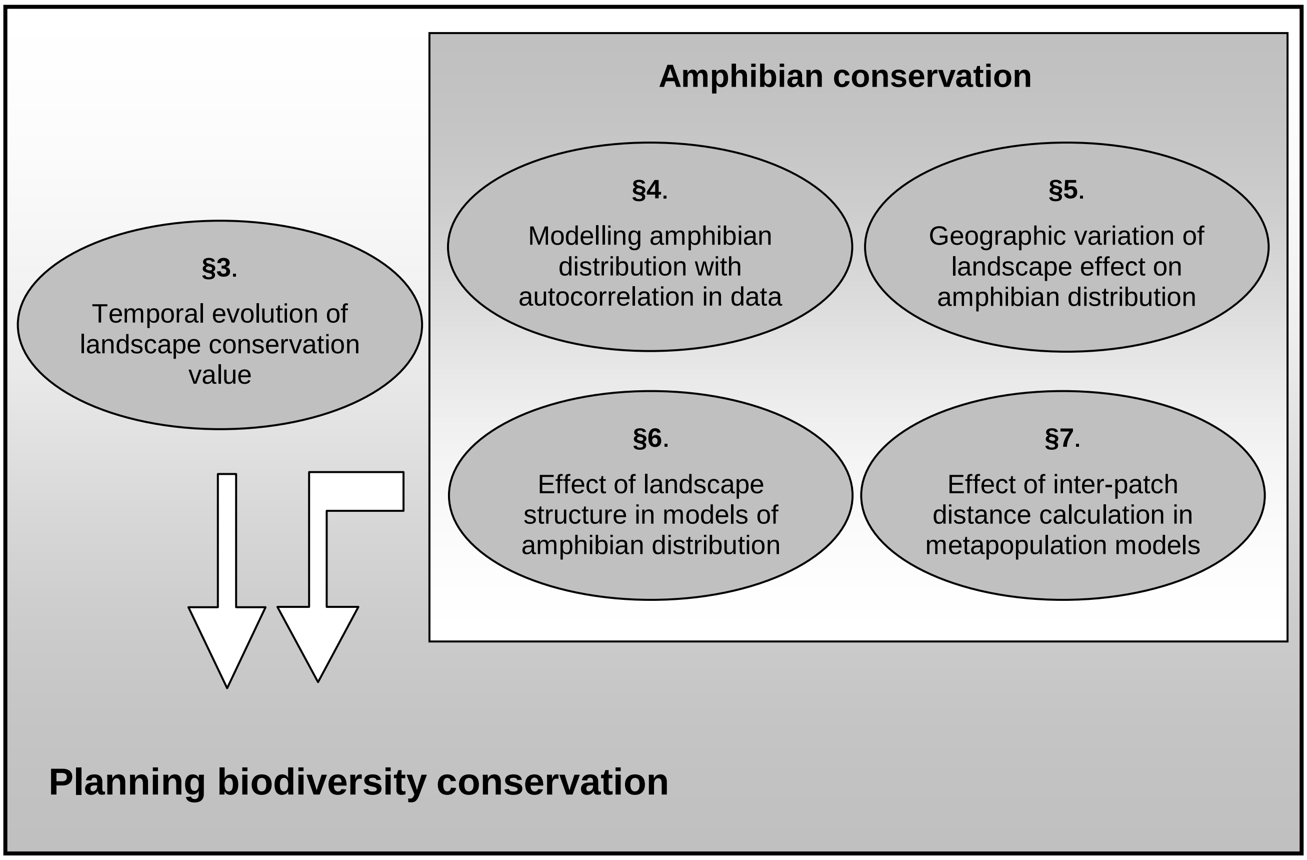

***Figure 5**. Structure and relationships addressed in this thesis in the context of biodiversity conservation planning.*

Specific objectives

This thesis addresses the following specific objectives:

Chapter 3:	(1) To develop a feasible method for the assessment of the conservation value of the landscape in the Rhone plain for the years 1900 and 2003 on the basis of land-cover maps and expert knowledge; (2) to locate hot spots where landscape transformation has mostly reduced the conservation value of the plain since 1900; and (3) to identify potential priority areas for landscape rehabilitation.
Chapter 4:	To assess the potential bias in logistic regression models when spatial autocorrelation in data is not accounted for by comparing logistic and autologistic regression estimates.
Chapter 5:	(1) To investigate the geographic variation in the effects of landscape composition around the ponds on the distribution of species; (2) to test the effect of pond connectivity; and (3) to determine the spatial scale of the effect of landscape composition on amphibian distribution.
Chapter 6:	(1) To assess the effect of pond scale and the surrounding terrestrial habitat on the distribution of two amphibian species by considering the area around the pond which is really accessible to moving individuals; (2) to compare the difference with the commonly used method considering circular areas. The proposed approach was called “Barriers-based buffers” (BBB).
Chapter 7:	(1) To assess the effect of landscape structure in metapopulation dynamic studies by comparing patch occupancy computed with Euclidean and least-cost inter-patch distance; (2) to determine the sensitivity of patch occupancy to colonization rate, extinction rate, and mean dispersal distance.

Chapter 3

Evaluation of the nature conservation value of the landscape over time: implications for rehabilitation projects[*]

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Abstract

In general, nature is undergoing gradual ecologically-negative change and landscape restoration is set to become a very important field in the future. In this paper, we document human-driven land-cover changes in an originally river-dominated region of Switzerland, the Rhone plain, which developed from a near-natural reference state in the early 20th century to a highly anthropogenic state in the early 21st. We present a method that uses land-cover data and expert knowledge to enable a spatially explicit assessment of changes in the nature conservation value of the landscape over time. Our results suggest that human activity has had a negative effect on the ecological state of over 97% of the plain since 1900. The hot spots which experienced the most negative ecological changes are related to wetland destruction. Our study proposes a methodological GIS-based approach for

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determining and locating the rehabilitation potential of the landscape. The method enables the rapid, ecologically relevant and spatially complete evaluation of a large and heterogeneous landscape and could constitute an important tool for communication, landscape decision-making and biological conservation management in landscape planning.

Keywords: Land cover changes, landscape history, reference state, fragmentation, GIS, Switzerland

Introduction

Nature is undergoing changes which are mostly negative, anthropogenic in origin, ominously large in scale and accelerating (Balmford and Bond 2005). In addition to the risk of species extinction arising from climate change (Thomas et al. 2004), anthropogenic habitat fragmentation and loss are recognized as major contributors to the general decline and future threat to biodiversity (Pimm and Raven 2000, Tilman et al. 1994). If the world's biological richness is to be conserved, natural and healthy ecosystems must be protected and recreated (Dobson et al. 1997). Given the limited financial, temporal and energy resources available, it is essential that priorities be set for conservation and restoration activities.

The conservation value of the landscape

Nature conservation can be defined as the preservation and protection of the natural richness of a landscape (i.e. soil, geomorphology, flora and fauna). The process of assessing the significance of an area for nature conservation is called ecological evaluation (Spellemberg 1992). Thus, the conservation value of a landscape represents its capacity to ensure the persistence of natural richness over the time. According to these definitions, the performance of an ecological evaluation basically involves classifying the area under analysis into units of varying significance in terms of nature conservation (Geneletti 2002), i.e. different conservation values. This requires a general evaluation concept which specifies both the conservation objectives and the criteria that express their fulfilment. Conservation objectives range from species-centred approaches focusing on the conservation of one or several endangered taxa to more process-oriented procedures aimed at the maintenance of functioning self-sustaining ecosystems (Geneletti 2002, Margules and Usher 1981, Noss et al. 1997, Spellemberg 1992). In recent decades, new evaluation criteria (e.g. connectivity, patch shape) have been related to the field of landscape ecology as it addresses the relationship between spatial patterns (landscape composition and configuration) and ecological processes (Forman and Godron 1986), therefore forming the base for the survival of species (Bridgewater 1993, Burke 2000, Hansson and Angelstam 1991).

Conservation value may vary spatially in a fragmented and heterogeneous landscape. Natural or near-natural ecosystems such as wetlands, forests or alluvial river systems are more significant in terms of conservation than intensively exploited or impaired components of the landscape matrix, such as agricultural lands, urban areas and road networks. However, the conservation value of the landscape also varies temporally, in particular as a result of human activities (Forman and Godron 1986). The rationalization and intensification of agricultural practices in Switzerland during the second half of the last century had an extremely negative impact on the capacity of the agricultural area to ensure the viability of a wide variety of species (Broggi and Schlegel 1990, 1998). Former natural structures such as trees, hedges and shrubs have either disappeared or have become isolated. Thus, temporal landscape dynamics are among the most important characteristics that describe a landscape (Forman and Godron 1986) and may have important implications for restoration projects (Egan and Howell 2005a).

Reference state and rehabilitation

The quantification of temporal landscape dynamics requires the definition of a reference state that describes the landscape in its pristine and generally less disturbed state. Several techniques can be used to establish the reference conditions of an ecosystem or a landscape. These include the study of historic records (e.g. written and oral histories, photographs, maps) and the analyses of proxy records derived from biological sources such as pollen, spores or macrofossils (White and Walker 1997). A reference state can support decision-making in landscape planning and biological conservation management and can also act as model or target for planning restoration projects, in particular when current conditions are seriously degraded and differ significantly with respect to the original state (Axelsson and Ostlund 2001, Christensen 1997, Gordon et al. 1997, Hohensinner et al. 2004, Jungwirth et al. 2002, Luyet 2005, Nordlind and Ostlund 2003, SER 2004, White and Walker 1997).

Nevertheless, historical analyses are generally carried out in places that have already been identified by previous investigations as suitable for restoration. Today, such reference conditions are used to drive restoration projects and not to locate them (Egan and Howell 2005b). The development of standardized methods which support decisions regarding the identification of areas most suitable for restoration at landscape and regional level is a recent and increasingly interesting research field (Hobbs and Norton 1996). Due to the increasing complexity of the ecological systems being studied, it is even more difficult to decide at a broader level what should be restored, where and how (Hobbs and Harris 2001).

In this study we used reference conditions as a model for the identification of locations in a given degraded and heterogeneous landscape where rehabilitation projects should take priority. Because it is recognized that ecological restoration will not necessarily translate into the re-establishment of the exact former state of an ecosystem or a landscape, we prefer to use the term rehabilitation (SER 2004). Rehabilitation shares with restoration a fundamental focus on historical or pre-existing landscapes as models or references, however the goal is not the exact reconstruction of the original state.

Goals

In this paper, we study the reference conditions and transformation over time of an originally river-dominated region of Switzerland, the Rhone plain. The objectives of the study are: (i) to develop a feasible method for the assessment of the conservation value of the landscape in the Rhone plain for the years 1900 and 2003 on the basis of land-cover maps and expert knowledge; (ii) to locate hot spots where landscape transformation has mostly reduced the conservation value of the plain since 1900; and (iii) to identify potential priority areas for landscape rehabilitation. It is our view that our approach could provide a useful starting point for the definition of conservation goals and for ecological rehabilitation projects in which the target state is based on an historical reference.

Material and Methods

Study area and land cover changes

The area studied is the section of the Rhone valley in Switzerland between Brig (678 m a.s.l.) and the mouth of the river Rhone into Lake Geneva (374 m a.s.l.) (Figure 1). The total area involved is 240 km^2. The length of the river, which is now almost completely canalized, in that area is approximately 120 km. The river Rhone drains a catchment area of 5,520 km^2 close to the mouth into Lake Geneva, and has an average annual discharge of 187 m^3 s^{-1} (Loizeau and Dominik 2000).

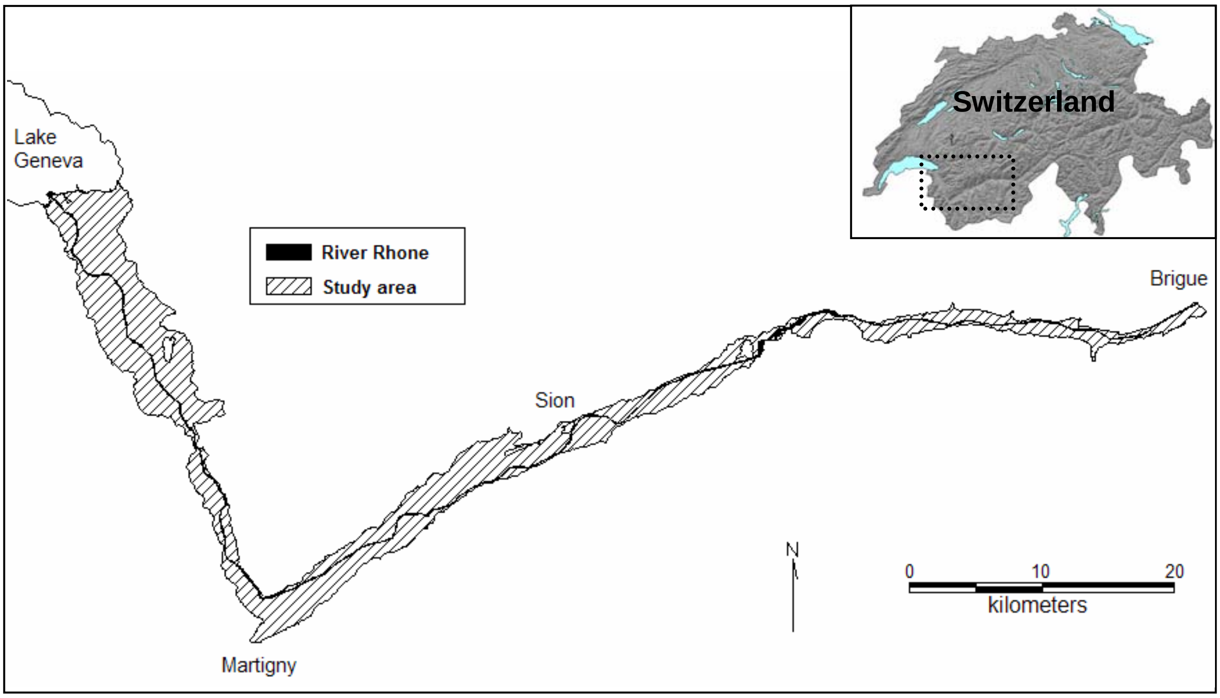

***Figure 1**. Location of the Rhone Plain in Switzerland. The current situation of the river Rhone is shown.*

The valley was formed by the sweeping advance of the Rhone glacier at the beginning of the Quaternary Period (Département Fédéral de l'Intérieur 1964). The river Rhone and its tributaries filled and formed the plain with their bed loads over the course of the centuries. The region has undergone fundamental compositional change over the past 150 years. The first systematic river correction, which was carried out in the late 19th century, almost completely destroyed the alluvial river-floodplain system, which covered 10.9% of the plain in 1850 and only 1.6% in 1900 (Zanini et al. submitted). The braided active channel of the river Rhone was restricted to a single mainsteam, resulting in a shoreline reduction of 150 km (45 %; Weber et al. submitted). Additional damage was caused to the ecological state of the plain after 1900 by the second river correction, the drainage of the plain, agriculture intensification and settlement development. Wetlands covered 6.1% of the plain in 1900 and only 1.3% in 2003. Furthermore, we observed a significant increase in urban area, in particular in the second half of the 20th century (1.4% in 1900 and 13.8% in 2003). Today, the Rhone plain constitutes a human-shaped landscape dominated by intensively exploited agricultural land (76.6%), in which the former natural ecosystems have almost completely disappeared (Zanini et al. submitted).

Despite the two systematic corrections of the Rhone, the anticipated level of flood security was not entirely attained, and considerable damage was caused to the region by repeated and severe flood events in 1935, 1948, 1987 and 1993 (Wallis 2000). As a result, it was decided in September 2000 to undertake a third correction of the river Rhone, with the help of which flood protection will be improved along a significant stretch of the river Rhone A simultaneous revaluation of ecological and socio-economic concerns is also planned (Wallis 2000).

Historical sources

Based on the historical topographic maps mentioned in Table 1, 15 land cover classes (Table 2) were identified and digitized using ArcMap^{TM} 8.3 (ESRI). These classes represent the most detailed information obtainable from the interpretation of topographical maps.

***Table 1**. Cartographical sources used to reconstruct the former state of the Rhone Plain and to digitize land cover.*

Period	Year of map publication	General context	Name	Scale
1900	1882-1904	Reference state (after first river correction, still with significant wetland area and extensive agriculture)	Siegfried Map	1: 50 000
2003	2003	Current state (significant agriculture intensification and urban development)	Digital National Map of Switzerland	1: 50 000

Table 2. *15 land-cover classes digitized from the historical topographical sources for the years 1900 and 2003. A buffer corresponding to an estimation of real width was set around the linear topographical elements (tributary, canal, highway, railroad and road).*

Land cover	Topographic map interpretation
Forest	Map signature for closed forest.
Wetland	Map signature for wetland.
Floodplain, Rhone river (natural active channel including floodplains)	Active side-arms or reaches of the river Rhone with intact floodplains, along one bank at least. According to Müller-Wenk (2004), intact floodplains are defined as areas between two arms of the river Rhone or outside of the furthermost arm carrying the signatures for gravel or open forest. Periodic inundations by the Rhone can be expected (absence of settlements and infrastructure). Both land and water area (mainstem, side-arms etc.) are included.
Rhone, canalized	Area occupied by river Rhone, but with none of the features mentioned under the floodplain, river Rhone.
Floodplain tributary	Alluvial area within the influence of a tributary of the Rhone.
Hill	Map signature for hill.
Dune	Map signature for hill and cited in the literature as a dune (Farquet 1924, Delarze pers. comm. 2004).
Urban area	Area including (1) >5 buildings within max. 100 m distance; (2) isolated, but large buildings covering approximately the surface of five smaller buildings (e.g. industry, factories).
Agricultural zone	Remaining area of the plain, essentially agricultural area.
Tributary	Running water originating in the mountains and flowing into another river or canal or into Lake Geneva (width 6 m).
Canal	Running water originating in the plain or appearing at the surface after being piped (width 4 m).
Highways	Highway: width 30 m.
Railways	Railroad: width 10 m.
Roads	Roads of first and second class. Width: 4 m in 1900 and 6 m in 2003.
Stagnant water	Stagnant water of natural or artificial origin.

Topographical maps of the plain were available for 1850 and were digitized in previous studies (Zanini et al. submitted). However, due to low spatial accuracy and a high level of incertitude with regard to land-cover identification arising from the measurement techniques and small map scale (1:100 000), it was not possible to use these data in this study. Thus, we used the year 1900 as the reference state, which is also supported by ecological elements. Indeed, although the first Rhone river correction (1863-1876) produced dramatic ecological consequences with regard to the alluvial ecosystems, the overall ecological value of the plain and its conservation potential for biodiversity remained high. Flooding episodes were still frequent (Wallis 2000) and several regions in the plain remained dominated by marsh, extensive agricultural practices and some unique ecosystems related to the Rhone alluvial system (e.g. sand dunes) were still present. Thus, as confirmed by several studies, overall species richness in the plain was still high in 1900 (Delarze 1982, Desfayes 1996, Farquet 1924, Gams 1916, 1927, Giugni 1985, Rey et al. 1985).

Data quality

The quality of the digitized data is crucial for any inter-year analyses. It may be influenced by the incertitude of cartographical sources, transformation through scanning and geo-referencing or the screen-digitations (Johnson 1990, Kienast 1993). Moreover, comparability between years is also influenced by data acquisition and generalization. In order to estimate the discrepancy between the 1900 and 2003 maps, the position of nine churches was compared. Churches were the topographical elements that could be identified most accurately at our working scale. Because the map scale is relatively small (1:50 000, 1 mm=50m!), we expected errors to occur, mainly due to geo-referencing. However, we observed a median discrepancy of only 24 m, which is sufficiently small to ensure limited errors in an inter-state comparison.

Estimation of the conservation value of the landscape

In terms of landscape patterns, historical topographical maps and aerial photographs provide an important basis for reference construction (Hohensinner et al. 2004, SER 2004), which is available for many regions. In contrast, historical information on the biotic (e.g. species richness) and abiotic (water quality, soil type) state of ecosystems is generally difficult to obtain and is often extremely fragmented (for several examples see Egan and Howell 2005a), especially if the study region is large (Van Diggelen et al. 2001). One way of dealing with this problem is to use expert knowledge. Expert knowledge offers significant support in conservation planning and ecological assessment when evaluation models based on empirical studies are not available (Balram et al. 2004, Hellier et al. 1999, Store and Kangas 2001).

We selected three experts who are familiar with the ecological characteristics of the ecosystems in the Rhone plain and their evolution over the last century. These experts are biologists by profession, live in the study area and work as environmental consultants in private offices. We asked them to estimate the land-cover conservation value in relation to the number and rarity of potentially present species of each land-cover class identified in 1900 (reference state) and 2003 (actual state).

The conservation value ranges from 0 (no conservation value) to 10 (maximum conservation value).

The conservation value of the entire plain (i.e. landscape conservation value) can be calculated using the following formula (equation 1):

$$C = \sum ps \qquad \text{(eq. 1)}$$

where *C* is the conservation value of the plain, *p* the proportion of the land-cover class and *s* its expert score. We used this weighted summation because (i) no synergic effect is considered in our evaluation and (ii) it is easy to explain and transparent (Janssen 2001).

However, this result cannot be represented spatially. Therefore, we estimated the landscape conservation value in regular cells of 250 x 250 m in accordance with the aforementioned formula with *p* as the proportion of each land cover class in the cell. A total of 3,143 cells were delineated in the Rhone plain. As suggested by EUROSTAT (2000) and Chetelat (2005), cell size may affect the results. A small cell size accentuates diversity between cells and, conversely, large cells limit variability. The cell size used in our study was chosen as the best compromise between the scale of our study area, the incertitude regarding the boundary of the digitized land cover classes and the narrow shape of the Rhone plain.

Finally, the difference between the conservation value of the current state (2003) and reference state (1900) was computed for each cell. The result of this difference is consecutively termed ecological alteration. Ecological alteration ranges from -10 to 10. A negative value is interpreted as a loss in landscape conservation value as compared with reference state. Conversely, a positive value represents a gain in landscape conservation value. The closer to zero the value, the smaller are the changes.

The expert evaluations were compared separately for each temporal state using the non-parametric Friedman-Test for related samples and the Wilcoxon-Wilcox-Test (*a posteriori*). All of the spatial analyses were computed using Mapbasic 7.5 and Mapinfo 7.5 software (Mapinfo corporation ©, 1985-2003). SPSS 11.0 for Windows was used for the statistical analyses.

Defining rehabilitation potential

According to the proposed methodology, the reference conditions and the estimation of the ecological alteration of the landscape over time enable the identification of areas in which anthropogenic landscape transformations caused the most negative ecological effects. These areas also have the higher rehabilitation potential because the deviation from near-natural reference conditions is the most significant, therefore the potential ecological gains from rehabilitation projects are greater. In all rehabilitation projects, reference conditions play a central role in determining the rehabilitation potential of a site (Egan and Howell 2005a, White and Walker 1997). Moreover, variations over time and historical aspects are not the only factors that can support the estimation of rehabilitation potential. Current conditions also have to be considered because the objective of rehabilitation projects is not only to re-establish former conditions, but also to fundamentally improve the current ecological state (Hobbs and Harris 2001). Hence, we assume that rehabilitation potential is the highest where (i) ecological alteration is the most negative and (ii) the conservation value is currently lower.

We proposed the use of a scale varying between 0 (no rehabilitation potential) and 5 (maximum rehabilitation potential). We considered a linear relationship between ecological alteration and rehabilitation potential (Figure 2), but assumed it to be 0 as long as the value of ecological alteration is positive. We also considered a linear relationship between conservation value in 2003 and rehabilitation potential. Finally, we calculated the mean between both rehabilitation potential values. Thus, for each cell in the landscape we obtained an estimation of its relative rehabilitation potential which varied between 0 and 5.

The proposed score scale and the linear function represent only one possible solution. The method is very flexible and can be quickly and easily adapted to the specific requests and strategies of project stakeholders and decision makers. This is an important point as the possibility of including various opinions and societal desires could influence the success of rehabilitation projects considerably (Hobbs and Harris 2001).

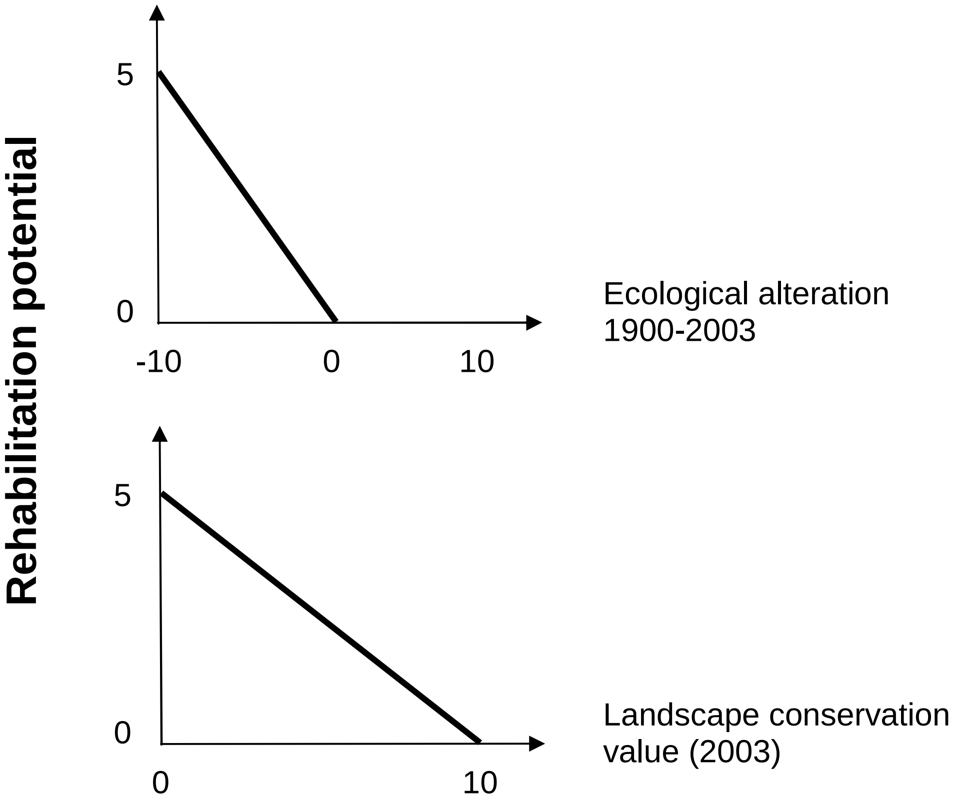

Figure 2. *Criteria used for the estimation of rehabilitation potential: the ecological alteration between 1900 and 2003, and the landscape conservation value in 2003. We assume a linear relationship between both criterion and the rehabilitation potential. Final rehabilitation potential is the mean between both estimations.*

Results

The area of natural habitats (in particular wetlands and forest) decreased between 1900 and 2003 (Table 3). In addition, experts estimated that an intrinsic degradation of the ecological quality of land cover also occurred among years. This is particularly evident in the case of agricultural area, which received a mean conservation value score of 6.3 in 1900 and a mean score of only 2.3 in 2003 (Δ =-4). In both temporal states, the alluvial floodplain area of the river Rhone has the highest mean value for conservation (9.7 and 7.7 respectively). Dunes and wetlands also obtained high scores. As expected, urban areas, roads and highway have a lower value. Based on the mean land cover scores and the formula (1), the conservation value of the entire Rhone plain corresponds to 6.5 in 1900 and 2.7 in 2003 (Δ = -3.8). This result is essentially dependent on the scores assigned to agricultural area which represents the predominant land cover in both temporal phases (78% of the Rhone plain area in 1900 and 73% in 2003).

Table 3. Land cover area (ha) and mean conservation value scores from the three expert evaluations (range is the difference between min and max expert score). Land covers are ranked in decreasing order for mean conservation score in 1900. Conservation value ranges from 0 (no conservation value) to 10 (maximum conservation value). The Rhone plain conservation value is computed using the formula in equation 1.

Land cover	**Area (ha)**			**Mean conservation score**				
	1900	**2003**	**Δ area**	**1900**	**Range**	**2003**	**Range**	**Δ scores**
Floodplain, river Rhone	389.6	131.8	- 257.8	9.7	1	7.7	2	-2.0
Dune	7.4	0	- 7.4	9.3	2	-	-	-
Wetland	1439.4	283.0	- 1156.4	9.0	2	7.3	1	-1.7
Hill	39.6	25.4	- 14.2	8.7	1	7.3	4	-1.4
Floodplain tributary	30.2	0.0	- 30.2	8.0	3	6.0	2	-2.0
Canal	202.7	127.5	- 75.2	7.3	2	3.0	3	-4.3
Stagnant water	9.3	153.6	+ 144.3	7.3	5	7.0	3	-0.3
Forest	2056.6	1227.8	- 828.8	7.0	3	6.7	3	-0.3
Agricultural zone	18 610.3	17 474.1	- 1136.2	6.3	4	2.3	1	-4.0
Tributary	85.4	47.6	- 37.7	6.0	2	4.3	5	-1.7
Rhone, canalized	568.2	573.3	+ 5.2	4.0	2	4.3	5	+0.3
Urban Area	321.8	3282.4	+ 2960.6	3.3	2	1.7	1	-1.6
Railways	131.9	156.3	+ 24.4	3.0	3	2.3	3	-0.7
Roads	83.2	256.7	+ 173.5	1.7	3	0.3	1	-1.4
Highways	0	236.6	+ 236.6	-	-	1.7	2	-
Mean				6.5	2.5	4.4	2.6	-1.6
Rhone plain conservation value				6.5		2.7		-3.8

Relative agreement was observed in the score attribution by the three experts (EXP) (Pearson's correlation coefficient; EXP1-EXP2: $r = 0.76$; EXP2-EXP3: $r = 0.74$; EXP1-EXP3: $r = 0.76$) which would indicate that the experts share a common appreciation of the conservation value of the different land cover classes. However, significant differences existed between the experts for the evaluations of the 1900 state (Friedman-Test, $p < 0.05$). EXP 2 assigned significantly higher scores than EXP 1 and EXP 3 (Wilcoxon-Wilcox-Test, $p < 0.05$); there were no significant differences between the scores allocated by EXP1 and EXP3. There were no significant differences in the expert evaluations for 2003 (Friedman-Test, $p = 0.736$).

The results of the ecological alteration and estimation of the rehabilitation potential are presented in Table 4. We assigned the cells in four classes of same size. According to the expert evaluations and computed land-cover changes, our method showed that ecological alteration in the Rhone plain was "negative" to "very negative" for more than 97% of the study area. For EXP3 ecological alteration was less negative than for the two other experts because the changes were classified as ecologically "very negative" for only 3.9% of the plain (as compared with 44.0% and 39.6% for EXP1 and EXP2, respectively). Moreover, positive ecological alteration, i.e. an increased conservation value, was found for only two experts and for an extremely limited area of the plain (0.9% for EXP2 and 2.8% for the EXP3).

Table 4. *Proportion of the plain corresponding to different classes of ecological alteration and rehabilitation potential value. The views of all three experts are presented.*

Ecological alteration classes	**Description**	**EXP1**	**EXP2**	**EXP3**
[-10,-5]	Very negative	44.0%	39.6%	3.9%
[-5,0]	Negative	56.0%	59.4%	93.3%
[0,5]	Positive	0	0.9%	2.8%
[5,10]	Very positive	0	0	0
<0	Negative and very negative	100%	99.1%	97.2%
Rehabilitation potential classes				
[0,1]	Very low	0.0%	1.9%	1.0%
[1,2]	Low	4.6%	4.6%	7.5%
[2,3]	Medium	39.3%	18.4%	85.2%
[3,4]	High	56.1%	74.4%	6.3%
[4,5]	Very high	0.0%	0.8%	0.0%

In order to identify spatially where ecological alteration is "very negative" and where the results for three experts are consensual, we superimposed the three maps of ecological alteration and selected those cells for which all three experts had the same class value. Figure 3 shows the hot spots of "very negative" ecological alteration for a section of the study area. The areas corresponding to "high" or "very high" rehabilitation potential were computed using the same methodological approach and are also illustrated for the same section of the plain (Figure 3). These hot spots generally overlapped. Positive ecological changes are not mapped as the results of three experts are not spatially consensual.

In Appendix 3 are presented the land-cover conservation value, the maps of ecological alteration and the maps of rehabilitation potential for all the experts separately.

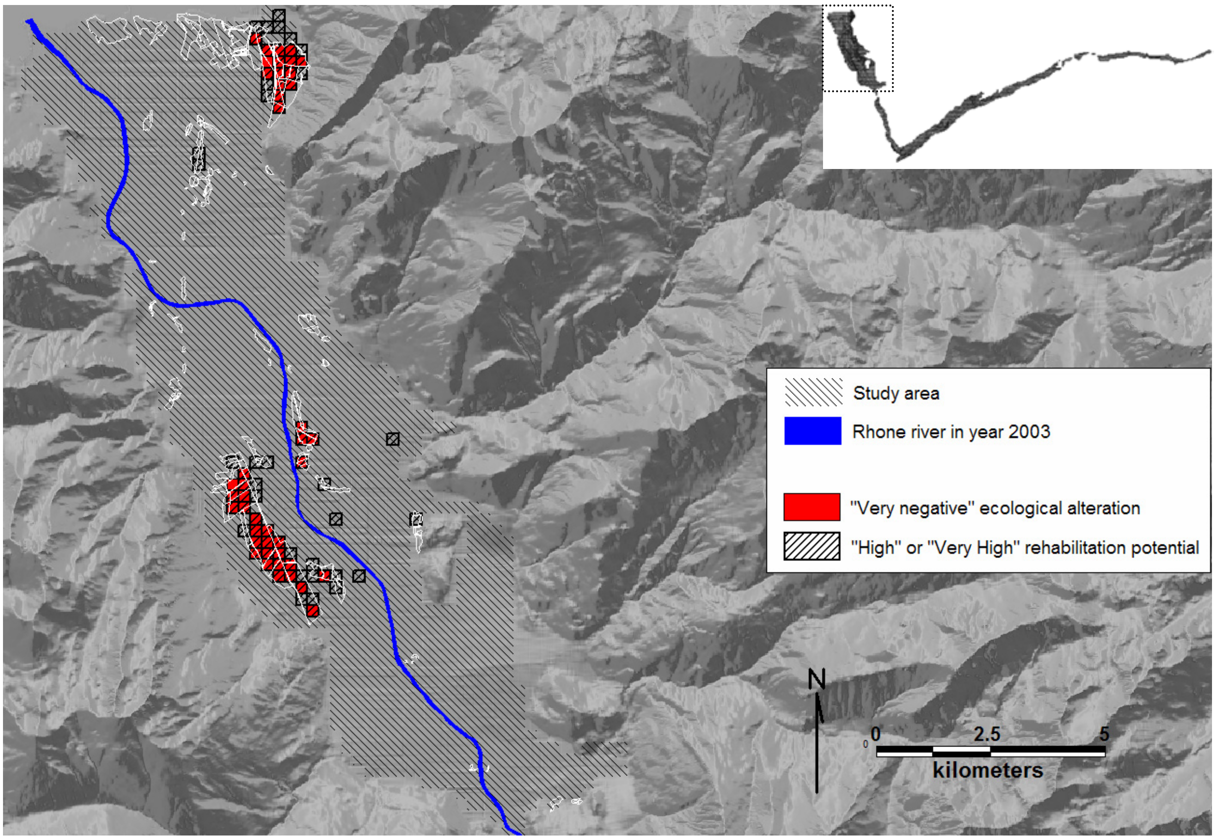

Figure 3. *Section of the Rhone plain (the Chablais) close to the mouth into Lake Geneva. The map shows the hot spots of "very negative" ecological alteration ([-10, -5]) and the hot spots of "high" or "very high" rehabilitation potential ([3, 5]), on which all three experts agreed. The white boundaries indicate the wetland perimeter in 1900 (MNT25, © Swisstopo 1995).*

Discussion

In this study, we presented a method for the quantification of the spatial and temporal variation in the nature conservation value of the landscape. Our approach enabled the localization of hot spots where land cover changes were most negative or positive from an ecological point of view. Our method is simple to understand, appropriate for different spatial scales and flexible because land-cover classes, cell size and expert scores can be modified easily and quickly. Rather than computing a mean value, we also identified consensus among experts so as to respect each specific expert opinion, which is very important for the communication and acceptance of results (Maystre and Bolliger 1999, Pictet 1996). Finally, due to its standardized and transparent method which indicates where the rehabilitation potential of the landscape is highest when an historical state is used as reference, our approach could have important implications for landscape planning. In this study, we presented and discussed the implications for rehabilitation projects. However, we also noted that the map produced, which provides information about the current conservation value of the landscape, could be very useful for the definition of conservation strategies, e.g. for the selection of area to be protected.

As is commonly acknowledged, the establishment of the reference state is a very difficult and time-consuming task and past data provide only snapshots of system parameters (Hobbs and Harris 2001). Problems arise both due to the lack of historical information and the difficulty in defining what a reference state is (Egan and Howell 2005b). If the reference constitutes a landscape that is entirely devoid of human influence, it would be necessary to obtain pre-historic information because human impact, e.g. in the Rhone plain, is documented back to the Neolithic period (Département fédéral de l’intérieur 1964), and this would be a difficult task. Around 1850, the river Rhone was still in a relatively natural state with high-quality longitudinal and lateral connectivity (Weber et al. submitted for publication). The fish-species richness of the river Rhone was also appreciably higher at the end of 19th century (19 species) than today (only 2 species; see Weber et al. submitted for publication). However, at this time landscape was also already partially shaped by human activity (agriculture, farming practices and forestry) (Bender 2001, Farquet 1924, Kuonen 1993). Several factors may influence the choice of the reference state, but, as suggested by Bradshaw (1997), the reference system is not necessarily intended to describe only the former state unaffected by humans. The reference must also be defined in accordance with the goals of the project, the availability of data and stakeholder acceptance. In our study, the 1900 state fulfilled these considerations.

For the Rhone plain we found that significant changes in landscape composition occurred over the past century with generally negative consequences for its ecological state. With the exception of stagnant water, which increased in area from 9.3 ha in 1900 to 153.6 ha in 2003 (+144.3 ha), the area of all natural habitats (see Table 3) decreased from 1900. The increase of stagnant water area is related to the development of gravel mining during the last century. This activity multiplies the number and size of ponds and associated pioneer habitats. Such ecosystems created by human activity are of particular importance for many endangered species in the region, for example the yellow bellied toad (*Bombina variegata;* Grossenbacher 1988). However, because of its small size and the generally extreme degradation of the ecological state of the study area in 2003 the effect of newly created stagnant water ponds on conservation value of the landscape was limited.

The hot spots which experienced the greatest negative ecological alteration are essentially located in the former wetland areas, which were still significant in size at the beginning of the last century (1439 ha, 6% of the plain), but have now almost entirely disappeared (283 ha, 1% of the plain). Wetland conversion was essentially due to agriculture rationalization and intensification. Indeed, previous studies revealed that 81% of the wetlands that existed in the plain in 1900 had been converted into agricultural area in 2003 and almost 7% had been converted into urban area (Zanini et al. submitted). The ecological importance of wetland for biodiversity conservation and the dramatic consequences arising their reduction have been documented for the plain. For example, between 1882 and 1982, at least 65 plant species associated with marsh area disappeared in the Chablais region on the right bank of the river Rhone (Figure 3) (Delarze et al. 1982). In the same region on the left bank of the Rhone,116 plant species disappeared between 1850 and 1985 (Giugni 1985) and 98 plant species probably became extinct in the regions close to the mouth of the Rhone into Lake Geneva (Morel 1985). Other species associated with wetland ecosystems also declined in the region. Among these, amphibians are emblematic of species that are sensitive to habitat degradation (Dodd and Smith 2003). According to the Swiss Red List, eight out of twelve species are endangered, vulnerable to or threatened with extinction within the study area, (Schmidt and Zumbach 2005). Many studies have noted the worrying threat to amphibian populations in the Rhone plain and have identified some possible causes such as the destruction of breeding ponds, road mortality, natural succession of the vegetation and expansion of the invasive species *R. ridibunda* (Berthoud 1976, ECOTOEC 1996, Farquet 1924, Grossenbacher 1988, Jordan et Rey 1973, Marchesi 1999, Praz 1983, Rey et al. 1985). Other possible causes exist, such as climate change, increased UV-B exposure, agrochemicals and chemical pollution, human exploitation and disease (Alford and Richards 1999, Blaustein and Kiesecker 2002, Kiesecker et al. 2001). However, in the context of the Rhone plain, the dramatic habitat destruction (in particular of wetlands) and fragmentation and their direct and indirect consequences are probably the main drivers of amphibian decline.

In addition to changes in landscape composition, which were considered in the present study, changes in landscape configuration have also triggered a reduction in the suitability of landscape for species persistence (Zanini et al. submitted). The number of forest patches increased by a factor of 2.6 (175%) from 1900 while their average size decreased by 78%. The number of wetland patches and their average size also decreased (by 66% and 40% respectively). Conversely, the number of urban area patches increased by 122% and their average size by 344%. This confirms the increasing of urbanization process with growing agglomerations and newly-created urban areas. As a result, because they were often isolated and stressed by the surrounding environment, the remaining natural areas offer fewer suitable living conditions for the species, (Zanini et al. submitted). Thus, it is our view that in order to obtain a more realistic ecological assessment, the approach proposed in this paper could be improved by considering supplementary criteria such as patch rarity, diversity, isolation, naturalness and exposure to disturbances (Geneletti 2002 2004a, 2004b, Lee et al. 1999, 2001, 2002, Lesslie et al. 1988, Morgules and Usher 1981, Spellenberg 1992). However, in the case of broad-scale landscape evaluation like this research, the utilization of multiple criteria may be inadequate due to (i) the complexity of the system under study (15 different land cover classes) and (ii) the subsequent potential difficulty in communicating the results to stakeholders (Jansenn 2001).

Assessment based on expert knowledge is usually used when it is impossible to carry out an objective evaluation due to the lack of data. In principle, by including expert knowledge, we fill the gaps in data with the subjectivity of the experts. In order to limit errors in evaluation and to approximate the conservation value of the landscape as accurately as possible, in our study we were very strict in the selection of experts. The evaluation was a difficult exercise, in particular for 1900 as very little descriptive information was available on the state of ecosystems, species richness and human impacts. This incertitude resulted in significant differences between the experts' evaluations carried out for 1900. In contrast, there were no significant differences between the evaluations for 2003, which would indicate the existence of a consensual perception of the conservation value of the landscape and validate the assessment of its current state. Thus, in order to reduce the discrepancies between the expert assessments, only the hot spots with very negative ecological alteration identified by all the experts were discussed.

In our study we estimated rehabilitation potential spatially and proposed that it be used to locate priority areas for rehabilitation. Decisions in the area of rehabilitation (or restoration) ecology could be driven and supported by historical information (Egan and Howell 2005a). However, we agree that historical information and rehabilitation potential is only one element that can be considered in the planning of rehabilitation and restoration projects. Lindenmayer et al. (2002) stressed that the complexity of ecological problems at landscape scale suggests that there may not be just one straightforward way for setting targets for urgently needed restoration projects. Instead, it will be important to adopt a risk-spreading approach which involves the implementation of a wide range of strategies for landscape restoration. Moreover, to succeed, restoration activities not only need to be based on sound ecological principles and information, they must also economically feasible and practically achievable (Hobbs and Harris 2001). This implies that political acceptability often plays a more important role in the setting of priorities and choice of options than any rational process (Hobbs and Harris 2001). It is our belief that *in situ* historical elements are essential components of the decision making process in this context. As citizens, resource managers, and policy makers become more familiar with well-validated and locally-generated pictures of landscape history, a shared understanding of present conditions and potential future scenarios becomes more possible, and a common vision of the future can emerge (Antrop 2005, Grossinger 2005).

Conclusion

The main contribution made by this study is its development of a feasible method for monitoring both spatial and temporal changes in nature conservation value and the identification of hot spots of landscape rehabilitation potential. Our approach is based on the historical reference state (1900) and on expert assessment of landscape conservation value. Due to the complex structure of fragmented and heterogeneous landscapes, significant assumptions and simplifications were made. However, simplification produced comprehensible results which can be quickly calculated and easily explained and understood (Jansenn 2001, Young and Jarvis 2001). As suggested by Hobbs and Harris (2001), assessment processes carried out in the context of restoration project can be complicated and expensive, and if they are too complicated or expensive, they will not be carried out.

Historical references are only one of the sources that may be considered in the planning of nature conservation measures. However, the use of a reference state as target for a rehabilitation project is an important step, in particular if current landscape conditions show dramatic degradation and information is required regarding the pristine state (e.g. Jungwirth et al. 2002). The proposed methodology represents an additional helpful element for landscape planning. It could play an important role in facilitating communication in participation processes and provide a useful tool for decision makers involved in projects at landscape level and for sustainable land-use policy which is an important element of the Swiss Landscape Concept (OFEFP 1998, Stremlow et al. 2003).

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Chapter 4

How wrong are we when modeling species distribution without accounting for spatial autocorrelation? The case of the clustered distribution of the agile frog (*Rana dalmatina*) in north-eastern Switzerland[*]

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Abstract

Modeling species distribution is important for the conservation and management of species. These models are based on the understanding of species-habitat relationships. However, spatial autocorrelations (SA) in data may affect the accuracy of these models. In spite of being frequently observed characteristic of spatial variables, SA is still rarely considered. In this study, we analyzed the effect of 7 landscapes variables on the distribution of the agile frog (*R. dalmatina*) in north-eastern Switzerland. Variables were extracted in 17 concentric discs of different radii, from 100 m to 3000 m, centered on agile frog breeding ponds. We described SA using Moran's I correlograms and we built autologistic models. An autologistic model is a logistic model that includes a measure of the spatial arrangement of the response variables as a covariate; usually called "autocovariate". Comparing logistic (without autocovariate) and autologistic models (with autocovariate) we found key differences in the statistical estimates. Because regression residuals of autologistic models are independent, while residuals for logistic models are autocorrelated, we

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conclude herein that logistic models are not the statistically correct option for our study. Using logistic regression could produce distortions in the results of the regression. In logistic models the positive effect of marsh cover is accentuated and a supplementary variable (density of second class roads) became significant at various distances from the ponds. Our study also emphasizes the importance of incorporating SA in statistical models of species distributions in order to avoid potential misinterpretation of species-habitat relationships.

Key words: autologistic/logistic regression, autocovariate, landscape structure, presence/absence, habitat modeling, conservation, amphibian.

Introduction

Spatial autocorrelation (SA) is the property of random variables to take values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected by randomly associated pairs of observations (Legendre 1993). Thus, the value of spatially autocorrelated variables can be in part predicted by values of the variables in the neighboring locations. In wildlife species distribution analyses, these patterns can be driven by multiple causes that may be exogenous (e.g. disturbances, historical events, land use) and/or endogenous (e.g. conspecific attraction, dispersal, predation) (Sokal and Oden 1978b, Legendre and Fortin 1989, Legendre 1993).

Ecologists are frequently interested in modeling species distribution based on environmental variables. However, classical statistics (e.g. logistic regression for binary responses) assumes independence of the observations. Incorrect inference can result from models because SA in residuals violates the assumption of independence of observation. Indeed, autocorrelation in error structure of an ANOVA or regression-type model reduces the degree of freedom of the associated statistical test (Legendre 1993). Even if SA does not necessarily generate bias (Diniz et al 2003), the computed statistical tests with dependent variables are generally too often declared significant under the null hypothesis (Type I error), the magnitude of habitat effects tend to be overestimated and the relative importance of different habitat variables can shift (Borcard et al. 1992, Legendre 1993, 1998, Gumpertz et al. 1997, Lennon 2000, Lichstein et al. 2002, Legendre et al. 2002). Despite this fact, SA is still rarely considered in models of wildlife-habitat relationships even if it is a frequently observed characteristic of the spatial variables (Lennon 2000, Dale and Fortin 2002, Klute et al. 2002, Lichstein et al. 2002, Keitt et al. 2002).

Various methods may be used to detect spatial patterns in the data (Legendre and Fortin 1989, Dale et al. 2002, Perry et al. 2002). Among them, in the case of a single variable, the most common is the Moran's I (Moran 1950, Appendix 4). This index is represented as a function of distance classes in correlograms. If SA is detected and not seen as a nuisance but rather as a part of the ecological process under study, then it is better to account for the SA in the statistical modeling rather than being avoided (e.g. by exclude autocorrelated observations). This is of interest because SA can in fact reflect ecological processes, such as dispersal. Logistic models that integrate the spatial patterns of the response variables are called autologistic models (Augustin et al. 1996). Some examples of autologistic models were proposed by Smith (1994) for mountain sorrel, Augustin et al. (1996) for red deer, Gumpertz et al. (1997) for diseases in bell peppers and Klute et al. (2002) for American woodcock distribution modeling.

In this study, we analyzed the distribution in north-eastern Switzerland of the agile frog (*Rana dalmatina*), a threatened amphibian species. While studies on the role of aquatic and terrestrial habitats in determining patterns of presence, abundance and richness of amphibians at breeding ponds has increased over the last few years (e.g. Vos and Chardon 1998, Pope et al. 2000, Houlahan and Findlay 2003, Ficetola and De Bernardi 2004, Pellet et al. 2004, Rubbo et al. 2004, van Buskirk 2005, Herrmann et al. 2005), the question of the bias in the regression analysis due to SA is rarely addressed (Knapp et al. 2003).

Our objective is to compare the results of logistic regression analyses on habitat determinants of agile frog pond occupancy using two different approaches. Firstly, we applied a regression analysis using a logistic model without incorporating SA. Secondly, we used an autologistic model, where SA was assessed and included as a covariate in the regression analysis. We expected to find that in the logistic analysis habitat covariate effect will be overestimated.

Methods

Species and study area

The agile frog (*Rana dalmatina*, Bonaparte 1840) is widely distributed in Europe (Nöllert and Nöllert 2003). However, in Switzerland this species have an extremely limited distribution and it is threatened to extinction (Schmidt and Zumbach 2005). Breeding, oviposition, and tadpole development take place in a wide range of wetlands, but usually in relatively sunny locations adjacent to forest patches (Geisselmann et al. 1971). Two months after the oviposition, metamorphosed froglets scatter into the terrestrial environment (Geisselmann et al. 1971).

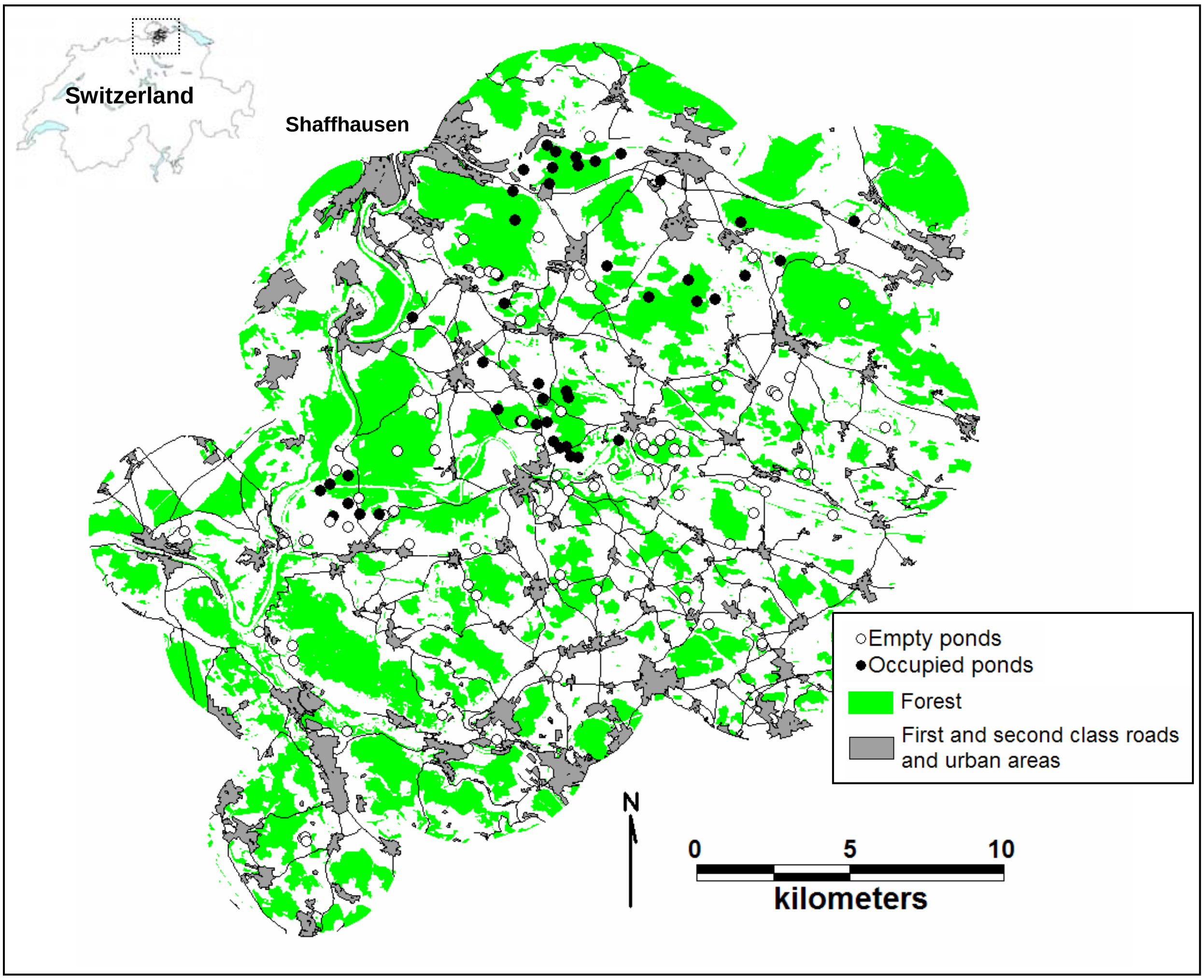

***Figure 1**. Study area and ponds visited (132) in north-eastern Switzerland. Black circle (46) shows ponds with at least one observation of agile frog reproduction between 1997 and 2003, white circle (86) illustrates ponds with no observations. Forest, roads and urban areas are showed within 3 km radius from ponds.*

We studied the distribution of the agile frog in 132 ponds in north-eastern Switzerland (Figure 1). Presence and absence of the species was determined by field surveys during the spring 2003, for the Swiss amphibian red list updating (Schmidt and Zumbach 2005). In addition, the distribution records were completed with data from the Swiss Amphibian and Reptile Conservation Program (KARCH). The specie was considered to be present in ponds if at least one of the breeding indicators (calling males, tadpoles, juveniles or amplexus) was detected on at least one occasion between 1997 and 2003. Agile frog distribution has been intensively monitored which help to minimize non-detection of the species (Pellet and Schmidt 2005). The Agile frog was found in 47 ponds (prevalence of 35.6%). The landscape in the region is typical for the Swiss plateau. The land-cover in the region is characterized predominantly by arable land (55%), forest cover (32%) and urban settlements (9%). The mean altitude of the ponds is 419 m a.s.l.

Landscape data extraction

Landscape variables were extracted from the VECTOR25 database, which represents the vector format of the 1:25000 topographical maps of Switzerland (SWISSTOPO 2003). Data precision is approximately 3-8 meters in flat areas (SWISSTOPO 2003). We selected 7 landscape covariates (predictors) which might affect the distribution of the agile frog (Table 1). In order to estimate the distance at which landscape variables affect the use of ponds by agile frogs, we used a multiple scale sampling (Pellet et al. 2004). The densities of each landscape variable (Table 1) were calculated based on 17 concentric discs of different radii centered on each of the breeding ponds (100, 200, …, 900, 1000, 1200, 1400, 1600, 1800, 2000, 2500 and 3000 m). We decided to include investigations across landscapes in large discs because recent studies suggest that the effect of adjacent land use can extend over comparatively large distances from ponds (Houlahan and Findlay 2003).

***Table 1**. Landscape variables extracted in each of 17 concentric discs of radii from 100 m to 3000 m.*

Variable	Description	Unit
AGRI	Proportion of arable lands and pastures	%
FOREST	Proportion of forest	%
MARSH	Proportion of marsh	%
BUSH	Proportion of bushes and hedgerows	%
URBAN	Proportion of urban areas	%
ROAD1CLASS	Total length of 1st class roads divided by the disc area	m/m2
ROAD2CLASS	Total length of 2nd class roads divided by the disc area	m/m2

Statistical analyses

We constructed Moran's I correlograms to investigate the degree of SA in response variables and predictors (Moran 1950, Legendre and Fortin 1989). Moran's I varies between [-1;1], with positive values representing a positive correlation. Moran's I was calculated in distance classes of 0-1000, 1000-2000, ..., 14000-15000 meters. 1000 permutations were calculated to determine if SA for variables was significantly different from zero (p value<0.05) in all distance classes. We used the ncf package of R 2.1.0 (Bjørnstad 2001-2004) to calculate Moran's I and associated statistics.

We built autologistic models to integrate the SA of the response variables (Augustin et al. 1996) (equation 1):

$$\text{logit}(p_i) = \beta_0 + \beta_1 X_{1i} + \ldots + \beta_n X_{ni} + \beta_m \Phi_i + \varepsilon \qquad \text{(eq. 1)}$$

where β_m is the parameter estimate for the autocovariate and ε the error term. Augustin et al. (1996) and Knute et al. (2002) used the following autocovariate term (equation 2):

$$\Phi_i = \frac{\sum_{j=1}^{k_i} \frac{1}{d_{ij}} y_j}{\sum_{j=1}^{k_i} \frac{1}{d_{ij}}} \qquad \text{(eq. 2)}$$

The autocovariate in the model represents the weighted average of the number of occupied ponds by species in a set (i.e. buffer distance of all the landscapes) of *Ki* neighbours of pond *i*. d_{ij} is the distance between patch i and j. y_i is a binary variable which indicates the state of occupancy of the patches j (y_i =1 if the species is present and y_i =0 if absent). In equation 2 the weight ($1/d_{ij}$) is the inverse of the Euclidean distance (d_{ij}) between breeding ponds *i* and *j* (Augustin et al. 1996). However, alternative measures of SA can be computed and introduced in autologistic models, assuming a negative exponential dispersal kernel ($e^{(-\alpha d_{ij})}$, Hanski 1994) (equation 3).

$$\Phi \exp_i = \frac{\sum_{j=1}^{k_i} e^{(-\alpha d_{ij})} y_j}{\sum_{j=1}^{k_i} e^{(-\alpha d_{ij})}} \qquad \text{(eq. 3)}$$

A negative exponential relationship is used in metapopulation analyses to weight the effect of distance on the estimation of patch connectivity. The parameter α scales the effect of distance to migration ($1/\alpha$ is the average migration distance of the species under study). Equation 3 allows the representation of species-specific dispersal parameters in the estimation of spatial autocorrelation. We found only one published work estimating dispersal distances for adult agile frogs (max of 300 m, Ponsero and Joly 1998) but there appears to be no published data giving dispersal distances for the juveniles. Due to the scarcity of this dispersal distance data we decided to carry-out the statistical tests assuming various dispersal distances: 100 m, 500 m, 1000 m and 2000 m. Thus, a total of 5 autocovariates were estimated.

We included in the autologistic model the autocovariate which explains the higher deviance (D^2) in the univariate logistic regression (Sokal and Rohlf 1995). We then built an autologistic model for each buffer radius, following three methodological steps: firstly, we used a logistic regression and we kept for further analysis all predictors (landscape variables) whose univariate regression coefficient was significant at the 0.25 level (Hosmer and Lemeshow 1989). Secondly, we ranked retained variables and the autocovariates in autologistic model by decreasing the value of the explained deviance (D^2). We then carried out a “both” stepwise regression using the minimum value of the Akaike Information Criterion (AIC) as the selecting criterion (Dalgaard 2002). “Both” stepwise regression removes (“backward” direction) and adds (“forwards” direction) successively the variables to the model. Thirdly, we retained in the final autologistic model only predictors whose explained deviance was significant at the 5% level (Hosmer and Lemeshow 1989). We made separate statistical analyses for each buffer radius (distance-dependent analysis), in order to estimate the spatial scale (i.e. the distance from the breeding pond) of the effect of the landscape variables (Vos and Chardon 1998, Houlahan and Findlay 2003, Pellet et al*.* 2004). An identical analysis was also computed without the autocovariate term in order to estimate the consequences on the results due to the exclusion of SA.

Results

Spatial autocorrelation patterns

The clustered distribution of agile frogs in this region is evident from the map in Figure 1. Three main population groups can be identified: in the north, centre and west of the study area, respectively. As expected, the clustered distribution is detected by Moran's I correlogram, which measured significant SA for the response variable (Figure 2). Agile frog presence was most strongly autocorrelated for the four smallest distance classes (until 4 km). The significant autocorrelation that was detected in classes between 7 and 9 km was driven by the distance separating the three clusters of occupied ponds. Significant SA was also detected in the landscape predictors (Table 2). The landscape predictors that were measured within large disc radii from breeding ponds were generally found to be more correlated than the predictors measured at shorter distances. Indeed, if the discs' radii are larger, then the overlapping area between discs is more likely to be larger. This correlation is more frequently significant for small Moran's I distance classes.

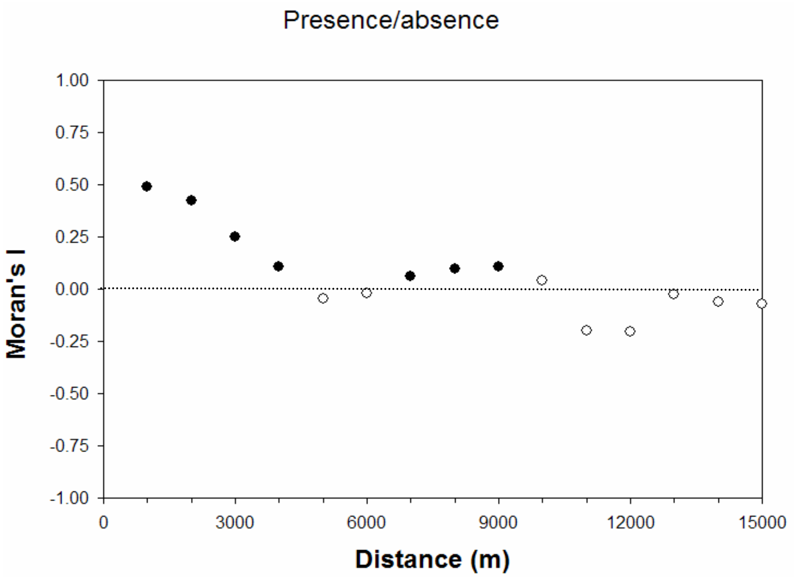

***Figure 2**. Moran's I correlogram for response variable (presence/absence) of agile frog distribution in 132 breeding ponds. Filled circles indicate Moran's I value significantly difference from zero (p<0.05)*

Table 2. *Moran's I value significantly different from zero (p<0.05, black squares) for all the landscape variables measured in discs with radii varying between 100 - 3000 m from breeding ponds of the agile frog. Moran's I is calculated in 1 km distances classes.*

	Moran's I distance classes [km]														
Landscape predictors	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
AGRI 100	■					■									
200	■					■			■						
300	■	■				■			■						
400	■	■				■			■						
500	■	■				■	■		■						
600	■	■				■	■		■						
700	■	■				■	■		■						
800	■	■				■	■		■						
900	■	■				■	■		■						
1000	■	■				■	■		■						
1200	■	■	■		■	■	■								
1400	■	■	■		■	■	■								
1600	■	■	■	■	■	■	■	■							
1800	■	■	■	■	■	■	■	■	■	■					
2000	■	■	■	■	■	■	■	■	■	■					
2500	■	■	■	■	■	■	■	■	■	■					
3000	■	■	■	■	■	■	■	■							
FOREST 100	■					■									
200	■					■			■						
300	■					■			■						
400	■	■				■	■		■						
500	■	■				■	■		■						
600	■	■				■	■		■						
700	■	■				■	■		■						
800	■	■				■	■		■						
900	■	■				■	■		■						
1000	■	■				■	■								
1200	■	■	■			■	■								
1400	■	■	■			■	■								
1600	■	■	■			■	■								
1800	■	■	■			■	■			■					
2000	■	■	■	■			■		■	■					
2500	■	■	■	■	■		■		■	■					
3000	■	■	■	■	■	■			■	■					
MARSH 100								■	■						
200								■	■						
300		■						■							
400	■	■						■						■	
500	■	■						■						■	
600	■	■						■		■					
700	■	■						■		■					
800	■	■						■	■	■					
900	■	■						■	■						
1000	■	■						■	■						
1200	■	■							■						
1400	■	■							■	■					
1600	■	■							■	■					
1800	■	■						■	■	■					
2000	■	■						■	■	■					
2500	■	■	■	■					■	■	■				
3000	■	■	■	■					■	■	■				
BUSH 100															
200															
300															
400	■														
500	■														
600	■	■								■					
700	■	■								■					
800	■	■													
900	■	■							■						
1000	■	■													
1200	■	■									■				
1400	■	■													
1600	■	■	■					■							
1800	■	■	■					■							
2000	■	■	■					■							
2500	■	■	■	■											
3000	■	■	■	■							■				

	Moran's I distance classes [km]														
Landscape predictors	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
URBAN 100	■									■					
200															
300															
400		■			■										
500		■			■										
600		■			■										
700		■			■										
800	■	■			■										
900	■	■			■										
1000	■	■			■										
1200	■	■			■										
1400	■	■			■										
1600	■	■			■	■				■					
1800	■	■			■	■				■					
2000	■	■	■		■	■									
2500	■	■	■	■	■										
3000	■	■	■	■	■	■									
ROAD1CLASS 100															
200	■	■				■									
300	■	■				■					■				
400	■	■				■	■				■				
500	■	■					■			■					
600	■	■					■			■			■		
700	■	■								■			■	■	
800	■	■	■							■			■	■	
900	■	■	■							■			■	■	
1000	■	■	■							■			■	■	
1200	■	■	■										■	■	
1400	■	■	■										■	■	
1600	■	■	■										■	■	
1800	■	■	■										■	■	
2000	■	■	■	■									■	■	
2500	■	■	■	■									■	■	
3000	■	■	■	■									■	■	
ROAD2CLASS 100				■											
200	■			■							■				
300	■		■	■							■				
400	■			■											
500	■		■	■			■								
600	■	■	■	■											
700	■	■	■	■											
800	■	■	■	■											
900	■	■	■	■											■
1000	■	■	■	■										■	
1200	■	■	■	■										■	
1400	■	■	■	■										■	
1600	■	■	■	■		■								■	
1800	■	■	■	■										■	
2000	■	■	■	■										■	
2500	■	■	■	■	■	■									
3000	■	■	■	■	■	■									

Logistic and autologistic regression

We found that all five autocovariates are highly significant and explained a deviance higher than 20% in univariate logistic regression (Table 3). The highest deviance (D^2=30.0%) is explained by the autocovariate with a mean dispersal distance of 1000 m. This autocovariate will be used in autologistic models.

Table 3. *Regression coefficients (β) and standard errors (SE) from the logistic regression using single autocovariates predictors. For autocovariate formulae explanations see equations 2 and 3. D^2 is the explained deviance.*

Autocovariates	**$1/\alpha$**	**β**	**SE**	**p-value!**	**AIC§**	**D^2**
$\Phi \exp_i$	1000	5.79	1.02	***	123.44	30.0%
$\Phi \exp_i$	2000	8.44	1.60	***	126.55	28.2%
$\Phi \exp_i$	500	4.00	0.69	***	129.49	26.5%
Φ_i	-	11.83	2.23	***	130.90	25.7%
$\Phi \exp_i$	100	2.54	0.47	***	139.93	20.4%

! *p≤0.05, **p≤0.01, ***p≤0.001 (likelihood ratio test).
§ Akaike Information Criterion.

The comparison between autologistic and logistic models revealed important differences (Table 4). The significant value of MARSH is accentuated and detected at all buffer radii, except at 600 and 700 m. In addition, a supplementary variable (ROD2CLASS) was significant, with a negative effect at several distances from the breeding ponds.

Moran's I correlograms indicated significant autocorrelation of regression residuals for small-distance classes for the logistic models (Figure 3, B), while the autocorrelation of residuals is not significant for the autologistic models (Figure 3, A).

In the autologistic model, only the autocovariate and at most the proportion of marsh area (MARSH) are retained (Table 4). MARSH was retained at short distances from the ponds (100, 200 and 300 m) and at larger distances (1600, 1800 and 2000 m) (Table 4). The best model was found for a distance of 1800 m and it explained 34.6% of the deviance. Adding landscape covariates, after the autocovariate, increases the explained deviance of the autologistic model by less than 5% (Figure 4).

Table 4. *Multiple autologistic and logistic models with landscape predictors computed at various distance from agile frog breeding ponds. The parameter estimates and their standard error are shown for each retained predictor. The predictors retained in the models allowed (i) for the construction of the most parsimonious model, and (ii) they significantly reduced the explained deviance at the 5% level. Bold indicates the most parsimonious models (min AIC).* D^2 *is the explained deviance.*

	Model predictors							
Distance (m)	**MARSH**		**ROAD2CLASS**		$\Phi\exp_i$!		**AIC§**	**D^2**
A) Autologistic models								
100	9.524 ± 5.400	*	-		5.77 ± 1.05	***	119.61	33.4%
200	32.412 ± 16.494	**	-		5.78 ± 1.06	***	118.09	34.3%
300	33.118 ± 19.127	*	-		5.51 ± 1.03	***	120.28	33.0%
400	-		-		5.79 ± 1.02	***	123.44	30.0%
500	-		-		5.79 ± 1.02	***	123.44	30.0%
600	-		-		5.79 ± 1.02	***	123.44	30.0%
700	-		-		5.79 ± 1.02	***	123.44	30.0%
800	-		-		5.79 ± 1.02	***	123.44	30.0%
900	-		-		5.79 ± 1.02	***	123.44	30.0%
1000	-		-		5.79 ± 1.02	***	123.44	30.0%
1200	-		-		5.79 ± 1.02	***	123.44	30.0%
1400	-		-		5.79 ± 1.02	***	123.44	30.0%
1600	113.360 ± 50.830	*	-		5.19 ± 1.05	***	120.04	33.2%
1800	**157.560 ± 58.513**	******	**-**		**5.16 ± 1.06**	*******	**117.62**	**34.6%**
2000	176.286 ± 69.598	*	-		5.07 ± 1.06	***	118.76	33.9%
2500	-		-		5.79 ± 1.02	***	123.44	30.0%
3000	-		-		5.79 ± 1.02	***	123.44	30.0%
B) Logistic models								
100	6.94 ± 2.94	**	-		-		162.53	7.1%
200	23.78 ± 9.89	***	-		-		160.74	9.3%
300	38.25 ± 15.30	***	-462.79 ± 232.25	*	-		158.71	10.5%
400	46.97 ± 16.99	***	-583.99 ± 267.25	*	-		157.92	11.0%
500	37.49 ± 17.97	*	-732.59 ± 290.58	**	-		161.16	9.1%
600	-		-988.30 ± 314.00	**	-		162.57	7.1%
700	-		-1159.58 ± 347.99	***	-		160.97	8.0%
800	48.66 ± 25.10	*	-1204.00 ± 387.80	***	-		156.64	11.7%
900	53.24 ± 26.79	*	-1249.00 ± 412.00	***	-		156.43	11.9%
1000	64.69 ± 30.19	*	-1231.00 ± 434.80	***	-		156.27	12.0%
1200	90.63 ± 36.83	***	-1196.340± 490.99	*	-		154.96	12.7%
1400	118.77 ± 43.73	***	-1186.33 ± 534.44	*	-		152.19	14.4%
1600	151.74 ± 54.15	***	-1208.06 ± 589.71	*	-		149.84	15.7%
1800	272.65 ± 62.46	***	-		-		148.04	15.6%
2000	**323.28 ± 72.25**	*******	**-**		**-**		**147.42**	**16.0%**
2500	363.20 ± 83.43	***	-		-		150.86	14.0%
3000	358.54 ± 114.62	***	-1468.88 ± 757.29	*	-		154.28	13.1%

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$ (likelihood ratio test).

! Autocovariate with average dispersal distance ($1/\alpha$) of 1000 m.

§ Akaike Information Criterion.

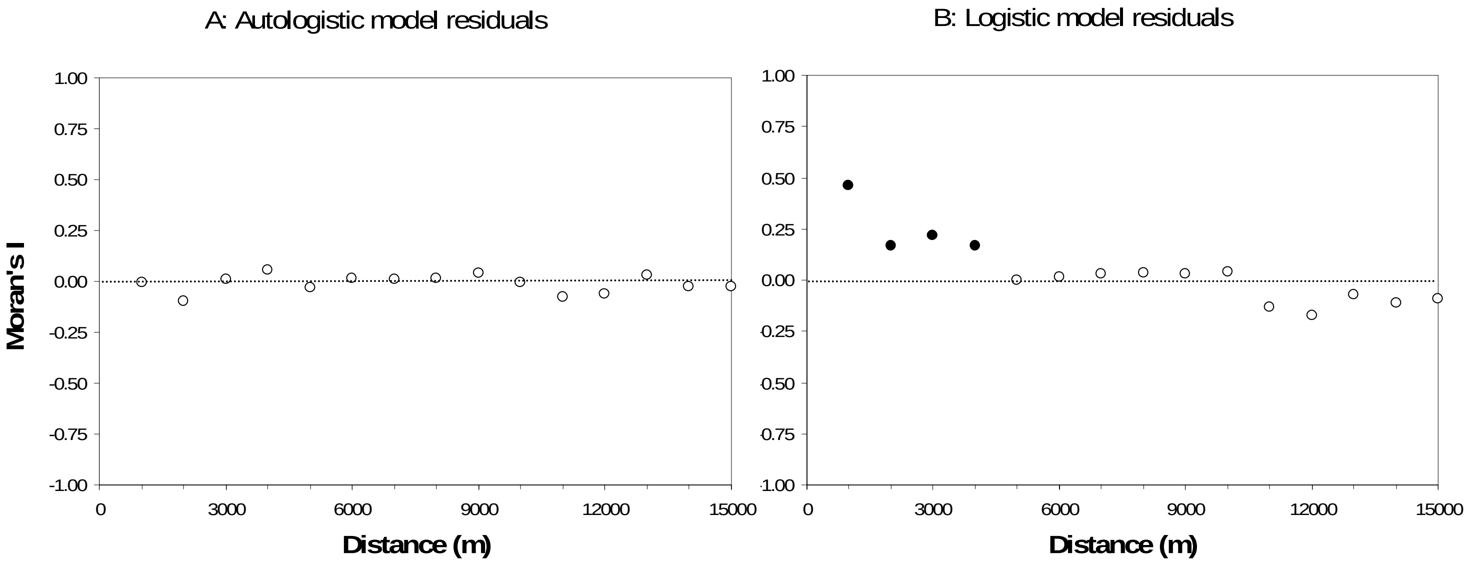

Figure 3. Moran's I correlograms of Pearson residuals from (A) autologistic and (B) logistic regression models for predicting agile frog presence in ponds based on the most parsimonious autologistic model (1800 m radius from ponds). Filled circles indicate Moran's I value significantly different from zero ($p<0.05$). No spatial autocorrelation was observed in residuals from autologistic model.

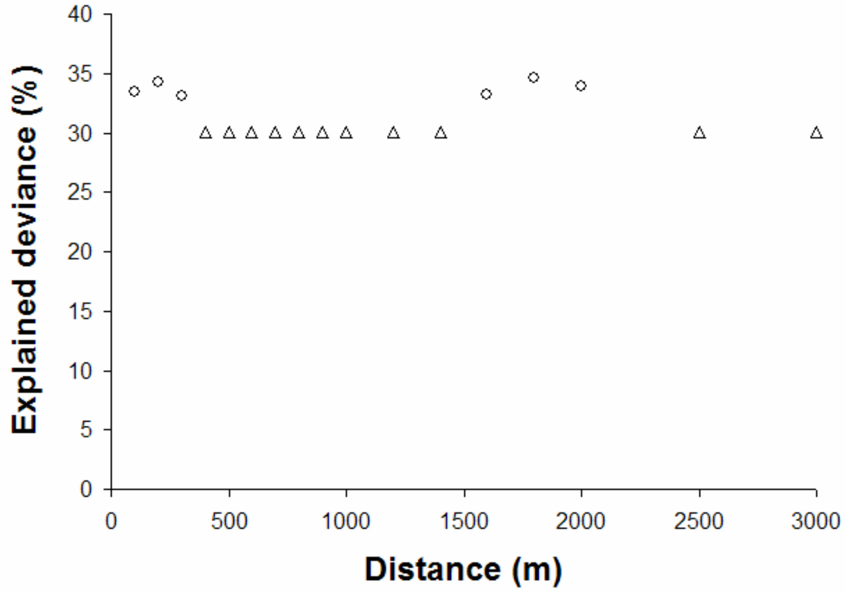

Figure 4. Explained deviance of autologistic regression models computed at different distances from agile frog breeding ponds. Triangles indicate models when only the autocovariate predictor was retained after variable selection. Circles indicate models with both autocovariate and MARSH variables.

Discussion

Legendre and Fortin (1989) underlined that ecologists have to consider *a priori* that their data are structured in space (i.e. autocorrelated). Ecologists therefore should test and describe spatial arrangements using structure functions. This is an imperative in order to avoid a distortion of the results (Lennonn 2000, Fortin and Payette 2002).

In this study, we describe SA in our data and we used autologistic regression to address the issue of non-independence of the data. Our results suggest that autologistic regression is a valuable solution and allows a better assessment of the species-habitat relationship and avoids the bias which may be encountered with the logistic regression analysis. These potential errors were observed in our case study, where logistics models proved inappropriate to investigate the effects of habitat variables on the distribution of agile frogs because the residuals of regression were dependent (Figure 3 A). Consequently, in logistic model the effect of marsh cover was accentuated and a new variable (ROAD2CLASS) was significant at various distances from the ponds. If we had ignored the spatial dependency in our data and had modeled using only logistic regression, we would have overemphasized the importance of the landscape variables because part of the effect due to the spatial dependencies between neighboring ponds would have been attributed to other variables. This has been underlined by other authors (Augustin et al. 1996, Gumpertz et al. 1997, Klute et al. 2002). In addition, the measurements of SA were improved in our study by using (i) a negative exponential relationship with distance among ponds rather than an inverse relationship and (ii) a parameter α which scales the effect of distance to migration. This approach allowed a species-specific description of spatial autocorrelation and thus a better assessment of the spatial information in the data.

For agile frog, we found that an average dispersal distance of 1 km was the distance giving the autocovariate the highest explained deviance (Table 3). This means that 1 km is the dispersal distance for which the observed patterns of presence/absence of species in ponds are better described. Other studies have stressed the importance of a 1 km radius distance from breeding ponds on colonization success and terrestrial habitat use for several amphibian species (Vos and Chardon 1998, Findlay et al. 2001, Marsh and Trenham 2001, Semlitsch and Bodie 2003). However, our result represent only an indication of the dispersal capacity of the species in our landscape, but not an empirical support, since actual distribution patterns could be driven by other factors, such as habitat quality or barriers to species movement. The estimation of dispersal capacity of the species can be done, for example, through field observations of terrestrial movement by radiotracking (Schabetsberger et al. 2004), harmonic direction (Pellet et al. 2006) or mark-recapture experiments (Vos et al. 2000).

Our approach could have several key implications because the non independence nature of the response variable can be expected to be important and frequent for amphibians. Amphibians are often poor dispersers relative to other vertebrates (Sinsch 1990), and a short distance between breeding ponds might be particularly important for their colonization (Sjogren 1991, Blaustein et al. 1994, Vos and Stumpel 1995, Marsh et al. 1999). In our study, the clustered distribution of the agile frog could be due to the dispersal process and colonization (by adults and juveniles) from surrounding ponds.

However, spatial patterns may be driven not only by biotic processes such as dispersal but also by species responses to variations in environmental factors. Environmental factors are themselves also spatially structured (Wagner and Fortin 2005): examples are historical events (e.g. fire), land use, or climate (Sokal and Oden 1978b, Legendre and Fortin 1989, Legendre 1993). It is difficult to discriminate between the relative effects of each of the possible potential causes affecting spatially structured variance. Wagner and Fortin (2005) represented the variance of a regression analyses in 4 components: (i) purely environmental effects (explained by regression models but not spatially structured), (ii) overlap of spatial and environmental effects (spatially structured explained variance), (iii) purely spatial effects (spatially structured explained variance) and (iv) unexplained variance that is not spatially structured. The autocovariate predictor in our autologistic model is able to explain the spatially structured variance of components (ii) and (iii). In other words, it considers a part of the variance possibly due to landscape covariates. This is one of the reasons that explains the low increment of explained variance (less than 5%, Table 4) when landscape covariates are added to the autologistic model.

The effect of marsh cover proportion (MARSH) was the most important among the landscape predictors used in this study. The positive association with MARSH is potentially driven by 4 factors: i) wetland vegetation and water pools, may limit the negative impacts associated with fertilizer, pesticide, and herbicide applications by serving as a sinks for pollutants (Schulz and Peall 2001, Moore et al. 2000, 2002). Arable land covers more than 55% of our study area, thus pond contamination due to agriculture practices may be important. ii) MARSH is a clear indicator of wet conditions in landscape, which may reduce the chances of desiccation when frogs forage away from ponds or hide during the day. iii) It may provide cover from which to escape predation. iv) It could indicate better landscape permeability to agile frog movement. This increases the probability that ponds will re-colonized after local extinctions (Sjogren 1991, Vos and Stumpel 1995). Some authors found the importance of hedgerows as potential dispersal corridors (Ficetola and De Bernardi 2004, Pope et al*.* 2000) and Vos (1999) demonstrating that displaced tree frogs make a preference for hedgerows as movement paths and actively avoid arable land.

Conclusion

Spatial autocorrelation is an important component of ecological systems and needs to be used in the spatial analyses of landscapes (Wagner and Fortin 2005). Once a spatial structure in regression residuals has been detected, it is imperative to remove it in order to avoid inaccurate conclusions about species-habitat relationships (Klute et al. 2002, Legendre et al. 2002). Integration of SA into ecological models (e.g., autologistic models) is imperative if we are to develop an understanding of the influence of environmental variables on species distribution.

In our study we found that autologistic regression is an appropriate technique to analyse dependent data because (i) its application is simple and well adapted for presence/absence data, (ii) these models can effectively avoid SA in regression residuals and (iii) autocovariates may represent spatial ecological processes, such as dispersion, which can be explicitly represented in the models. Autologistic regression analysis is a practical tool to enable the estimation of both the effect of species-habitat relationship and the effect of spatially structured species distribution.

If spatial structure continues to be ignored as an inconvenience, the understanding of inter-relationships between patterns of environmental variables and species spatial distributions will remain confused (Lennon 2000, Wagner and Fortin 2005).

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Chapter 5

Assessing geographic variation in the effects of landscape composition on the distribution of amphibians[*]

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Abstract

Understanding and predicting species distribution is of fundamental importance for ecology, conservation and management. Effective and optimal management strategies can only be formulated after relationships between species distribution and environmental factors have been identified. However, distribution models are usually established for only a single region and it is unknown whether the identified relationships between the distribution of a species and environmental variables can be transferred to another geographic area. We studied the distribution of amphibian species in five geographically distinct areas of Switzerland to address the question of whether the effect of landscape variables varied among regions. We analyzed the effect of 17 variables extracted in concentric disks of varying width (from 100 meters to 3 km) describing landscape composition around ponds at different spatial scales. We used data on the occurrence of 6 amphibian species in a total of 655 breeding sites. We also tested whether spatial proximity to neighboring populations (i.e.

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connectivity) was an important determinant of species distribution. We used logistic regression and information-theoretic model selection to evaluate 585 candidate models for each species. We found that the explained deviance of each species' best models varied between 5% and 32%. Models that included interactions between a region and a landscape variable performed best for three more widely distributed species. For two out of three rarer species, the best models did not include interactions, but different regions had different probabilities of pond occupancy for the same value of the landscape variable. This suggests that caution is needed when predictions of species occurrence are made in separate geographic regions. The spatial scale at which landscape variables affected species distribution varied from a hundred to several km, which was in agreement with several recent studies suggesting multi-scale effects of habitats variables. Thus, different species are affected by different landscape variables at different spatial scales and these effects may vary geographically. We also found that connectivity was generally more important (in terms of explained deviance) than landscape variables, the latter having only marginal effects. This suggests that metapopulation processes may play a more important role in species distribution than habitat characteristics. In conclusion, there is probably no single conservation strategy for terrestrial habitats that equally benefits all species.

Key words: *Bufo bufo*, *Rana temporaria*, *Rana esculenta* complex, *Rana dalmatina*, *Hyla arborea*, *Triturus alpestris*, habitat modeling, conservation, connectivity, metapopulation, interactions, presence/absence, model selection.

Introduction

Predictive distribution models play an important role in ecology, conservation and management (Guisan and Zimmermann 2000, Lehmann et al. 2002, Guisan and Thuiller 2005). These models of the distribution of species can be used to learn which factors positively and negatively affect the presence of species at particular sites. This is an essential prerequisite for understanding both the general ecology of species and their successful management. A large number of studies deal with the issue of how biodiversity responds to landscape structure, the importance of amount and arrangement of specific habitat types, and isolation of populations (Andren 1994, Turner 1996, Fahrig 2003, Elith et al. 2006). These studies produce statistical relationships between predictor variables and the occurrence of species. The resulting information is then used to make recommendations about habitat management. One desirable feature of such statistical models is their generality. Indeed, in the context of predictive distribution models, the important question is whether the results of one study on one species in one region can be transferred to the same species in a different region. This question has only rarely been addressed (Graf et al 2006, Menendez and Thomas 2006, Randin et al. in press). We therefore analyzed data on the distribution of amphibians, a highly threatened group of vertebrates (Houlahan et al. 2000, Stuart et al. 2004) where species-specific knowledge of the effects of landscape structure are urgently needed (Cushman 2006). We asked whether the effects of predictor variables were homogeneous across different regions or whether they varied geographically.

The effects of habitat fragmentation and landscape scale predictors on amphibian populations has been the subject of a large number of studies (e.g. Fahrig et al. 1995, Vos and Chardon 1998, Pope et al. 2000, Joly et al. 2001, Houlahan and Findlay 2003, Pellet et al. 2004a,b, Van Buskirk 2005). These studies produced varying results depending on the species, region and habitat studied. Predictors did or did not affect species and the effects were variable across regions. For example, Pellet et al. (2004b) identified a set of land use types that affected the distribution of the European tree frog (*Hyla arborea*) in western Switzerland whereas Van Buskirk (2005) noted that the European tree frog was the only species not affected by the structure of the landscape surrounding the breeding ponds in eastern Switzerland. Similarly, for *Bufo americanus*, Lehtinen et al. (1999) found a positive effect of forest cover on the occurrence of the species in two regions of Minnesota (USA), while a negative association was reported by Guerry and Hunter (2002) in Maine (USA). Knutson et al (1999) analyzed the effect of landscape factors on anuran abundance and found that species-landscape associations were different in two areas. Lehtinen et al. (1999) described differences between two Minnesota eco-regions in amphibian assemblage response to habitat loss and fragmentation. Johansson et al. (2005) showed clear but regionally contrasting effects of habitat structure on the population size and genetic diversity of the common frog in Sweden. Such differences among studies call into question the utility of predictive distribution models for species conservation and management.

A further line of research into the landscape ecology of amphibians investigated the spatial scale at which landscape factors affect the presence of amphibians in ponds (e.g. Vos and Stumpel 1995, Pope et al. 2000, Johnson et al. 2002). Again, different studies have produced quite different results about the relevant spatial scales. For example, Houlahan and Findlay (2003), Gibbs et al. (2005) and Price et al. (2005) reported that land-use effects peaked at distances of several kilometers. Other reported that far smaller distances were important (less than 1000 m; e.g. Pellet et al. 2004b, Porej et al. 2004, Herrmann et al. 2005, Mazerolle et al. 2005). Recently, Loman and Lardner (2006), found that in experimental conditions the water quality of farmland ponds in Southern Sweden has no effect on the reproductive success of two frog species. Their results indicate that other factors (i.e. the terrestrial habitat quality and the metapopulation structure) have to be considered in order to understand the drivers of distributional patterns.

Connectivity may also determine the presence or absence of a species in a pond. Suitable ponds may be unoccupied if they cannot be colonized. We expected that pond connectivity is an important predictor because it increases the probability that an “empty” pond is being colonized (e.g. Laan and Verboom 1990, Vos and Stumpel 1995, Sjögren 1991). Thus, because the distribution of species may be determined by both landscape and connectivity, it is important to include and differentiate their relative contribution in distribution models. This aspect has been only rarely addressed (Pope et al. 2000, Knapp et al. 2003, Denoel and Lehmann 2006).

Our goal was to investigate the following research questions: (1) Is there geographic variation in the effects of landscape composition around the ponds on the distribution of species? (2) Is there an effect due to pond connectivity? (3) What is the spatial scale of the effect of landscape composition? We examined landscape-level habitat relationships and geographic variations thereof for five anuran and one caudate amphibian species by measuring associations with their presence in 655 ponds in five different regions of Switzerland. The proportion of human-induced or natural uninhabitable habitats (e.g. urban and arable lands) and more natural areas (e.g. forest) varied widely across the region studied.

Materials and Methods

Study areas and species

Five areas were selected in intensively cultivated and densely inhabited regions of Switzerland (Zurich, Bern, Vaud, Valais and Ticino), all below 1000 m (Figure 1). The areas differ in important aspects of land use. Arable land and pastures are predominant in all three regions located in the Swiss Plateau (Zurich, Bern and Vaud). Vineyards are one of the predominant forms of agriculture (12%) in Valais (VS). Ticino (TI) is, on the other hand, mainly forested (47%) and is the most urbanized region (16%). General landscape statistics are presented in Table 1.

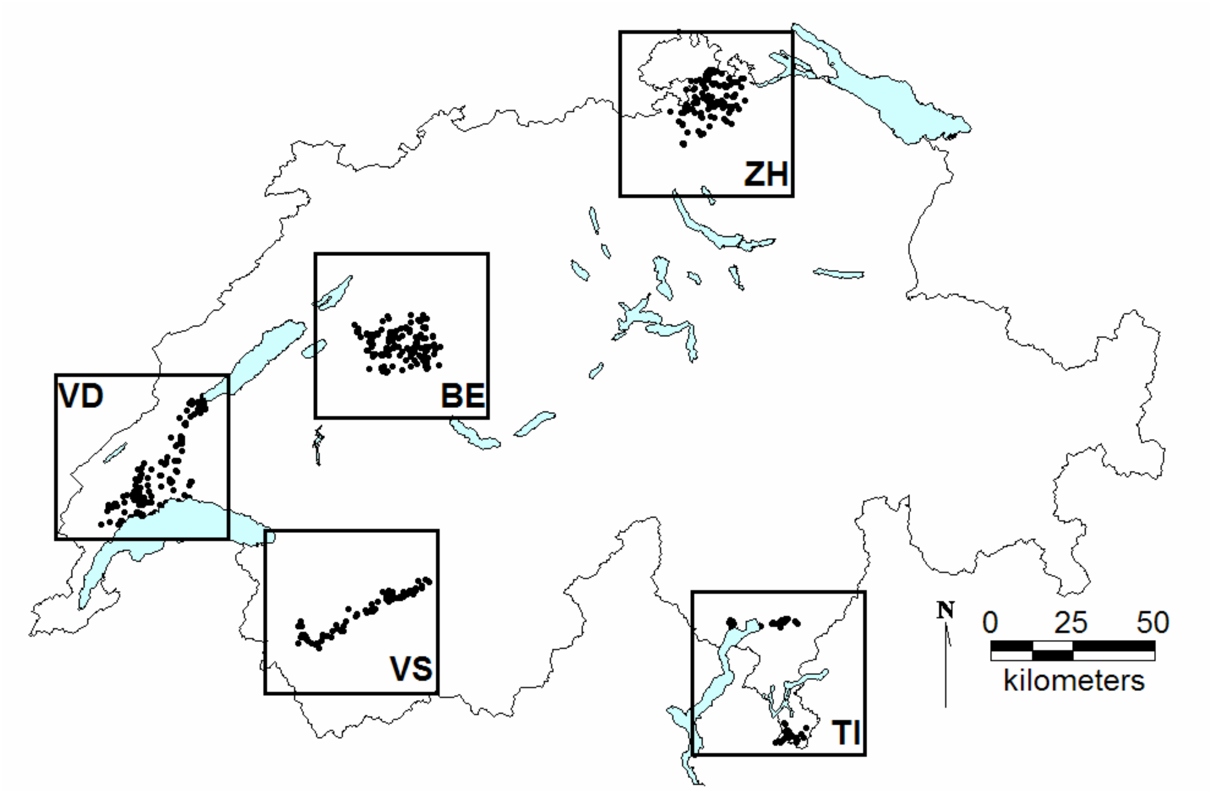

Figure 1. *Location of the 5 study areas and the 655 amphibian breeding ponds in Switzerland (VD= Vaud, BE=Berne, ZH=Zurich, VS=Valais, TI=Ticino).*

***Table 1**. Site occupancy, landscape composition and mean altitude of ponds among the five study regions. Total sample size is 655 ponds*

			Regions		
	ZH (n=132)	**BE (n=215)**	**VD (n=150)**	**TI (n=70)**	**VS (n=88)**
Species (proportion of sites occupied)					
Common Toad (*Bufo bufo*)!	0.20	0.36	0.31	0.30	0.42
Common frog (*Rana temporaria*)!	0.61	0.47	0.52	0.37	0.56
Water frog (*Rana esculenta* complex)	0.59	0.29	*	0.51	*
Alpine newt (*Triturus alpestris*)!	0.36	0.31	0.23	*	*
Agile Frog (*Rana dalmatina*)	0.35	*	*	0.71	*
Tree frog (*Hyla arborea*)	0.33	*	0.32	*	*
Landscape composition (proportion)					
Urban	0.09	0.14	0.10	0.16	0.11
Forest	0.32	0.28	0.19	0.47	0.36
Arable lands and pastures	0.55	0.56	0.54	0.24	0.28
Vineyard	0.01	0.00	0.03	0.03	0.12
TOTAL	0.97	0.98	0.86	0.90	0.87
Mean pond altitude (m)	419	564	525	314	530

! Commoner species in Switzerland (Schmidt and Zumbach 2005)
* Species absent from region or proportion of sites occupied <15% (see text)

Amphibian distribution has been intensively monitored in 665 ponds in these regions in recent years. All sites were visited multiple times such that non-detection of species that were present is unlikely to be a problem (Pellet and Schmidt 2005, Mazerolle et al. 2005). Species occurrence data were collected by the Swiss Amphibian and Reptile Conservation Program (KARCH). Species were considered present in ponds if one of the breeding indicators (calling males, tadpoles, juveniles or amplexus) was detected at least once between 1997 and 2003. This also ensures that year-to-year variability in species presence is buffered.

Because we wanted to explore species-habitat relationships with sufficient statistical power, we analyzed species distribution only in regions where species occupancy was higher than 15%. Rarer species that also occurred were therefore excluded. Given this criterion, we selected six species: five anurans (*Bufo bufo*, *Rana temporaria*, *Rana esculenta* complex, *Rana dalmatina* and *Hyla arborea*) and one newt (*Triturus alpestris*). As a consequence of the threshold for inclusion in the study, *B. bufo* and *R. temporaria* were studied in all the five regions, *R. esculenta* complex and *T. alpestris* in three regions and, on the other hand, *R. dalmatina* and *H. arborea* in two regions only (Table 1).

According to the red list of endangered amphibian species in Switzerland (Schmidt and Zumbach 2005), *B. bufo* is vulnerable and *R. dalmatina* and *H. arborea* are endangered. *Rana esculenta* complex is near the threatened category whereas *Rana temporaria* and *Triturus alpestris* are of least concern.

Landscape variables

Landscape variables were extracted from the VECTOR25 database, which is the vector format of the 1:25,000 topographical maps of Switzerland (SWISSTOPO 2003). Data precision is approximately 3-8 meters in flat areas (SWISSTOPO 2003). We selected 17 landscape variables (Table 2) representing different types of land cover which have been shown to affect amphibian distribution in Switzerland (Pellet et al. 2004b) and which were available for all the studied sites. Landscape variables characterize the landscape composition (i.e. the type and amount of landscape components (Forman and Godron 1986) in the landscape surrounding the breeding ponds.

***Table 2**. Landscape composition variables (17) extracted in each of 17 circles of radii from 100 m to 3000 m from ponds. A total of 289 variables (17 variables x 17 circles) describe the landscape around each breeding pond.*

Variable	Description	Unit
AGRI	Proportion of arable lands and pastures	%
FOREST	Proportion of forest	%
LAKE	Proportion of lakes	%
URBAN	Proportion of urban areas	%
VINE	Proportion of vineyards	%
ORCHARD	Proportion of orchards	%
MARSH	Proportion of marsh	%
BUSH	Proportion of bushes and hedgerows	%
MINERAL	Proportion of mineral extraction sites (gravel pits)	%
MAINRIVER	Proportion of main rivers	%
RIVER	Total length of rivers divided by the disk area	m/m2
ROAD1CLASS	Total length of 1st class roads divided by the disk area	m/m2
ROAD2CLASS	Total length of 2nd class roads divided by the disk area	m/m2
ROAD12CLASS	Total length of 1st class roads + 2nd class roads divided by the disk area	m/m2
HIGHWAY	Total length of highway divided by the disk area	m/m2
RAILROAD	Total length of rail road divided by the disk area	m/m2
HEDGE	Total length of hedgerows divided by the disk area	m/m2

In order to estimate the distance at which the adjacent landscape affected amphibian presence in a breeding pond, we extracted landscape composition variables at multiple spatial scales (Pellet et al. 2004b). These variables were calculated on the basis of 17 concentric disks of different radius (100, 200, …, 900, 1000, 1200, 1400, 1600, 1800, 2000, 2500 and 3000 m) centered on each of the breeding ponds. Large scales were chosen because recent studies suggest that land use at 2000 m and beyond could affect amphibian species occurrence (e.g. Houlahan and Findlay 2003). Variables measured at different scales were labeled by adding the radius of circle to the name of the land use (i.e. FOREST100, FOREST200, …). Thus a total of 289 landscape variables (17 variables x 17 disks) were measured for each breeding pond. Automated variable extraction was programmed in Mapbasic 7.5 software (Mapinfo corporation © 1985-2003).

Connectivity

To estimate the effect of connectivity on species occurrence we computed an additional variable ($CONNECT_i$, equation 1) measuring the connectivity of each patch *i*, assuming a negative exponential dispersal kernel. The negative exponential relationship weights the effect of distance on patch connectivity and is derived from metapopulation theory (Hanski 1999).

$$CONNECT_i = \sum_{j \neq i} e^{(-\alpha d_{ij})} y_j / \sum_{j \neq i} e^{(-\alpha d_{ij})} \qquad \text{(eq. 1)}$$

In equation 1, d_{ij} is the distance between patch *i* and *j*. y_j is a binary variable which gives information about the state of occupancy of the patches *j* (y_j=1 if the focal species is present and y_j=0 if absent). The parameter α scales the effect of distance to migration (1/α is the average migration distance of the species). Because no information is available on the dispersal distance of the species in the study area and the literature on the distance of species movement is limited and often only approximate (e.g. the maximal distance of dispersion of adults, but a maximum does not characterize a population well) (Smith and Green 2005), we analyzed the effect of different average migration distances (100 m, 500 m, 1000 m and 2000 m). These preliminary analyses showed that the strongest association between the occurrence of all the species and the variable $CONNECT_i$ is obtained when an average migration distance of 1 km is used (Zanini et al., unpublished data).

Spatial autocorrelation (SA) is often encountered in ecological data (Lichstein et al. 2002) and may be source of problems if not properly addressed. Indeed, if the presence of species in a breeding pond could be in part predicted by their presence in the neighboring ponds (positive SA), then observations are not statistically independent and consequently we might encounter statistical errors (incorrect estimation of the degree of freedom). The magnitude of habitat effect tends to be overestimated and the relative importance of different habitat variables can shift (Borcard et al. 1992, Legendre 1993, Augustin et al. 1998, Lichstein et al. 2002, Klute et al. 2002, Legendre et al. 2002). Here, we ensure the correct applicability of statistical tests because $\mathrm{CONNECT}_i$ is an extension of the measure of SA proposed by Augustin et al. (1996), which is used to integrate the spatial variance of response variables with presence/absence data and species-specific dispersal parameters (Zanini et al. submitted).

Statistical analyses

We used binary logistic regression (presence/absence of the focal species being the response variable) to investigate the effect of various models on species occurrence (Hosmer and Lemeshow 1989). We designed models starting with the simplest one (univariate) and finishing with the most complex (Table 3). The first 3 candidate models included a single factor each: region (R), altitude (A), and CONNECT (C). We also considered models that included all pair-wise combinations of these variables and a model that included all three variables. Next, we considered models with the three basic variables R, A, and C where a landscape variable was added. This landscape variable was one land use type at one distance (e.g FOREST100: % forest in a buffer of 100 m). Finally, we added the interaction landscape variable by region to test whether landscape composition affected species in the same way in all regions. We fitted 585 models to each of the 6 amphibian species.

***Table 3**. Summary of the 585 candidate models used for modeling the distribution of 6 amphibian species in five regions of Switzerland.*

Model predictors	**#**
REGION	1
ALTITUDE	1
CONNECT	1
REGION+ALTITUDE	1
REGION+CONNECT	1
ALTITUDE+CONNECT	1
REGION+ALTITUDE+CONNECT	1
REGION+ALTITUDE+CONNECT+Landscape	289
REGION+ALTITUDE+CONNECT+Landscape+INTERACTION*	289

Notes: For a description of Landscape variables see Table 2. # indicates the number of models.
* region-by-landscape interaction

We used an information-theoretic model selection approach to identify the models that were best supported by data (Burnham and Anderson 2002). We used Akaike's information criterion (AIC) to rank models according to their strength support from the data and the Akaike weight (*w*) to estimate the relative weight evidence for each model (Burnham and Anderson 2002). *w* can be interpreted as the probability that model *i* is the best model for the observed data, given the candidate set of models. The sum of the Akaike weight of all models is 1.

We determined the relative importance of spatial scale on species distribution by cumulating the Akaike weight of models incorporating landscape variables measured in the same circle radius around ponds (e.g. accumulated Akaike weight at 100m=*w*(AGRI100)+*w*(FOREST100)+…+*w*(HEDGE100)).

Statistical procedures were implemented in R 2.1.0 (R Development Core Team 2005).

Results

Landscape variables, geographic variation and connectivity

The results of model selection are shown in Table 4. The models best supported by the data always included region, altitude, connectivity, a landscape variable and in about half of the cases an interaction. The explained deviance of the best models ranges between 5% (*B. Bufo*) to 32% (*R. dalmatina*) and the Akaike weights ranged between 0.07 (*R. dalmatina*) to 0.45 (*R. esculenta* complex). The best model included interaction between landscape variable and region for the three more widely distributed species (*B. bufo*, *R. temporaria* and *T. alpestris*). The landscape variables interacting with region were HEDGE1000, VINE2500 and RIVER3000, respectively. However, the best models for these three widespread species explained only a small proportion of the deviance and had low Akaike weights (Table 4). The effects of landscape variables on predicted occupancy and their interaction with region are shown in Figure 2. The occupancy probability of a site was associated positively, negatively or not affected by landscape variable as a function of the region.

For the three rarer species (*R. esculenta* complex*, R. dalmatina* and *H. arborea*), the best models did not include interactions, but other top-ranking models with high Akaike weights included it (Table 4). The landscape variables retained in the best models were MARSH100, MARSH200 and FOREST100, respectively. Even if there were no interactions between the landscape variable and region in the best models, different regions had different probabilities of occupancy for the same value of the landscape variable (i.e. there is an effect of the region on pond occupancies; Figure 2). For example, no matter how much marsh was present, the predicted occupancy of *Rana esculenta* complex was always highest in Bern and lowest in Ticino (Figure 2). For only one species, *R. dalmatina*, the predicted occupancy with the best model is not affected by region.

Connectivity alone explained about more than half of the deviance that the best model for each species explained (Table 4). For species where the models explained a substantial amount of deviance, connectivity alone explained 27%, 18% and 18% (for *R. dalmatina, R. esculenta* complex and *H. arborea*, respectively). The absolute effect of connectivity varied across regions (but note that we did not include connectivity-by-region interactions; Figure 3). For some species (e.g. *Rana esculenta* complex), we predicted markedly different probabilities of occupancy at the same level of connectivity whereas for other species predicted occupancy at all connectivities was the same in all regions (e.g. *Rana dalmatina*).

Table 4. *Model selection results. Models are ranked by their Akaike weight (in decreasing order). For clarity, models that include landscape variables with Akaike weight <0.05 are not shown.*

Species	**Model structure†**			**K‡**	**Regression coefficients**		**AIC§**	**Akaike weight**	**D^2!**
		Landscape (L)			**C**	**L**			
Bufo bufo									
	R+A+C+	HEDGE1000	INTERACTION	6	0.55	527.00	803.73	0.11	5%
	C			2	1.73		811.06	0.00	2%
	A+C			3	1.58		811.30	0.00	2%
	R+C			3	1.26		812.17	0.00	2%
	R+A+C			4	1.24		813.76	0.00	3%
	R			2			816.06	0.00	2%
	R+A			3			817.42	0.00	2%
	A			2			819.70	0.00	1%
Rana temporaria									
	R+A+C+	VINE2500	INTERACTION	6	3.63	-0.44	832.98	0.33	13%
	R+A+C+	VINE3000	INTERACTION	6	3.63	-1.08	834.24	0.17	13%
	R+A+C+	VINE2000	INTERACTION	6	3.43	-5.52	834.31	0.17	13%
	R+A+C+	VINE1800	INTERACTION	6	3.43	-2.68	835.52	0.09	12%
	A+C			3	2.79		846.16	0.00	7%
	C			2	2.85		846.95	0.00	7%
	R+A+C			4	2.63		850.89	0.00	8%
	R+C			3	2.73		854.13	0.00	7 %
	R+A			3			896.18	0.00	3%
	R			2			904.04	0.00	2%
	A			2			905.61	0.00	1%

Species	Model structure†			K‡	Regression coefficients		AIC§	Akaike weight	D^2!
		Landscape (L)			C	L			
Extension of Table 4									
Rana esculenta complex									
	R+A+C+	MARSH100		5	2.77	6.86	442.99	0.45	24%
	R+A+C+	MARSH100	INTERACTION	6	2.75	8.37	446.33	0.08	24%
	R+A+C+	MARSH200		5	2.68	12.81	447.28	0.05	23%
	R+A+C			4	2.80		455.47	0.00	22%
	A+C			3	3.14		460.09	0.00	20%
	C			2	3.91		469.62	0.00	18%
	R+C			3	3.70		472.21	0.00	18%
	R+A			3			483.96	0.00	16%
	A			2			504.04	0.00	12%
	R			2			539.88	0.00	6%
Triturus alpestris									
	R+A+C+	RIVER300	INTERACTION	6	1.80	-478.75	582.00	0.12	7%
	R+A+C+	RIVER200		5	1.84	-182.75	582.15	0.11	6%
	R+A+C+	RIVER300		5	1.78	-218.53	582.71	0.08	6%
	R+A+C+	RIVER200	INTERACTION	6	1.84	-344.03	583.05	0.07	6%
	C			2	2.34		590.62	0.00	3%
	R+A+C			4	1.90		591.71	0.00	4%
	A+C			3	2.31		591.76	0.00	3%
	R+C			3	2.14		592.62	0.00	3%
	R+A			3			600.33	0.00	2%
	R			2			604.78	0.00	1%
	A			2			607.89	0.00	0%
Rana dalmatina									
	R+A+C+	MARSH200		5	4.81	28.12	201.42	0.07	32%
	A+C			3	4.66		207.40	0.00	28%
	C			2	4.91		207.63	0.00	27%
	R+C			3	4.73		209.32	0.00	27%
	R+A+C			4	4.73		209.33	0.00	28%
	R+A			3			257.34	0.00	10%
	R			2			258.43	0.00	9%
	A			2			264.67	0.00	7%
Hyla arborea									
	R+A+C+	FOREST100		5	4.13	-2.04	283.53	0.44	23%
	R+A+C+	FOREST100	INTERACTION	6	4.11	-2.18	285.42	0.17	23%
	R+A+C+	MARSH100	INTERACTION	6	4.26	9.70	287.80	0.05	22%
	C			2	4.19		295.52	0.00	18%
	A+C			3	4.10		296.98	0.00	18%
	R+C			3	4.21		297.36	0.00	18%
	R+A+C			4	4.10		298.01	0.00	18%
	R+A			3			351.49	0.00	3%
	A			2			352.07	0.00	2%
	R			2			358.68	0.00	0%

† Variable abbreviations are R=REGION, A=ALTITUDE, C=CONNECT, L=Landscape composition variable (see Table 2), INTERACTION=interaction REGION:Landscape

‡ Number of parameters (intercept parameters is considered).

§ Akaike Information Criterion

! Explained deviance

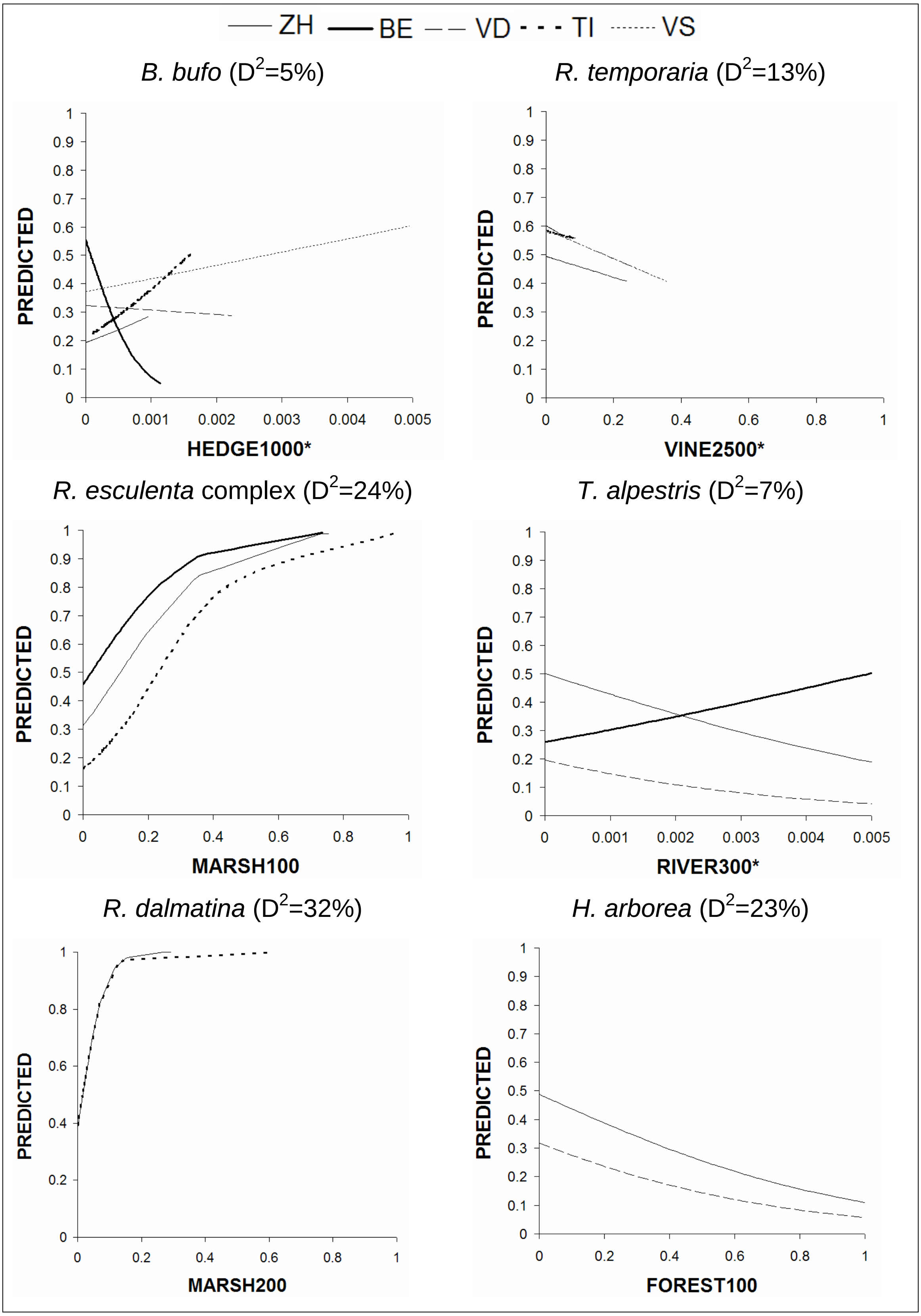

Figure 2. *Prediction of the probability that ponds will be occupied depending on landscape variables. Predictions are based on the best model (Table 4) and using the mean value of ALTITUDE and CONNECT across regions. Asterisks indicate the best model that includes the interaction REGION:Landscape. For R. temporaria only three lines are observable because predictions for BE, TI and VS overlapped. Regions: ZH=Zurich, BE=Berne, VD=Vaud, TI=Ticino, VS=Valais. D^2 is the deviance explained by the model. See Table 2 for landscape variable explanation.*

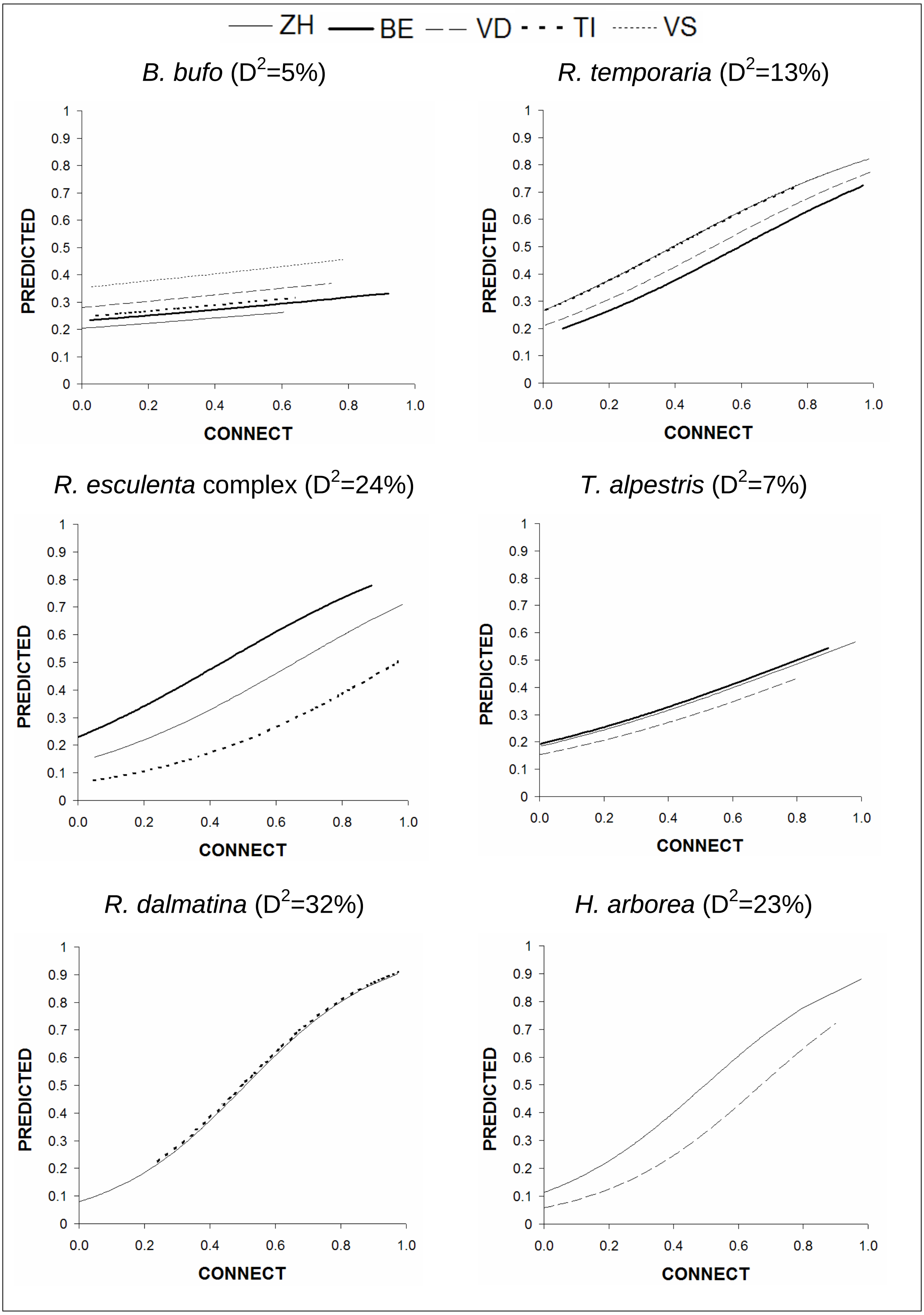

***Figure 3**. Prediction of the probability that ponds will be occupied depending on connectivity of sites (CONNECT). Predictions are based on best model (Table 4) and using the mean value of ALTITUDE and landscape variable across regions. For R. temporaria only three lines are observable because predictions for ZH, TI and VS overlapped. Regions: ZH=Zurich, BE=Berne, VD=Vaud, TI=Ticino, VS=Valais. D^2 is the deviance explained by the model. See Table 2 for landscape variable explanation.*

Spatial scale of landscape composition effect

In Figure 4 we illustrated the accumulated Akaike weights of models as a function of the circle radius within which we study the landscape effect. The relative effect of landscape variables was different between species. It seemed possible to rank species according to their sensitivity to the circle size. Thus, from small to large circle radii, the species sensitivity to landscape composition follows this order: *H*. *arborea*, *R. esculenta* complex, *T. alpestris*, *R. dalmatina*, *B. bufo* and *R. temporaria*. For *H*. *arborea*, *R*. *esculenta* complex and *T. alpestris*, the landscape within a circle of 100-300 m radius around the pond best explains pond occupancy. For *R*. *dalmatina* the landscape within a circle of 600 m radius better explained pond occupancy, while for *B*. *bufo*, the radius extent was around 1000 m. Finally, for *R*. *temporaria* the landscape within a circle of 2500 m around the pond best explained pond occupancy.

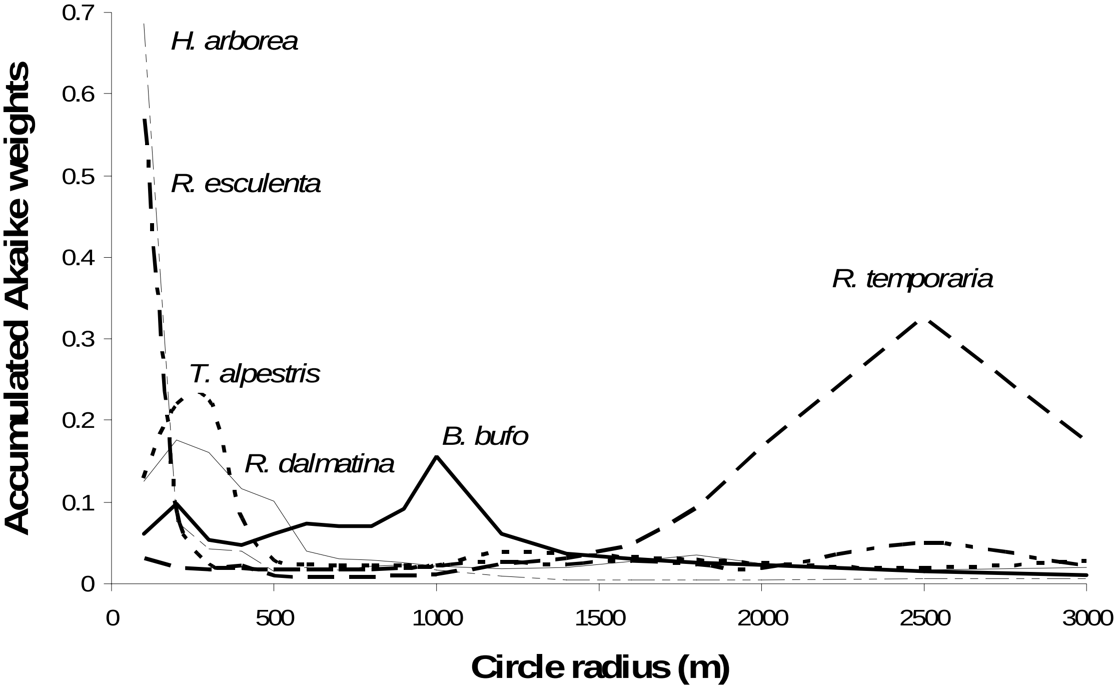

Figure 4. *Accumulated Akaike weights of models by circle radius. Circles are the sampling area within which the landscape effect is assessed and they are centered on ponds.*

Discussion

Our main finding indicated that predictors of amphibian species occurrence had regional specificity. We demonstrated that for the three widely distributed species, the models best supported by data incorporate an interaction between region and landscape composition predictors. For less common species, models that included interactions between region and landscape factors were less supported by the data. However, the region had an effect on pond occupancy for two out of three rare species. Furthermore, we found that connectivity of ponds was an important predictor of species distribution, the effect being most important for the rare species. Finally, we noted that the landscape composition seemed to play a more important role at a larger distance from the breeding site for species having higher seasonal mobility.

Geographic variation in the effects of landscape variables

We found that the effect of landscape composition on species occurrence varied across regions. Hedgerows for example, negatively affected the occurrence of *B. bufo* in the region of Bern, positively in Ticino and had a very weak overall effect in Vaud (Figure 2). It is difficult to provide a biological explanation of how such region-by-landscape variable interactions arise. We believe that landscape variables act in concert with other habitat characteristics and this may result in the fact that a landscape variable affects species distribution differently in different regions. This is not surprising (but see Menendez and Thomas 2006), because one environmental factor is unlikely to play a role independently from others and a context-dependent effect of environmental variables on species seems to be a more realistic view (Blaustein and Kiesecker 2002).

Region-by-landscape variable interactions suggest that models are specific to a region and cannot be generalized to other regions or that the transfer to other regions would require that the biological mechanism creating the interaction is understood and its effect can be predicted. Because the mechanisms creating the interaction can be related to a large set of factors specific to the region (e.g. spatial arrangement of habitats, presence of introduced species, water chemistry, history of experiencing particular stressors, diseases, predators …) it seems difficult and probably time- and cost-consuming to detect it. Thus, from a conservation point of view the region-by-landscape interaction is bad news. We therefore suggest a cautionary use of predictive habitat models in conservation.

However, region-by-landscape interactions had a stronger support from the data for species where the overall explanatory power (i.e. proportion of deviance explained) was low. This was the case for the more widely distributed species (Table 4). Our models explained more deviance and had weaker evidence for interactions for the less widely distributed species (*R. esculenta* complex*, R. dalmatina* and *H. arborea*). These species are of conservation concern and there is a greater need to quantify habitat-species associations and build valid predictive models of their distribution. For these three species, geographic variations in landscape composition effects seemed unlikely to be a great nuisance. This is a positive result for these endangered species and the people who manage them.

The role of connectivity

Our results showed that connectivity is strongly and positively associated with species occurrence. Populations' connectivity has been showed to be a key to the regional viability of amphibian populations (Semlitsch and Bodie 1998, Marsh and Trenham 2001), especially because amphibian populations experience relatively frequent local extinctions and recolonizations (Edenhamn 1996, Alford and Richards 1999, Vos et al. 2000, Trenham et al. 2003). The maintenance and improvement of inter-population individual exchange is therefore a crucial requisite for regional amphibian population persistence.

The positive effects of increasing connectivity indicate that amphibians are spatially organized in clusters of occupied ponds. Because immigration rates increase with proximity to neighboring occupied ponds (e.g. Sjögren 1991, Hanski 1999), rescue effects may maintain populations in ponds that are reproductive sinks most of the time. If there is a source-sink structure, then amphibians may occupy suboptimal ponds (Pulliam 2000). In addition, metapopulation theory suggests that suitable patches could be unoccupied (Hanski 1999). Consequently, because the distribution of species is not only related to habitat quality, some misinterpretation of habitat effect may occur. This is especially important for amphibians due to their breeding site fidelity (Sinsch 1990). For example, Schmidt and Pellet (2005) showed that the distribution of two anuran species was best predicted by the number of calling males in previous years rather than habitat variables, supporting the idea that population processes are more important determinants of distribution than habitat characteristics. This, in turn, makes it difficult to successfully predict amphibian habitat associations and may justify the generally weak effect of landscape variables on species occurrence found in this study.

The effect of landscape composition

Although our study areas are all strongly affected by human activities (Table 1), we did not find evidence for the expected negative effects of anthropogenic landscape elements such as urban area or road density (e.g. Vos and Chardon 1998, Knutson et al. 1999, Pellet et al. 2004b, Rubbo and Kiesecker 2005). One explanation may be that the variability of urban and road density value across ponds is too low to induce a detectable effect. An alternative reason could be that these predictors have no direct effect on amphibian distribution and that more proximal variables (e.g. traffic index rather than road density) should be used in order to define more causal relationships (Fahrig et al. 1995, Pellet et al. 2004a). Also, because we found that the most important variables represented relatively natural land covers, our results suggest as long as there is suitable habitat, the species will persist. In other words, the critical elements seem to be the availability of suitable habitats more than the amount of anthropogenic stressors. If this is true, then the areas with low anthropogenic stressors are not necessarily more favorable for species persistence than the areas with higher anthropogenic stressors when they have the same amount of suitable habitats. These considerations deserve additional investigation, in order to completely understand the contribution of suitable and unsuitable habitats to species distribution.

The spatial scale of the landscape effect

Several studies have found that landscape features can be important up to several kilometers away from breeding ponds (e.g. Houlahan and Findlay 2003, Gibbs et al. 2005, Price et al. 2005). However, in our study, we found better support for landscape effects at a relatively small spatial scale. The landscape effect ranges between hundred meters to 1 km, except for *R. temporaria,* for which the effect peaked around 2500 m (Figure 4). This agreed with other work which also found a landscape effect at less than 1 km (e.g. Porej et al. 2004, Herrmann et al. 2005, Mazerolle et al. 2005, Pellet et al. 2004a).

A potential important factor determining the extent of this scale is the mobility of the species. Here mobility refers to the distance covered each year between aquatic and terrestrial habitats. Species which exhibit greater annual mobility are expected to be more sensitive to landscape composition at a greater distance from aquatic habitats (Weyrauch and Grubb 2004). Our results partially support this assertion. As expected, we found that less mobile species are affected by landscape composition at shorter distances (e.g. *R. esculenta* complex, Holenweg and Reyer 2000). *R. temporaria* (highly mobile species, Blab 1986) are on the contrary affected by landscape composition up to larger distances from breeding ponds than other species (Figure 4). Nevertheless, we failed to find a large spatial scale for the effect of landscape composition on *B. bufo* occurrence. This toad is known to be a highly mobile species, using terrestrial habitat at several km from aquatic site (Heusser 1968).

The species-specific response to the scale of landscape has important implications for species conservation and management. First, variables measured at only one landscape scale (e.g. within 200 m radius from ponds) did not adequately predict occurrences of all species. In the same way, conservation measures at a given scale are unlikely to have similar effects on all species. Our results join the growing body of evidence that management strategies for amphibian habitats should be conducted at multiple scales (Mazerolle and Villard 1999, Johnson et al. 2002, Price et al. 2004, Van Buskirk 2005).

Conclusion

The definition of efficient conservation strategies to reverse amphibian declines will be a great challenge for the coming years and will largely focus on the restoration and creation of suitable breeding habitats. We have shown that pond connectivity is an important predictor of many species occurrences. This underlines the necessity of preserving a functional network of habitat patches. This is especially true for the rarer species.

We also found evidence for a strong regional variability of the effect of landscape on species occurrence. This is a central but poorly understood issue, which needs additional research in order to determine the generalization conditions of predictive habitat models (Graf et al. 2006, Menendez and Thomas 2006, Randin et al. in press). Finally, we found that landscape composition hundreds of meters away from the pond affected species occurrence. This stresses again the importance of incorporating also landscape features at large-scale into the management strategies for amphibian species.

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Chapter 6

The effects of landscape structure on the occurrence of two anuran species: a barriers-based buffers approach*

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Abstract

Species movement and accessibility to terrestrial habitats are dependent on landscape permeability. *Corridors*, such as river banks or hedgerows, favor movement while *barriers*, such as built areas and road network, are obstacles. However, in amphibian autoecology the common practice is to use predictive variables extracted from circular buffers around ponds for the development of species-habitat models. The main assumption is that species are affected by a particular landscape element equally in every direction from a given pond. In accordance with previous considerations, this could be erroneous since barriers or inhospitable surfaces may reduce movement patterns and reshape the ideal circular surface into a non-circular. In this study, we developed a method to determine the effect of habitat variables on amphibian species distribution considering physical barriers of their movement around ponds. We studied two amphibian species: the common toad (*Bufo bufo*) and the common frog (*Rana temporaria*) in a highly fragmented landscape in the Rhone plain, Switzerland. We computed pond scale and

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landscape scale variables (up to 3 km) within (i) “circulars buffers” (CB) and (ii) “barriers-based buffers” (BBB). BBB were produced by reducing the boundaries of CB according to barriers in the study area. Our results show that the BBB approach increases the explanatory power for (i) the majority of the predictors and (ii) the multiple models representing the effects of landscape variables at various distances from the ponds. These results suggest that the proposed BBB approach is ecologically more valid than to the traditional CB analyses of species-habitat relationship. Our study clearly shows the necessity to consider landscape permeability in species distribution models in order to avoid incorrect inferences.

Key words: *Rana temporaria*, *Bufo bufo*, movement, landscape permeability, barriers, landscape resistance, circular and non-circular buffers, conservation, Switzerland

Introduction

Amphibian populations have been declining worldwide for several decades (Houlahan et al. 2000) and are more threatened than either birds or mammals (Stuart et al. 2004). A series of factors affecting amphibian populations have been identified. Amongst these factors, we can list climate change or increased UV-B exposure and, at a more local scale, habitat destruction, agrochemicals and chemical pollution, (invasive) introduced species, human exploitation and disease (for a review see Alford and Richards 1999). Information on the effect of habitat variables on the distribution of species may be very useful for conservation and landscape planning, for example by assisting managers in identifying suitable sites for new pond creation (e.g. Vos and Chardon 1998, Pellet et al. 2004a).

Habitats surrounding breeding ponds are indispensable for the survival of ponds-breeding and dual (aquatic and terrestrial) life-cycle amphibian species. The effect of this surrounding landscape on amphibian occurrence in ponds is traditionally analyzed within circular buffers (concentric disks) centered on ponds (e.g. Knuston et al. 1999, Findlay et al. 2001, Guerry and Hunter 2002, Pellet et al. 2004b, Rubbo and Kiesecker 2005, van Buskirk 2005, Denoel and Lehmann in press) and by using circular buffers of different radii to estimate the scale-dependency effect (e.g. Findlay and Houlahan 1997, Vos and Chardon 1998, Pope et al. 2000, Carr and Fahrig 2001, Joly et al. 2001, Johnson et al. 2002, Houlahan and Findlay 2003, Pellet et al. 2004a, Knutson et al. 2004, Herrmann et al. 2005). The use of circular buffers assumes that the landscape has an isotropic effect on the species presence, so that species are affected by a particular landscape element equally in every direction from a given pond. However, it is likely that frictions in the landscape, such as barriers or inhospitable surfaces, reduce movement patterns (e.g. Marsh et al. 2005, Gibbs 1998) and reshape the ideal circular surface into a non-circular form, which would better reflect the real use of terrestrial landscapes by amphibians. Accordingly, the effect of the terrestrial habitats surrounding the breeding ponds may be better described studying non-circular buffer areas around the ponds. Ray et al. (2002) found that land-use variables computed in friction-based buffers from breeding ponds, improved the prediction of toad presence when compared to circular zones. As a consequences, it is likely that not taking landscape permeability (i.e. the quality of a heterogeneous land area to provide passage for animals (Singleton et al. 2002)) into account may produce distortions (under- or over-estimations) of habitat effect on species distribution and consequently errors in conservation planning.

Landscape permeability is fundamental for species persistence because it determines the possible movement for an individual. Movements can lead to the access of resources, genetic exchanges among populations, colonization of new habitats and re-colonization after local extinction (Hanski 1999). The effect of landscape permeability on movement can be important especially for ground-dwelling animals, such as amphibians, which are more sensitive to the physical quality of the landscape (Wiens 1997). However, in spite of its importance, estimating landscape permeability is difficult task because of the lack of information about the permeability of different land-uses and the difficulty of ascribing a permeability coefficient to each habitat type (Pither and Taylor 1998). For amphibians, such information is usually time- and cost-demanding because it requires intensive fieldwork and expensive radio-tracking equipment (Vos 1999). An alternative is the use of expert knowledge to appreciate land-use friction to species movement. This approach introduces the subjectivity of expert assessment but may be valuable in landscape planning and biodiversity conservation (Ray et al. 2002, Vuilleumier and Prelaz-Droux 2002, Adriaensen et al. 2003, Chardon et al. 2003, Joly et al. 2003, Verbeylen et al. 2003).

The goal of our study is to assess the effect of local scale (ponds) and landscape scale variables (terrestrial habitat surrounding the ponds up to 3 km) on the occurrence of two widely distributed amphibian species. We test whether species occurrence is predicted better by landscape variables extracted within 1) traditional circular buffers or 2) non-circular buffers based on the terrestrial area potentially accessible by individuals. We call these buffers "Barrier-based buffers" (BBB) because they were computed by removing from circular buffers (CB) the areas non accessible due to impassable barriers. Our hypothesis is that landscape variables within BBB better explain species distribution than CB. We assume that BBB more realistically represents the use of terrestrial habitats by amphibians.

Methods

Study area and species

The study area is located in southwestern of Switzerland, in the Rhone Plain (Valais) below 1000 m a.s.l. (Figure 1). The plain has an average width of 2-3 kms and is bordered to the south and to the north by the Swiss Alps. Apart from villages and small cities (13.8%), agriculture (essentially orchard and vineyards) is the predominant land-use in the plain (76.6%) (Zanini et al. submitted). The canalized Rhone river, the highway and the railway divide the study area lengthwise (Figure 1).

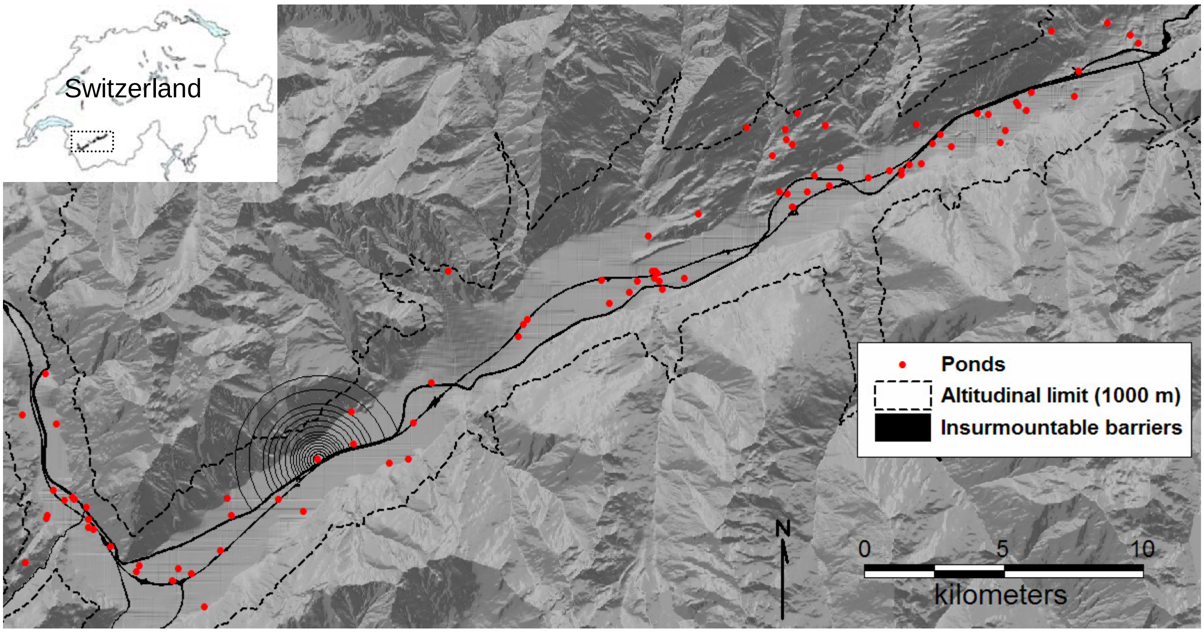


Figure 1. *Study area and 88 visited ponds in the Rhone plain, Central Valais, Switzerland. We show, with the example of one pond, the 17 non concentric disks (i.e. barrier-based buffers) from which landscape variables are extracted. The radii of buffers vary from 100 m up to 3 km. In order to not overload the map, land-uses are not shown. (MNT25, © Swisstopo 1995).*

We studied two amphibian species: 1) *Bufo bufo* (the common toad), which used to be well distributed all over Switzerland but is now in decline (Schmidt and Zumbach 2005), and 2) the *Rana temporaria* (the common frog), which is still widespread in Switzerland and currently not threatened (Schmidt and Zumbach 2005). Species were considered present in ponds if at least one of the breeding indicators (calling males, tadpoles, juveniles or amplexus) was detected at least once between 1997 and 2003. Data on presence/absence of the species in 88 ponds (Figure 1) was provided by the Swiss Amphibian and Reptile Conservation Program (KARCH) and by Paul Marchesi (Environmental office DROSERA SA). *B. bufo* was found breeding in 37 of the 88 sites (prevalence of 42%), while R. temporaria was breeding in 49 (prevalence of 56%).

Pond scale predictors

Pond scale habitat variables were collected during field surveys in July and August 2004 (Table 1). Two persons visited each breeding site once.

The abiotic factors, fish presence, the vegetation cover and the land-cover in a radius of 30 meters around the ponds (Table 1: A, C and D) were estimated by eyesight. The presence/absence of fish (Fish) was determined upon whether it individuals were seen or not. Temporary breeding site (Dry) were determined if there was no water visible in the pond during the visit.

Three measures were made to access the chemical characteristics (water pollution) of the water for each site (Table 1, B): (i) pH (water acidity), (ii) conductivity (dissolved ions) and (iii) nitrate (concentration of nutrients). Measurements of pH and water conductivity were made 1 m from the bank in three different locations around the pond using a pH-meter (WTW model pH 330) and a conductivity-meter (HACH model 44600). The mean values of the pH and conductivity were used for statistical purpose. Water samples were taken from each breeding site and analyzed the same day using a spectrophotometer in order to assess the nitrate concentrations, (HACH model DR/2000, Cadmium reduction method (0-132mg/l N03-), 500nm).

***Table 1**. Pond scale predictors measured on each of 88 ponds during July and August 2004.*

Predictor abbreviation	Description
A) Abiotic factors and fish presence	
Typ	type of site (swamp, pond, gravel pit, puddle, pool, canal, other)
Sub	type of substratum (gravel, alluvial soil, peat, sand/clay, calcareous, concrete, other)
Surf	surface of water body (m^2)
Per	perimeter of water body (m)
Depth	depth of the pond (m)
Sun	evaluation of the hours of direct sunshine in hours
Dry	summer draining (binary variable)
Wbank	slope of the bank that is weak (<30°) in %
Mbank	slope of the bank that is medium (30°- 60°) in %
Abank	slope of the bank that is steep (>60°) in %
Fish	presence-absence of fish (binary variable)
B) Water chemistry	
pH	mean of three pH measurements (mg/l)
Cond	mean of three conductivity measurements (mS/cm)
NO3-	nitrate concentration (mg/l)
C) Ponds vegetation (%)	
Alg	cover of floating algae
Float	cover of floating plants
Nofloat	surface of the pond which is not covered with floating algae or plants
Up	cover of standing plant
Shrub	cover of shrubs
Tree	cover of trees
Open	surface of the pond which is not covered with shrubs or trees
D) Land-cover in a radius of 30 meters around the ponds (%)	
Pal30	cover of aquatic zones
Marsh30	cover of marsh
Grav30	cover of gravel
Rude30	cover of pioneer vegetation
Agri30	cover of cultivated land
Grass30	cover of grassland, meadow, pasture or lawn
Bush30	cover of shrub
Forest30	cover of forest
Built30	cover of built land

Landscape scale predictors and barrier-based buffers (BBB)

Landscape variables in the wider surroundings of the breeding sites, were measured using Mapbasic 7.5 and Mapinfo 7.5 GIS software (Mapinfo corporation © 1985-2003), and based on land-use data derived from the VECTOR25, the vector format of the 1:25000 topographical maps of Switzerland. The Swiss Federal Office of Topography provides this database and its precision is approximately 3-8 meters (SWISSTOPO 2003). Landscape variables (Table 2) were measured in so-called "barrier-based buffers" (BBB) around the ponds and for comparison also in classical circular buffers (CB).

BBB represent an approximation of the potential amphibian movement area around the breeding sites. This area depends on how landscape favors or hinders amphibian movement. In order to estimate this potential amphibian movement area, we first computed 17 CB of different radius centered on each breeding ponds (100, 200, 300, …, 900, 1000, 1200, 1400, 1600, 1800, 2000, 2500 and 3000 m). The largest discs were chosen according to potential amphibian mobility and based on recent studies suggesting that landscape variables within 2000 m and beyond could affect amphibian species occurrence (e.g., Houlahan and Findlay 2003).
Secondly, we deleted the surfaces in each CB likely to be inaccessible to *B. bufo* and *R. temporaria*, i.e. surfaces separated from the central breeding site by barriers defined as insurmountable for both species. In our study, we considered three linear topographical elements as insurmountable barriers: the Rhone River, three additional canalized rivers and the highway (Figure 1).

Finally, we extracted the landscape variables from each of these BBB (Table 2). The 14 variables represent different land-uses that may potentially affect amphibian distribution (Pellet et al. 2004a), and which cover together 100% of the surface in the buffers. The analysis of land-use at various buffer radii around the breeding sites (multi-scale sampling) allowed us to estimate the distance at which landscape variables affect the amphibian use of ponds (Pellet et al. 2004a).

We acknowledge that the analysis made for the different buffer radii are statistically not independent, because larger buffers include the smaller ones.

Table 2. *Landscape scale predictors (14) representing different land-uses in barriers-based buffers (BBB) and circular buffers (CB) of radii between 100 and 3000 meters around the breeding sites. The surface of BBB is also used as a predictor.*

Predictor abbreviation	Description
Agri	surface of arable land and pasture (m^2)
Forest	surface of forest (m^2)
Lake	surface of lakes (m^2)
Urban	surface of urban areas (m^2)
Vine	surface of vineyards (m^2)
Orchard	surface of orchards (m^2)
Marsh	surface of marsh (m^2)
Bush	surface of bush (m^2)
Mineral	surface of mineral extraction sites (m^2)
River	total length of rivers (m)
Road1class	total length of 1st class roads (m)
Raod2class	total length of 2nd class roads (m)
Railroad	total length of rail roads (m)
Hedge	total length of hedgerows (m)
BBB area	Surface of barriers-based buffers (m^2)

Statistical analysis

We computed Moran's I (Moran 1950, Legendre 1993) for distance classes of 1 km to ensure that the ponds were independently distributed over our landscape and not located in clusters of occupied and empty ponds (i.e. no spatial autocorrelation). 1000 permutations were calculated to determine if spatial autocorrelation was significantly different from zero (p value<0.05) for all distance classes. We used the "ncf" package of R 2.1.0 (Bjørnstad 2001-2004) to calculate Moran's I and the associated statistics.

We tested associations between amphibian occupancy and habitat variables (at pond and landscape scale) with logistic regression models (Sokal and Rohlf 1995). We used habitat variables as explanatory variables (predictors) and the presence or absence of a species as the binary response.

We first analyzed all predictors separately using univariate models. All predictors whose explained deviance (D^2) and regression coefficient were both significant at the 5% level were considered relevant (Hosmer and Lemeshow 1989). Then, we used multiple logistic regression in order to analyze the effect of buffer radius and the simultaneous action of the variables. We built up a model for each one of the eighteen spatial scales (pond scale and 17 buffers radii) considering pond scale predictors together with landscape predictors from same size buffers. Having one model per buffer radius allowed us to identify the radius around the breeding sites, which was best correlated with species occurrence.

The multiple logistic regressions analyses followed two methodological steps: 1) we used the previous results of the univariate logistic regression and we kept all predictors whose regression coefficient was significant at the 0.25 level for further analyses (Hosmer and Lemeshow 1989). Secondly, we ranked this variables in the multiple logistic model by decreasing p-value and we carried out a “both” stepwise regression using the stepAIC function from package MASS of R 2.1.0 (R Development Core Team 2004).

We used the Akaike Information Criterion (AIC) to rank final models according to their strength support from the data and the Akaike weight (*w*) to estimate the relative weight evidence for each model (Burnham and Anderson 2002, Johnson and Omland 2004). Best models have min *AIC* value. *w* can be interpreted as the probability that a model *i* is the best model for the observed data, given the candidate set of models. The sum of all Akaike weights is 1. Explained deviance was adjusted taking into account the number of observations and the number of parameters in the model (adjusted D^2) (Guisan and Zimmermann 2000). The same statistical procedure was used for CB and BBB.

Results

Characteristics of ponds, landscape predictors and barrier-based buffers

Moran’s I statistics indicated that there was no spatial autocorrelation in response variables. The observations of species in ponds were independently distributed validating the species-habitat statistical tests.

General statistics of pond scale variables revealed alkalinity (pH: 8.10±0.058) and oligotrophic conditions (Cond: 0.61±0.045 mS/cm; NO3-: 2.42±0.522 mg/l). The standard error (SE) of nitrate values was relatively large, which indicated a high dispersion around the mean value. The nitrate concentration varied between 0 and 29.04 mg/l. In 80% of the breeding sites it was lower than 3.3 mg/l. The surface of the water body fluctuated between 20 m^2 and 80 000 m^2 (7613±1622 m^2). Fish were observed in 30 of the 88 breeding sites. In the surroundings of the breeding sites agriculture area were predominant. For example in a radius of 300 m, arable land, pasture, vineyards and orchards together made up 69%, forest 11% and urban area 10% of the land-cover.

As expected, differences in area of BBB and CB raised as the buffer radii increased (Figure 2). At 1000 m radii, the mean value of the BBB corresponded to 62% of the CB area with the same radius. The proportion was lowest at 3000 m radius (45%). This confirmed that in our study, selected insurmountable barriers considerably reduced potential amphibian accessibility to the terrestrial habitat.

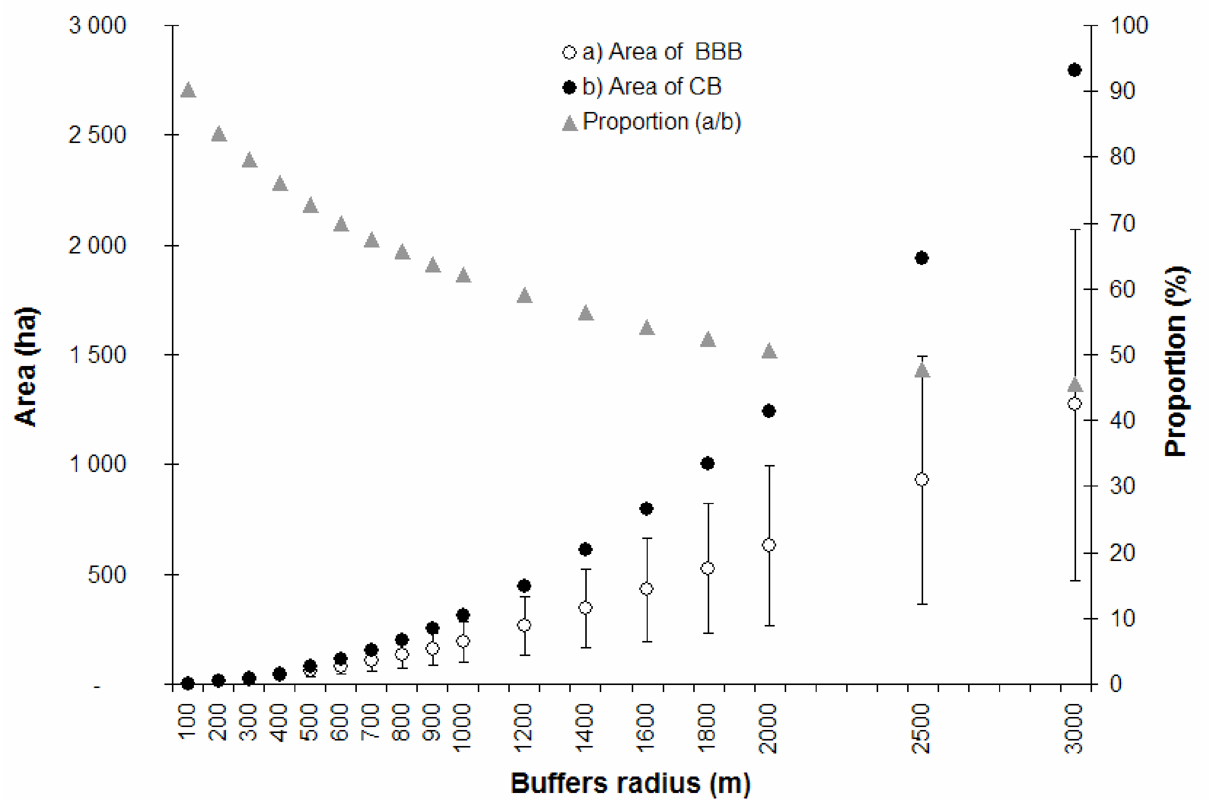


Figure 2. *The mean area of buffers surrounding the ponds at different radii for barrier-based buffers (BBB) and circular buffers (CB). BBB correspond to CB reshaped according to major amphibian movement barriers (see the text for more details).*

Single predictors' effect

We observed differences on predictors' effect between BBB and CB approach (Table 3). We first presented the results from the BBB analyses and then the differences with respect to the CB analyses.

***Table 3**. Explained deviance (D^2) for single variable models at pond scale (A) and at landscape scale level (B). Only the variables with regression coefficient and explained deviance significant at the 5% level are presented.**

Bufo bufo

A) Pond scale predictors

Surf	6
Depth	4

B) Landscape scale predictors and buffer radius (m)

		100	200	300	400	500	600	700	800	900	1000	1200	1400	1600	1800	2000	2500	3000
Agri	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CB	(-) 4	(-) 5	(-) 4	(-) 4	-	3	4	-	-	-	-	-	-	-	-	-	-
Forest	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lake	BBB	5	5	-	-	-	-	-	-	-	-	-	-	-	-	-	4	5
	CB	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mineral	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CB	-	4	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Road1class	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CB	-	-	-	-	-	-	(-) 4	-	-	-	-	-	-	-	-	-	-
Road2class	BBB	-	-	-	-	-	-	4	5	4	5	4	4	3	4	3	-	-
	CB	-	-	-	-	-	-	-	-	4	4	-	-	-	-	-	-	-

Rana temporaria

A) Pond scale predictors

Built30	(-) 4

B) Landscape scale predictors and buffer radius (m)

		100	200	300	400	500	600	700	800	900	1000	1200	1400	1600	1800	2000	2500	3000
Agri	BBB	-	-	-	-	-	-	-	-	-	-	-	5	7	9	10	**13**	**12**
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bush	BBB	-	-	-	7	6	6	8	8	9	9	7	10	**11**	9	7	-	-
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-
Forest	BBB	5	7	6	7	9	10	**11**	**12**	**12**	**13**	**13**	**12**	**11**	10	9	9	9
	CB	5	6	4	5	6	6	6	6	6	6	5	4	4	-	-	-	-
Hedge	BBB	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	7
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-
Mineral	BBB	-	-	-	-	-	6	8	8	8	8	10	10	10	**11**	**12**	**11**	**11**
	CB	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
Orchard	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CB		(-) 4	(-) 5	(-) 7	(-) 8	(-) 7	(-) 7	(-) 6	(-) 6	(-) 6	(-) 5	(-) 6	(-) 6	(-) 5	(-) 4	-	-
River	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	5	6
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Road1class	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CB	-	-	-	-	-	(-) 4	(-) 4	(-) 4	(-) 4	(-) 5	-	-	-	-	-	-	-
Road2class	BBB	-	-	-	4	5	7	8	7	7	8	8	7	6	7	6	7	7
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urban	BBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
	CB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BBB area		4	5	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-

* BBB: barrier-based buffers, CB: circular buffers, bold indicates D^2>10% and (-) indicates negative regression coefficients.

For *B. bufo*, the area of the ponds (Surf) and their depth (Depth) had a positive effect (Table 3). The forest surface had a significant effect only in the largest buffer radius, whereas area of lake (Lake) had a significant effect in the smallest and in the largest buffer radii. The density of second class roads (Road2class) had a significant and positive effect in radii between 700 and 2000 meters (Table 3). Explained deviance was always inferior to 6% revealing that any single variable had an important explanatory power.

We found that, at the pond scale, the occurrence of *R. temporaria* was negatively associated with the surface of urban area within 30 m from the ponds (Built30). In addition, eight landscape variables had a positive and significant association in various buffers radii (Table 3). The highest explained deviance (13%) was found for forest area (Forest) within buffer of 1000 m and 1200 m radii, and for agriculture area (Agri) at a radius of 2500 m. The majority of the significant associations explained less than 10% of the deviance, but globally the correlations were more important for *R. temporaria* than for *B. bufo*. There were 1) three types of land-use, which had a significant positive influence in several buffer radii (Forest, Bush and Mineral); 2) three had a low explained deviance and a not well supported correlation (River, Urban and Hedge) and 3) two had a positive and relatively strong effect (Agri and Road2class). We also found a positive association with the area of the buffers (BBB area) between 100 and 400 m.

The most evident differences of CB variables effect compared to BBB are (i) the apparition of significant negative effects of some variables (e.g. Road1class and Orchard) and (ii) the general reduction of the model explained deviance (e.g. Forest) (Table 3). This will be discussed later.

The spatial scale of the landscape effect

Multiple logistic models were computed with variables from identical buffer radius. Doing so, it was possible to compare models and determine the distance from the ponds where the landscape was most associated with species occurrence. Three main results should be emphasized in relation to BBB. 1) We found that using multiple regression models (Table 4) allowed us to explain a larger proportion of the deviance than using single covariate models (Table 3). The adjusted explained deviance was around 40% for the best multiple models and for both species (Table 4). 2) The models based on the sole pond scale predictors had a limited capacity to support data (*w*=0.001 for *B. bufo* and *w*=0.000 for *R. temporaria*) (Table 4) and the addition of landscape variables considerably increased the weight of the models. 3) The best models were found at 700 m buffer radius in the case of *B. bufo* (w=0.490) and at 2000 m for *R. temporaria* (w=0.242) (Table 4). However, we found substantial support (ΔAIC<3) as well for others models and for both species. Figure 3 shows the distribution of the Akaike weight as a function of buffer radii.

Table 4. *Model selection, number of parameters (k), explained and adjusted deviance (D2, adj.D2). Models are ranked in an increasing AIC order. w is the Akaike weight of the model.**

Bufo bufo

Barrier-based buffers

Radius	k	D2	adj.D2	AIC	ΔAIC	w
700	12	47%	39%	88.004	-	0.490
800	12	46%	38%	89.066	1.062	0.288
600	12	44%	36%	90.795	2.791	0.121
500	12	42%	34%	93.361	5.357	0.034
1200	9	35%	28%	96.120	8.116	0.008
300	13	41%	32%	96.430	8.426	0.007
1600	8	33%	27%	96.450	8.446	0.007
3000	9	34%	28%	96.516	8.512	0.007
1400	9	34%	28%	96.546	8.542	0.007
2000	9	34%	28%	96.839	8.835	0.006
1800	8	32%	27%	96.876	8.872	0.006
900	11	37%	29%	97.247	9.243	0.005
1000	11	37%	28%	97.811	9.807	0.004
2500	8	31%	25%	98.061	10.057	0.003
400	11	36%	28%	98.114	10.110	0.003
100	8	31%	25%	98.921	10.917	0.002
200	7	28%	22%	100.747	12.743	0.001
pond	6	26%	21%	100.888	12.884	0.001

Circular buffers

Radius	k	D2	adj.D2	AIC	ΔAIC	w
1000	8	38%	33%	90.149	-	0.621
1200	8	35%	29%	93.658	3.509	0.107
900	9	37%	30%	93.789	3.640	0.101
1400	8	34%	28%	95.610	5.460	0.040
400	11	38%	30%	95.758	5.608	0.038
800	8	33%	27%	96.204	6.055	0.030
300	10	35%	28%	97.352	7.203	0.017
600	10	34%	27%	98.658	8.508	0.009
500	9	32%	25%	99.391	9.241	0.006
700	9	32%	25%	99.727	9.577	0.005
100	7	28%	23%	100.051	9.902	0.004
200	7	28%	23%	100.057	9.908	0.004
pond	6	26%	21%	100.888	10.739	0.003
1600	6	26%	21%	100.888	10.739	0.003
1800	6	26%	21%	100.888	10.739	0.003
2000	6	26%	21%	100.888	10.739	0.003
2500	6	26%	21%	100.888	10.739	0.003
3000	6	26%	21%	100.888	10.739	0.003

Rana temporaria

Barrier-based buffers

Radius	k	D2	adj.D2	AIC	ΔAIC	w
2000	10	47%	41%	83.631	-	0.242
2500	10	47%	41%	84.364	0.733	0.168
3000	10	46%	40%	85.543	1.911	0.093
900	9	44%	38%	85.681	2.050	0.087
1000	12	49%	42%	85.748	2.117	0.084
1800	10	45%	39%	86.465	2.834	0.059
800	10	45%	39%	86.508	2.877	0.058
1200	12	48%	40%	86.819	3.187	0.049
700	10	44%	38%	87.148	3.517	0.042
400	10	44%	38%	87.483	3.851	0.035
1400	10	44%	37%	88.058	4.427	0.026
600	10	44%	37%	88.241	4.610	0.024
500	11	44%	37%	89.262	5.631	0.015
1600	11	43%	36%	90.439	6.808	0.008
200	10	40%	34%	91.957	8.326	0.004
300	11	42%	35%	92.017	8.386	0.004
100	9	38%	31%	93.264	9.633	0.002
pond	7	29%	24%	99.938	16.307	0.000

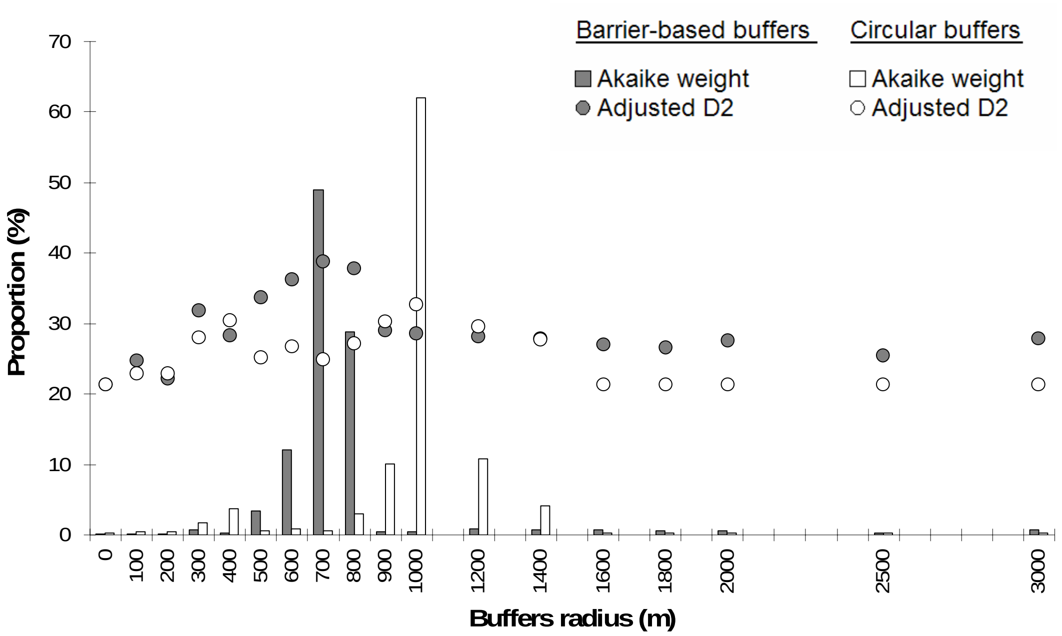
Circular buffers

Radius	k	D2	adj.D2	AIC	ΔAIC	w
1000	10	44%	37%	87.918	-	0.278
1400	9	42%	36%	88.696	0.778	0.188
1200	10	42%	35%	89.939	2.021	0.101
2000	9	40%	34%	90.705	2.787	0.069
900	10	41%	35%	90.802	2.884	0.066
800	11	43%	35%	91.113	3.196	0.056
2500	8	38%	32%	91.347	3.429	0.050
1600	9	39%	33%	91.367	3.450	0.050
700	10	41%	34%	91.813	3.895	0.040
1800	10	40%	33%	92.399	4.481	0.030
600	10	39%	32%	93.225	5.307	0.020
400	10	39%	32%	93.418	5.500	0.018
500	10	39%	32%	93.960	6.042	0.014
200	10	38%	31%	94.968	7.050	0.008
100	9	36%	29%	95.806	7.888	0.005
3000	8	34%	28%	95.810	7.892	0.005
300	10	36%	29%	97.456	9.539	0.002
pond	7	29%	24%	99.938	12.021	0.001

adj.D2=1-[(n-1)/(n-k)](1-D2), n is the number of observations (88), k is the number of model parameters (Guisan and Zimmermann 2000).

When we examined the landscape using CB, then the results are quite different. The best model was found at 1000 m buffer radius for both species (w=0.621 for *B. bufo* and w=0.278 for *R. temporaria*) (Table 4). This suggested that, for *B. bufo*, CB overestimate the scale of the effect of landscape (Figure 3). For *R. temporaria*, the difference between CB and BBB contrasted less.

Bufo bufo



Rana temporaria

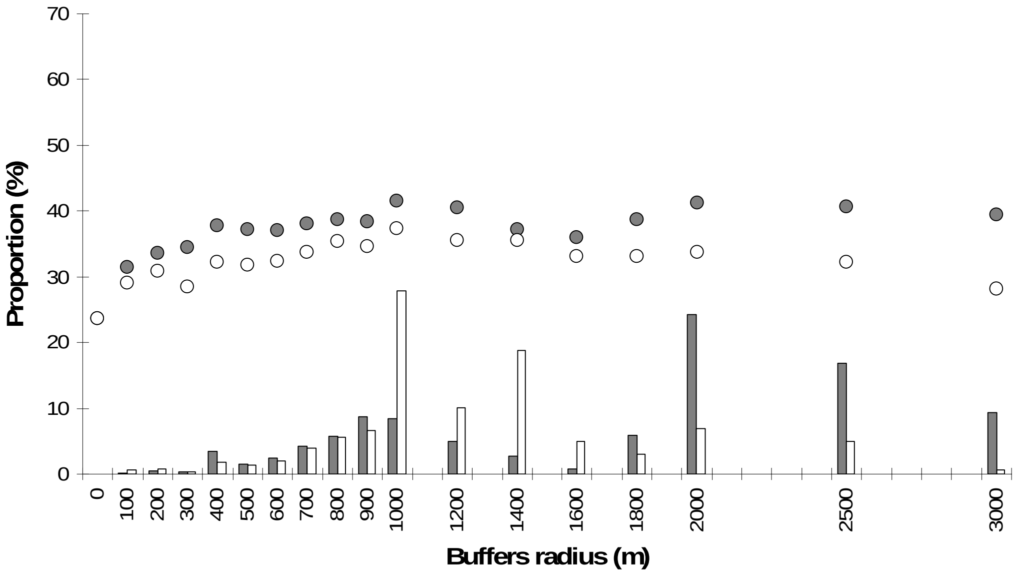


Figure 3. *Proportion of adjusted explained deviance (Adjusted D*^{2}*) and Akaike weight for models built up within each buffers radii. Grey color represents the results for barrier-based buffers and white colors the ones for the circular buffers.*

A difference between BBB and CB multiple models was also found for the adjusted explained deviance. Generally, the adjusted explained deviance was lower in CB than in BBB (Figure 4). The only exceptions were buffers of 400, 900, 1000 and 1200 m radii for *B. bufo*. The maximum difference was found between 500 and 800 m for *B. bufo* (14.0% at 700 m) and at more than 2000 m for *R. temporaria* (11.3% at 3000 m) (Figure 4).

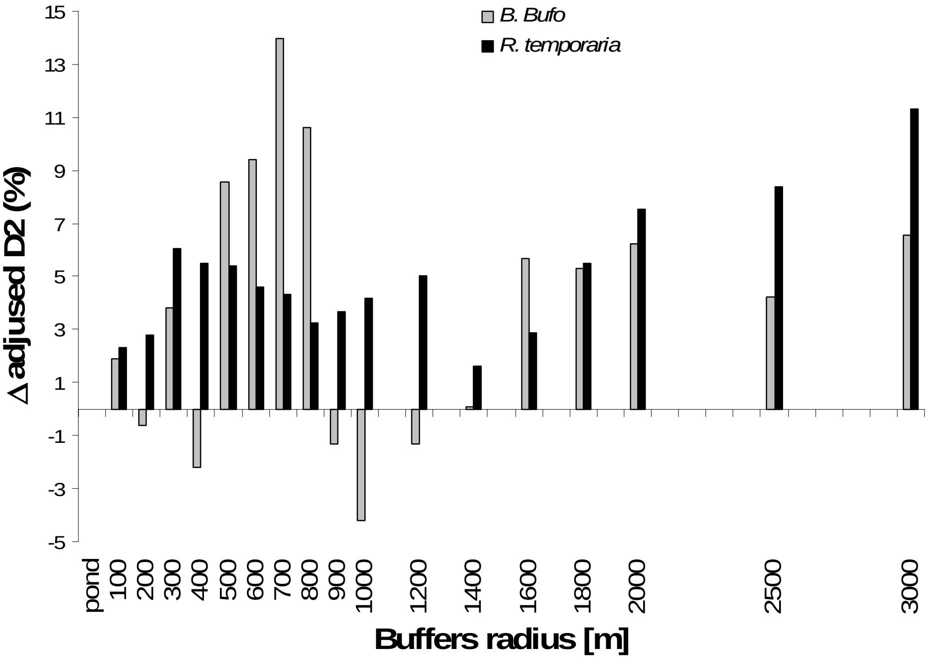


Figure 4. *The difference between the adjusted explained deviance of multiple regression models computed with barrier-based and circular buffer variables (BBB and CB). Difference varies as a function of species and buffers radius.*

Discussion

In this study we developed a method to determine the effect of habitat variables on amphibian species distribution considering physical barriers (i.e. an approximation of real landscape permeability) to their movement around breeding ponds. We proposed to reshape the currently used “circular buffers” (CB) centered on each pond into “barrier-based buffers” (BBB). Our results showed that the BBB approach increases the explanatory power for (i) the majority of the predictors considered individually in logistics models and for (ii) the multiple models representing the effect of landscape variables at various distances from ponds. These results suggested that the BBB approach is ecologically more appropriate than traditional CB analysis of species-habitat relationship. Our results are consistent with the only found study, which trying to consider landscape permeability in distribution models for amphibians (Ray et al. 2002). In addition, the differences in statistical estimates of habitat variables between BBB and CB (Table 3) stress the necessity to consider landscape permeability in species-habitat relationship studies in order to avoid potential distortions of the results and errors in the definition of conservation strategies. Among the most evident likely distortions that we found in our study, there is the overestimation of the negative effect of “first-class road” and “orchard area”, and the underestimation of the positive effect of the forest area.

The fact that the effect of habitat variables in the BBB approach generally better explained species occurrence than traditional CB models implies that the species distribution is affected by the considered barriers. This was not an obvious result because the species response (e.g. population extinction or population size reduction) to an environmental stressor (e.g. road construction, water pollution, habitat destruction or fragmentation) is unlikely to occur immediately. Rather, species responses were expected to be gradual, after the apparition of the environmental stressor, and will only be detected sometime later. For example, Findlay and Bourdages (2000) found that wetland biodiversity loss in response to road construction is better associated with past, rather than present, road densities. The effect of roads construction on ponds diversity may not actually become evident for decades. Similarly, a time lag between landscape changes and the reaction of species was found for beetle distribution by Petit and Burel (1998). The effects of barriers in our study were detected because the time already elapsed since their construction was sufficiently long to observe ecological response. For our study, time lags varied between decades (highway construction and tributaries canalization, SRCE 2006) and centuries (Rhone river canalization, Wallis 2000).

Pond scale and landscape scale variables were both correlated with the presence of *B. bufo* and *R. temporaria*. This was confirmed by previous studies on amphibians (e.g. Pope et al. 2000, Johnson et al. 2002, Pellet et al. 2004b, van Buskirk 2005) and others taxa (Mazerolle and Villard 1999) underlining the multi-scale effects of habitats on species distribution. In our study, pond scale predictors together with landscape scale predictors allowed us to develop more accurate models than those using pond scale variables alone. This may be due to the relatively high mobility of the species; distances of more than 3 km have been observed for *B. bufo* (Heusser 1968, Moore 1954, in Smith and Green 2005) and

Baker and Halliday (1999) showed that *R. temporaria* and *B. bufo* were able to colonize new ponds at distances up to 950 m from existing ponds. High terrestrial mobility implies that individuals can interact with landscape not only in the neighborhood of the breeding sites but also at greater distances.

The strongest habitat-species association was found between forest area and *R. temporaria* occurrence (Table 3). The positive effect of forests on amphibian occurrence, abundance and richness in breeding ponds is one of the most consistent landscape-scale habitat relationships reported in the literature. Forests may be associated with anuran occurrence because they (i) represent undisturbed habitats compared with agricultural or urban areas, (ii) provide dispersal corridors between breeding and non breeding habitats, and (iii) ensure terrestrial habitat quality essential for hibernation, estivation and foraging (Kolozsvary and Swihart 1999, Knutson et al 1999, Lehtinen et al. 1999, Findlay et al. 2001, Guerry and Hunter 2002, Houlahan and Findlay 2003)..

According to our results, the length of second-class roads around the breeding sites seems to have a positive influence on the presence of *B.bufo* and *R.temporaria* (Table 3). This is quite surprising, as in most studies, road density has been identified as having a negative influence on presence, abundance and richness of amphibians (Vos and Chardon 1998, Findlay et al. 2001, Houlahan and Findlay 2003, Pellet et al. 2004). The main causes for this negative correlation were traffic induced road mortality (Van Gelder 1973, Fahrig et al. 1995, Carr and Fahrig 2001, Mazerolle 2004) and constraints to dispersal (deMaynadier and Hunter 2000). However, our results can be explained by the fact that habitats associated with second class roads, such as ditches, may constitute dispersal corridors. Amphibians may prefer ditches for their movements, as they are often humid and provide a hidden passage protecting against predation (Mazerolle 2005). This is especially true in the Rhone plain where climate is the driest in Switzerland (Encyclopedie Valais 2004). However, correlations found in our study were not intended to highlight causality effect. For a clearer interpretation, more proxy relationships between roads and species occurrence should be computed, such as traffic intensity indexes (e.g. Pellet et al. 2004a). Unfortunately, this proxy analysis was not feasible in our study because of the lack of data.

We also found a surprisingly positive association between agricultural land (pasture and arable land) and species occurrence. This result was unexpected because modern agricultural practices are known as one of the main causes of habitat loss and disturbance for anurans spending time underground (Kolozsvary and Swihart 1999, Joly et al. 2001, Dodd and Smith 2003). We believe that distinguishing among arable land and pasture area may help to refine the models and perhaps obtain more specific results.

Data on pond scale characteristics were collected during August and September 2004, i.e. after the breeding period of *B. bufo* and *R. temporaria* (Brodmann 1982). It would have been more appropriate to measure these variables in early spring when both species can be found in the water. This temporal inconsistency may partly explain the limited explained deviance (D^2<6%) and the number of significant pond scale variables. Nevertheless, we found that depth and ponds size are positively associated with the presence of *B. bufo*. This was consistent with other studies, suggesting that *B. bufo* prefers breeding in deep and permanent water bodies (Berthoud and Perret-Gentil 1976, Brodman 1982, Babik and Rafinski 2001). In addition, a negative effect of built-up areas within 30 m from the breeding sites was found for *R. temporaria*. Urban areas are inhospitable habitat for anurans. Housing, paved and industrial areas have replaced their natural habitats, induced wetland contamination and reduced accessibility to water bodies (e.g. Knutson et al. 1999, Pellet et al. 2004a, Rubbo and Kiesecker 2005).

Conclusions

Increasing urbanization and habitat alterations make it particularly important to find ways to assess the real impact of land-cover changes on the distribution of natural populations. In our study, we proposed a relatively simple approach to include the effect of barriers to amphibian movement in distribution models. Complex simulations of species movement within the area surrounding a breeding site can be made (e.g. Ray et al. 2002, Joly et al. 2003) but gaps in knowledge regarding permeability of landscape elements to amphibian movement constrain those approaches as exploratory tools (Joly et al. 2003). Validation is still difficult, but a great deal of interest exists in such studies that are trying to join these least-cost path modeling approaches with field observations of terrestrial movements by radiotracking (Vos 1999, Schabetsberger et al. 2004) or harmonic direction (Leskovar and Sinsch 2005, Pellet et al. 2006).

The proposed BBB approach is potentially applicable to any species functioning on a spatially defined patch basis (e.g. pond site for reproduction or nesting place). Many applications may be found in conservation biology (i) for identifying habitat effect in realistically species accessible areas (ii) for testing hypotheses on the effect of barriers on species movement and (iii) for analyzing response time of the considered species to environmental stressors at landscape scale. Our results show that studies on species distribution modeling should consider landscape permeability in order to obtain more accurate results. We suggest that such studies are essential for the development of valuable conservation strategies.

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Chapter 7

How does the landscape affect patch occupancy in metapopulation models? Comparing Euclidean vs landscape-based inter-patch distance*

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Abstract

Dispersal barriers and corridors between habitat patches can strongly affect colonization processes, and therefore patch occupation probability (=occupancy). However, most metapopulation dynamic models assume that heterogeneity in the landscape between patches can be neglected, basing dispersal on the Euclidean (shortest) distance between patches. For heterogeneous landscapes inter-patch distance should take into account the resistance of landscape features to movement, as with the least-cost algorithms implemented in Geographic Information Systems (GIS). In this study, we explore how patch occupancy is sensitive to Euclidean versus a landscape-based distance (least-cost algorithm). We illustrate our method with two metapopulations of the Yellow-bellied Toad (*Bombina variegata*) in the Rhone plain,

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See Appendix 5 for details on populations' size of the Yellow-bellied toad in the Rhone plain.

Switzerland. Our results reveal patch occupancy to be highly sensitive to the distance algorithm. Obviously, the least-cost-distance produces lower patch occupancy than Euclidean distance. However, some patches are more affected than others. This allows us to identify which patches are the most sensitive to the inter-patch landscape; i.e., from a conservation point of view, those patches where improving connectivity (e.g., by building vegetated corridors, removing barriers to dispersal) might be a valuable management scenario. Additionally, we show that it is more important to measure accurately the species mean dispersal distance than its colonization and extinction rates. We offer two main conclusions: (1) from a theoretical standpoint, we show that inter-patch landscape affects patch occupancy and we identify which patches are the most sensitive; (2) from a conservation standpoint, we propose a method to identify which patches should be considered a priority for landscape management.

Keywords: Spatially-realistic metapopulation model, dispersal distance, population viability analyses, landscape resistance, connectivity, conservation, *Bombina variegata*, Switzerland

Introduction

Species extinction is often caused by habitat fragmentation and destruction (Tilman et al. 1994, Pimm and Raven 2000, Stuart et al. 2004). One important consequence of fragmentation is that isolation of suitable habitat patches hinders dispersal and colonization (Hanski and Simberloff 1997, Hanski 1999). In these fragmented landscapes, metapopulation modeling is being increasingly used for the design of species conservation strategies (McCullough 1996, Akçakaya and Sjogren-Gulve 2000, Hanski 2004). Metapopulation models estimate the probability that the metapopulation will persist for a given time into the future. Various types of models have been devised, each requiring different kinds of data, and addressing different questions (Akçakaya and Sjogren-Gulve 2000). Among these, patch-occupancy models need only a small number of parameters, which is a great advantage for their application (Akçakaya and Sjogren-Gulve 2000, Sjögren-Gulve and Hanski 2000). Patch-occupancy models assume that patches are either occupied or empty, without explicitly modeling local population dynamics (Sjögren-Gulve and Hanski 2000). Local extinction and colonization depends on patch sizes and spatial configuration. These models aim at estimating the probability of each patch to be occupied (=occupancy) and the equilibrium proportion of occupied patches.

The inter-patch distance (i.e. the distance separating two patches) is a central parameter in metapopulation modeling. If the inter-patch distance increases, colonization likelihood, and thus patches occupancy, decreases (Hanski 1999). However, measuring inter-patch distance is far from obvious because it depends on how much the landscape features occurring between patches facilitate or impede the movement of organisms (Taylor et al. 1993, Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001). Therefore, any realistic measurement of inter-patch distance must explicitly take into account the behavioral responses of the focal organism to the various landscape features. Accordingly, the interpatch distance is not the Euclidean (shortest) distance, but a complex function of the landscape resistance to movement (Johnson et al. 1992, Wiens 1993, Ricketts 2001). For example, Ricketts (2001) found that butterfly movement through coniferous forest was 3-12 time less likely than movement through willow thickets. Meadows separated by coniferous forest are thus more isolated than meadows separated by willows. Mazerolle (2005) showed that ditches constitute dispersal corridors for green frogs. Mazerolle and Desrochers (2005) found from a field experiment that 72% of translocated individuals from northern green frogs and northern leopard frogs avoided disturbed surfaces. In another experimental study, Rothermel and Semlitsch (2002) noted the avoidance of open-canopy habitat by juvenile American toads. The combining of metapopulation models with landscape ecology is an emerging field (Wiens 1997, With 2005) with important implications for the reliability and interpretation of patch occupancy. There is a danger of formulating incorrect conservation strategies if the landscape structure among patches is neglected and the inter-patch distance is measured as the Euclidean distance (Wiens 1997).

In spite of the recognized importance of inter-patch landscape structure for species movement, from a practical point of view, it is time- and cost-consuming to quantify the movement behavior of a species to landscape elements (e.g. Vos 1999, Pither and Taylor 1998, Stevens et al. 2004). Thus, several studies have attempted to measure landscape-explicit inter-patch distances by means of simulations (e.g. Ferreras 2001, Arnaud 2003, Adriaensen et al. 2003, Chardon et al. 2003, Verbeylen et al. 2003). These approaches are based on least-cost distance algorithms, which assume that each landscape feature category (e.g., forest, roads, agricultural areas,

…) has a specific resistance (or suitability) to species movement (Formann 1995). For example, Verbeylen et al. (2003) found that the presence of red squirrels in wooded patches is better explained by isolation measures when Euclidean distance was replaced by a least-cost distance. Similarly, Chardon et al. (2003) found that in predicting Speckled wood butterfly occurrence, the connectivity based on the least-cost distances algorithms had a significantly better predictive power than that based on Euclidean distance.

Hence, it may be expected that more realistic and valuable results can be obtained when the inter-patch distances in metapopulation models are not Euclidean but based on the effect of landscape features between patches upon the movement of organisms. The inclusion of inter-patch distance measurement into metapopulation analyses is of increasing interest but we found no example in the literature (Guisan and Thuiller 2005, but see Hirzel 2001).

The goals of our study are (i) to compare patch occupancy results as computed with Euclidean and least-cost inter-patch distance and (ii) to assess the sensitivity of patch occupancy to other crucial parameters in metapopulations analyses: colonization rate, extinction rate, and mean dispersal distance. We finally discuss implications of our approach for conservation. The method has been applied to two metapopulations of yellow-bellied toads (*Bombina variegata*).

Methods

Species and study area

The Yellow-bellied Toad (*B. variegata* Linnaeus, 1758) is a small toad, known to use a wide range of different ponds for spawning with a preference for small, temporary and sunny ponds (Grossenbacher 1988, Barandun and Reyer 1997). Nowadays, these conditions essentially occur in man-made habitats (Nöllert and Nöllert 2003). Males and females mostly staying close to breeding ponds but regularly move to nearby forests during the dry period and in autumn (Barandun and Reyer 1998). Colonization of new habitats is rapid (Barandun and Reyer 1997) because adults are good dispersers and can move more than 1 km (Plytycz and Bigaj 1984) with a maximal distance recorded of 1.5 km in one year (MacCallum et al. 1998). In

Switzerland, *B. variegata* occurs below 1000m a.s.l. (Grossenbacher 1988) and is considered as threatened to extinction (Schmidt and Zumbach 2005).

In the Rhone plain (Figure 1), *B. variegata* populations are nowadays isolated from the other populations in Switzerland and during last decades they experienced a worrying decline (Marchesi 1999). The landscape of the plain is mainly composed of agriculture (77%, essentially orchard and vineyard). Urban areas cover 14% of the plain and forest areas almost 5% (Zanini et al. submitted). The Rhone river and the highway divide the plain longitudinally.

We studied separately the metapopulations M1 (western part of the Rhone plain) and M2 (central part) (Figure 1), because they are too distant (16.7 km) to exchange individuals. Ponds were visited at least three times from 1997 to 2003 during the breeding season. Population size is based on the number of calling males corresponding to four abundance classes (Grossenbacher 1988, Figure 1).

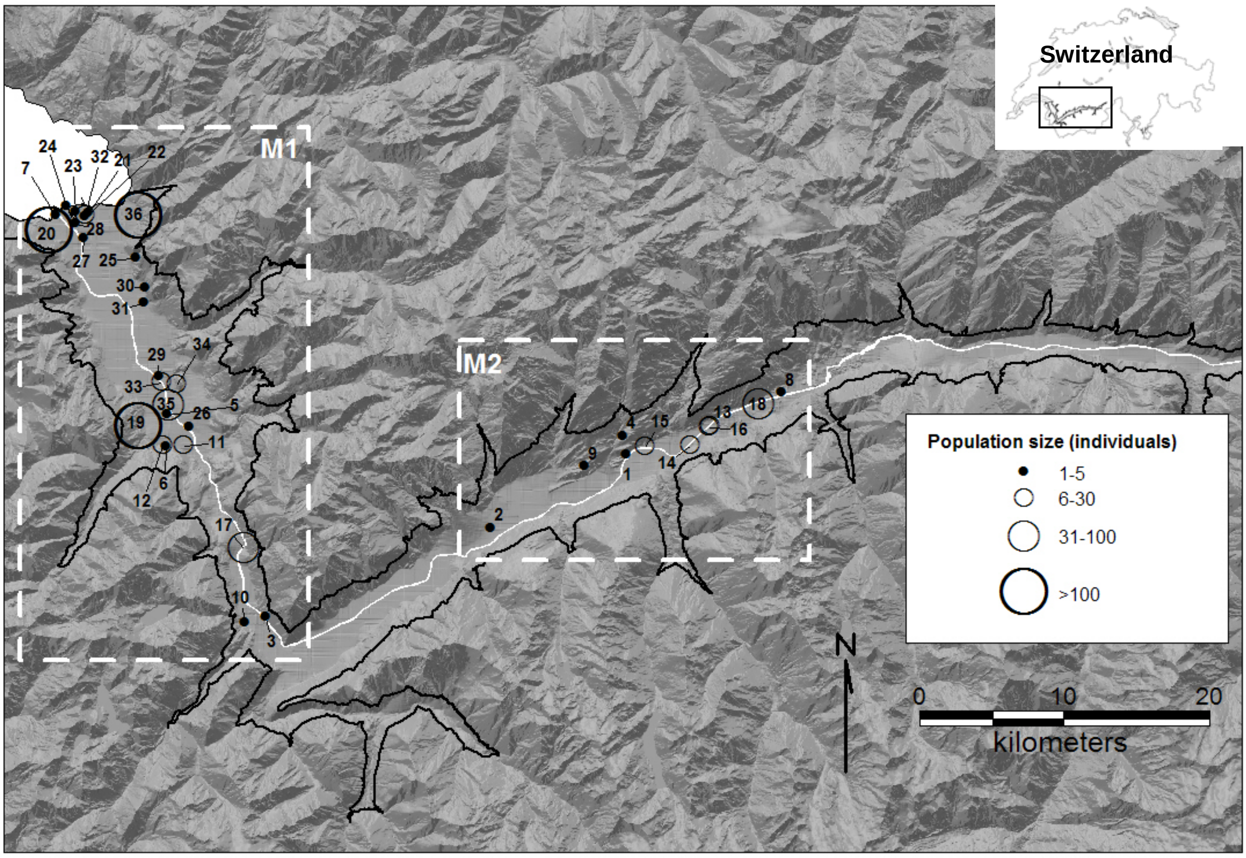


Figure 1. B. variegata *local populations (breeding ponds) in the Rhone plain, Switzerland. Metapopulations M1 and M2 are composed of respectively 26 and 10 populations (black, numbered circles). For clarity only the Lake Geneva (North-West of the study area) and the Rhone river are shown. The black line represents the 1000-m altitudinal limit. (MNT25, © Swisstopo 1995).*

Metapopulation dynamics

We modeled metapopulation dynamics using Hanski and Ovaskainen (2000) and Ovaskainen and Hanski (2001, 2003) patch occupancy models. The deterministic model used is a spatially-realistic, finite-patch version of Levins' metapopulation model (Levins 1969). Patch size and location are taken into account in the dynamics of the system. The occupancy of patch *i* at time *t+1* is:

$$p_{i,t+1} = p_{i,t} + c_i(1 - p_{i,t}) - e_i p_{i,t} \qquad \text{(eq. 1)}$$

where the patch colonization rate is:

$$c_i = c\sum_{j \neq i} \exp(-\alpha d_{ij}) N_j p_{j,t} \qquad \text{(eq. 2)}$$

and patch extinction rate is:

$$e_i = e\frac{1}{N_i} \qquad \text{(eq. 3)}$$

N_i is the carrying capacity of patch *i*, d_{ij} is the distance between patches *i* and *j*, e and c are species extinction and colonization rates, respectively. The dispersal function is a negative exponential, with a mean dispersal distance of $1/\alpha$. The expected patch occupancy resulting from a dynamic equilibrium between extinction and colonization was computed by means of numerical simulations.

Metapopulation model parameters

We used pond population size classes (middle-range value, see Figure 1) as carrying capacity (N_i) instead of pond area, which is a poor indicator of habitat quality (Barandun and Reyer 1997). The mean dispersal distance ($1/\alpha$) was not available for *B. variegata* in the study area and literature is fragmentary. We assumed a mean dispersal distance of 1000 m as a realistic estimation (Plytycz and Bigaj 1984, MacCallum et al. 1998). We found no information regarding species specific colonization (c) and extinction rate (e). Thus, we used, arbitrary but realistic intermediate values of $c = 0.35$ and $e = 0.5$.

Due to the absence of empirical data supporting these baseline parameter estimates, we tested three values of $1/\alpha$, c and e: the baseline estimates times 75%, 100% and 125%. We ran this sensitivity analyses for both metapopulations M1 and M2. We reported the patch occupancy computed with all possible combinations of parameters values. We also tested previous models with two inter-patch distances (d_{ij}): 1) the Euclidean distance and 2) the least-cost distance (cf. next section). Thus, for each patch we obtained 54 occupancies.

Least-cost distance

We used the COSTGROW (Eastman 1999) least-cost algorithm to incorporate landscape structure into inter-patch distance estimation (Vuilleumier and Prelaz-Droux 2002). The algorithm input consists of two grid-maps: (1) a map of habitat patches, and (2) a map of landscape features, where every cell has a resistance coefficient. The resistance can be thought of as an energy cost or fitness cost paid by an individual crossing the cell. Landscape features that favour movement (e.g. forest or wetland) are given low resistance values, while features that hinder movement get higher values (e.g. building and highway) (see Table 1). The least-cost distance between a patch and a focal cell is measured by the minimum amount of resistance summed up on a path from the patch to the focal cell. Least-cost distance is symmetrical. Movement is possible in 8 directions, diagonal movements being 1.41 times more costly. Least-cost distance can be interpreted as a species-specific distance measure weighted by the intervening landscape structure (Ferreras 2001, Adriaensen et al. 2003, Chardon et al 2003, Verbeylen et al. 2003).

***Table 1**. Landscape feature categories and their resistance coefficients (expert estimates) to* B. variegata *movement.*

Categories of landscape features	Resistance coefficients
Forest, wetland, bush, alluvial area and canals	1
Arable lands and orchards	5
Vineyard	10
Main roads*	20
Canalized rivers (concrete bank) with high water flow and canalized Rhone river	150
Railways*, highways*, buildings, Lake Geneva and altitudes > 1000 m	Impassable

* Except bridges and viaducts.

Although resistance coefficients are best measured with empirical data (Stevens et al. 2004) no such information was available for *B. variegata*. Thus, we had to rely on expert-based estimates (Table 1). Cells above the altitude of 1000 m a.s.l. are absolute barriers for *B. variegata* in Switzerland (Grossenbacher 1988). The railways, building and highways are also assumed to be absolute barriers (except viaducts and bridges). The resistance coefficients are relative values expressed as multiples of the base resistance (=1) caused by favourable landscape. For instance, a resistance coefficient of 5 indicates a cost 5 times higher than the reference landscape. For each patch we computed a map of least-cost distances (Figure 2), which were used to extract least-cost distances between all pairs of patches. Then, this least-cost inter-patch distance was multiplied by the size of a grid cell (10m) to make comparison with Euclidean distance easier. Indeed, Euclidean and least-cost distances have the same value if all landscape features between two patches have a resistance coefficient of 1 (Table 1). Otherwise, the least-cost distance is always higher than the Euclidean distance.

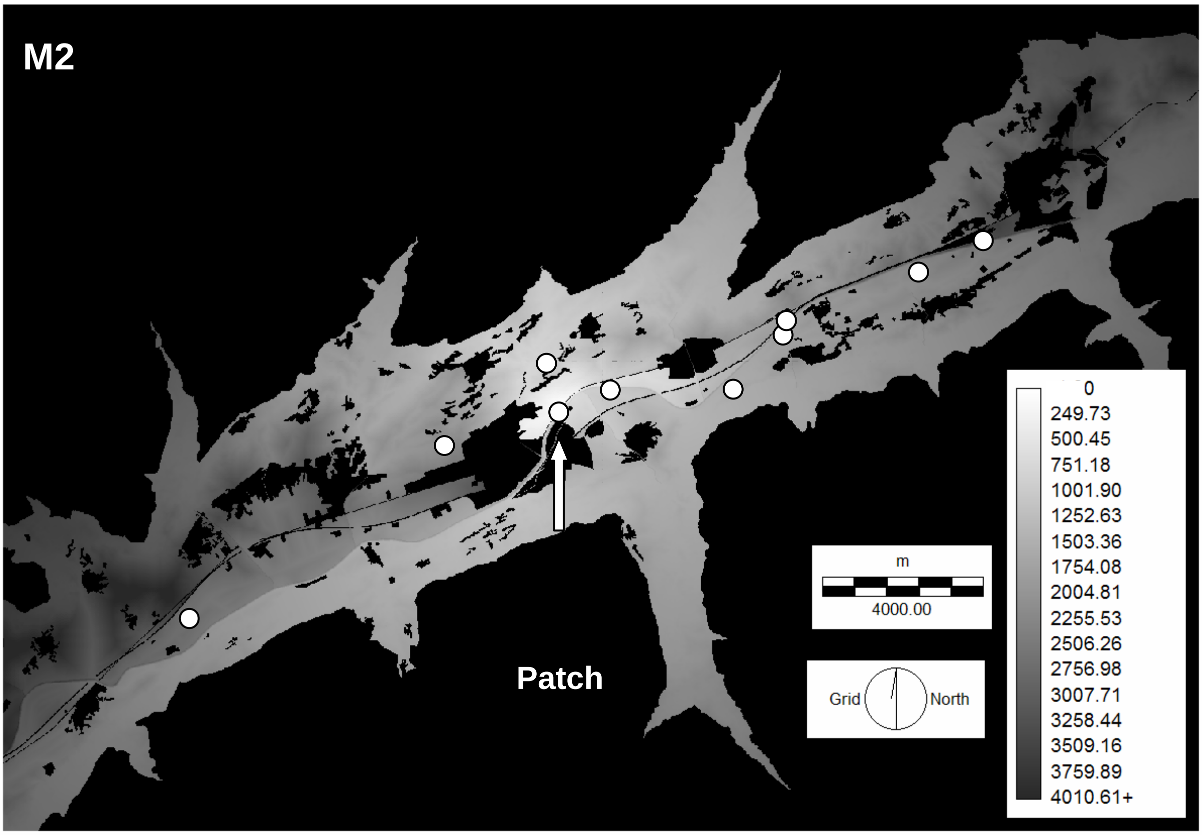


Figure 2. *Map of least-cost distance from patch 1 in the metapopulation M2. White circles indicate patches. The least-cost distance from patch 1 increases with grey color intensity. Black color indicates impassable areas. Grid-size is 10 m.*

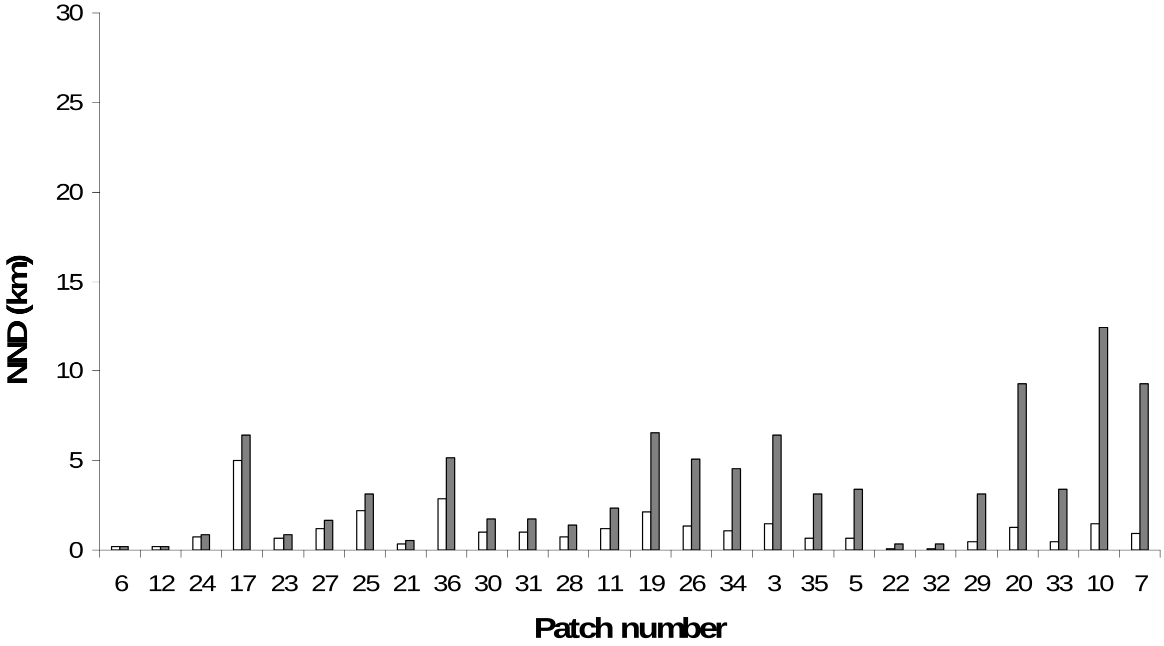
Results

Description of inter-patch distances

On average, the least-cost distance was almost two times higher than the Euclidean distance in metapopulations M1 (respectively 11.4 km and 20.0 km) and three times higher in metapopulation M2 (respectively 7.6 km and 21.2 km). Similarly, the average nearest neighborhood distance (NND) with the least-cost algorithm was almost three times higher than with the Euclidean algorithm in metapopulation M1 (respectively 1.1 km and 3.6 km) and four time higher in metapopulation M2 (respectively 2.1 km and 8.0 km). Thus, landscape structure has a stronger negative effect on inter-patch distance in metapopulation M2 than in metapopulation M1. This suggests the presence of more frequent barriers hindering *B. variegata* movement in metapopulation M2 than in metapopulation M1.

However, when Euclidean and least-cost distances were compared for each patch, the ratio was extremely variable. In metapopulation M1 the ratio of the NND varied from 1.1 (patch 12) to.10.0 (patch 7) In metapopulation M2 the ratio varied from 1.3 (patch 14) to 7.5 (patch 8) (Figure 3). Spearman's rank determination coefficients (r^2) between Euclidean and least-cost distances were r^2=0.77 for M1 and r^2=0.73 for M2. This indicates that Euclidean distance explains approximately 75% of the inter-patch distance, with the remaining 25% being due to inter-patch landscape features.

A) Metapopulation M1



B) Metapopulation M2

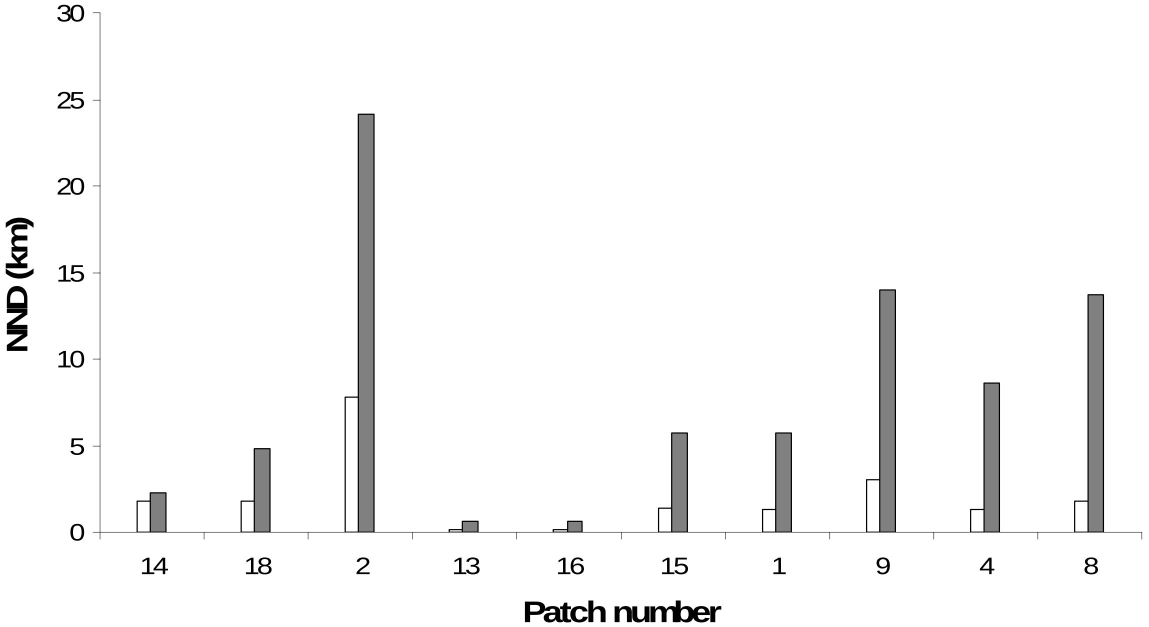


Figure 3. *Euclidean and least-cost nearest neighborhood distance (NND) between patches in metapopulation M1 and M2. White: Euclidean distance; grey: least-cost distance. Patches are sorted by increasing ratio between least-cost and Euclidean distance.*

Patch occupancy

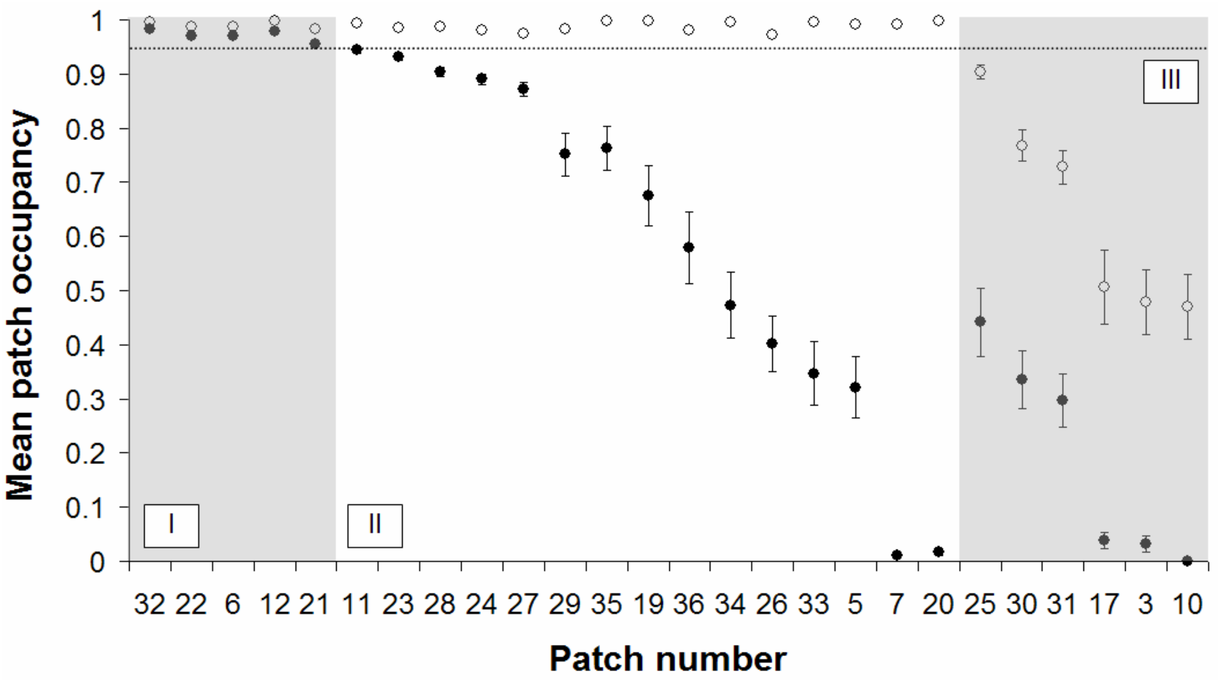
Obviously, in both metapopulations, mean patch occupancy was smaller when least-cost distance was substituted to Euclidean distance (Figure 4). However, the amplitude of this discrepancy varied among patches. In M1, this discrepancy was the smallest for patches 6, 21, 22 and 32, where both Euclidean and least-cost had mean patch occupancy >0.95 (Figure 4, A.I). The highest discrepancy in M1 was found for patches 7 and 20 where Euclidean distance occupancy was respectively 0.99 and 1.00, while least cost-distance occupancy respectively 0.01 and 0.02 (Figure 4, A.II). Finally, some patches had both Euclidean and least-cost distance <0.95 with in addition important mean occupancy discrepancies (Figure 4, A.III). The same structure of the results have been found for metapopulation M2, where the smallest discrepancy was found for patches 16, 13 and 14 (Figure 4, B.I). Furthermore, we noted the smallest discrepancy for patch 2 where both Euclidean and least cost distance had patch occupancy near zero (Figure 4, B.III). The highest difference was observed for patch 8 where occupancy for Euclidean distance is 0.95 and 0.00 for the least-cost distance (Figure 4, B.II).

In addition, our results showed that many patches had high mean patch occupancies (>0.95) when Euclidean distance was used but low mean patch occupancies (<0.95) when least-cost distance was used (Figure 4, A.II and B.II). This indicates that patches can be geographically close to surroundings patches (potentially well connected) but effectively separated from them by ecological barriers.

Sensitivity to metapopulation parameters

As expected, the species-specific colonization factor (*c*) and the average dispersal distance ($1/\alpha$) were positively correlated to the mean occupancy of patches in both metapopulations (Figure 5), while the species-specific extinction factor (*e*) was negatively correlated to it. However, while these effects were weak for *c* and *e* (the inter-quartile ranges overlap), the effect was much stronger for the average dispersal distance $1/\alpha$ (Inter-quartile ranges do not overlap, Figure 5). These results did not depend on the distance algorithm used.

A) Metapopulation M1



B) Metapopulation M2

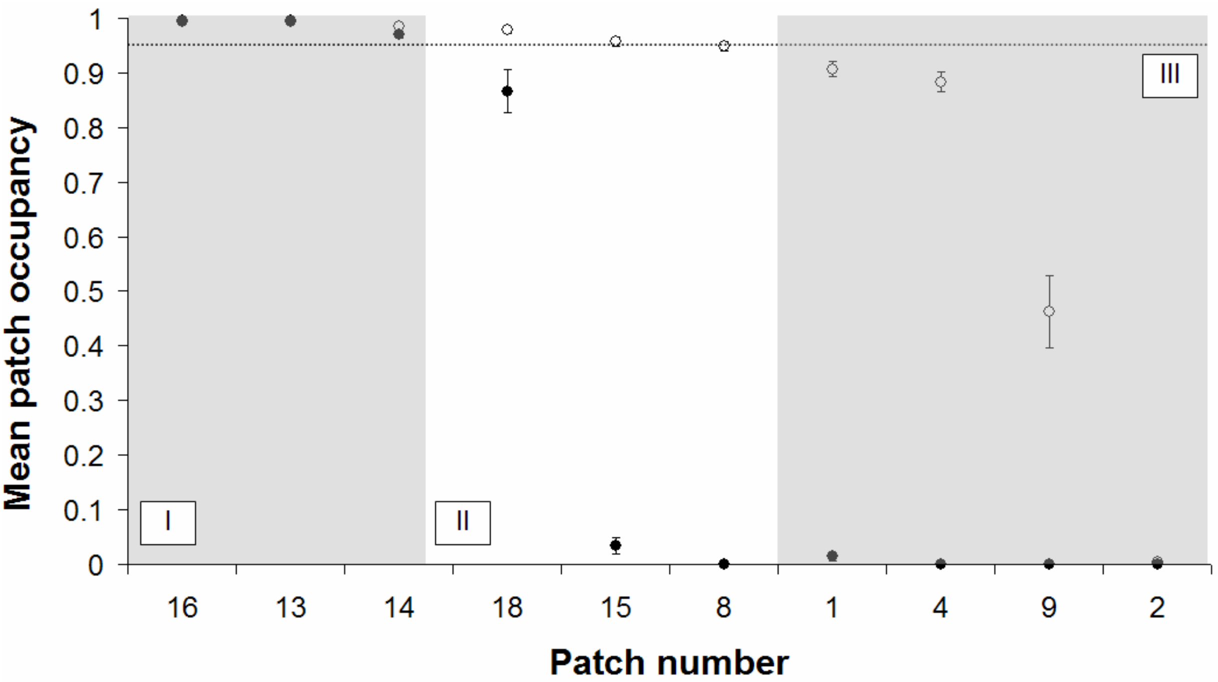
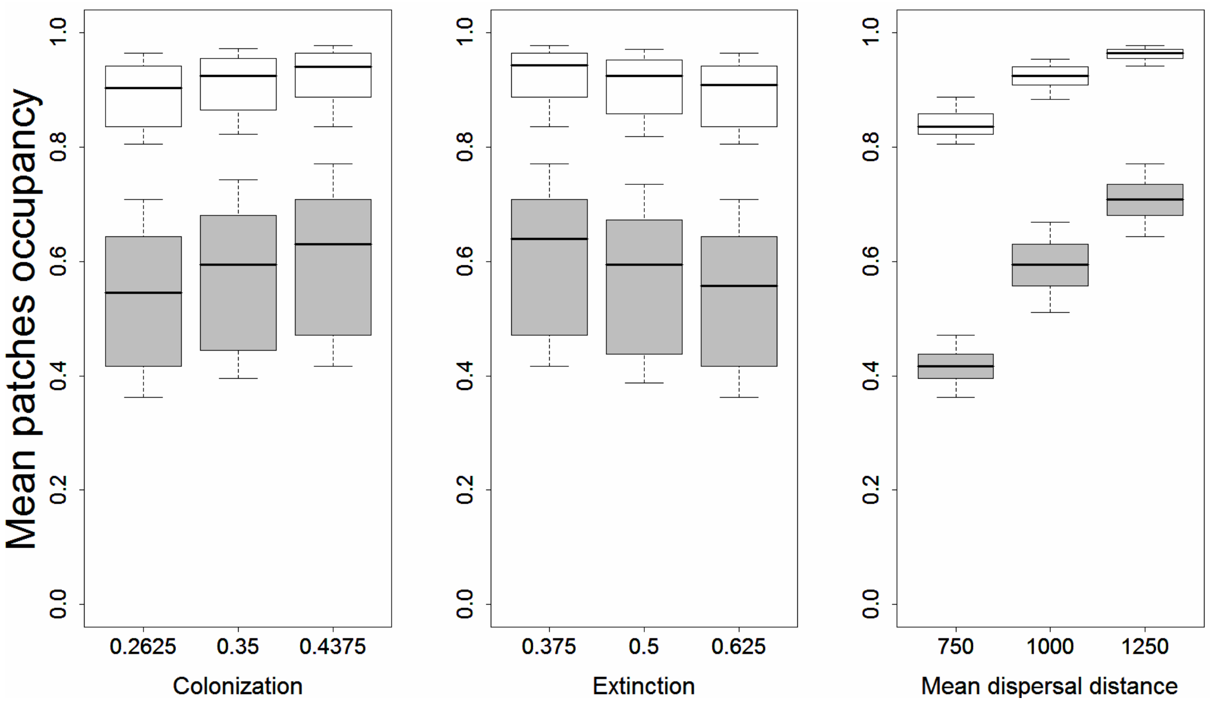


Figure 4. *Mean patch occupancy in metapopulation M1 and M2 over the 27 combinations of parameters (e, c, 1/α) (standard error expressed by the error bars). White dots: Euclidean distance; black dots: least-cost distance. Patches are sorted by they Euclidean occupancy and difference between Euclidean and least-cost occupancy. Dotted line indicates 0.95 mean patch occupancy. I) Mean patch occupancy >0.95 for both distance algorithms; II) Mean patch occupancy >0.95 for Euclidean distance only; III) Mean patch occupancy <0.95 for both distance algorithms. Region II indicates putative patches for landscape management.*

A) Metapopulation M1



B) Metapopulation M2

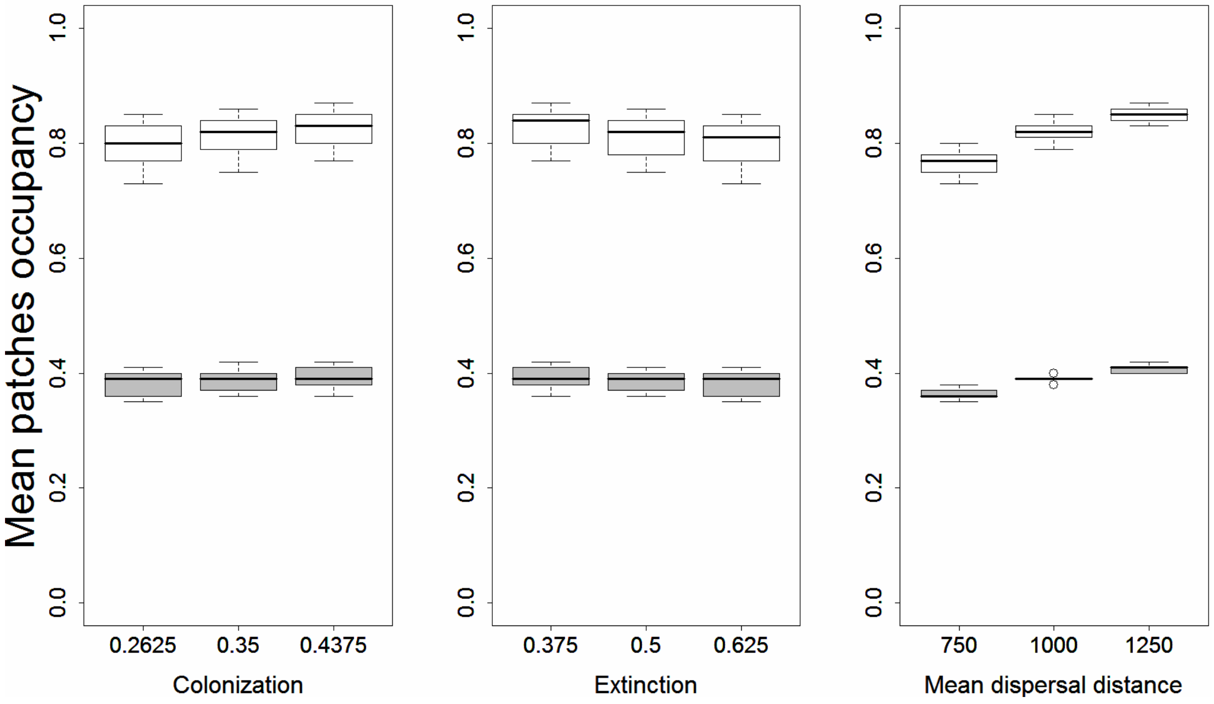


Figure 5. *Boxplots of the mean patch occupancy as a function of colonization rate (c), extinction rate (e) and mean dispersal distance in meters (1/α) for metapopulation M1 and M2. White: Euclidean distance; grey: least-cost distance. Only 1/α shows non-overlapping inter-quartile ranges. Each box represents the median (bold line), the inter-quartile range (rectangle) and the most extreme value no more than 1.5 times the inter-quartile range (whiskers).*

Discussion

Effect of distance measurement on patch occupancy

Our results show that patch occupancy is sensitive to the inter-patch distance measurement. The Euclidean distance is the shortest distance separating two patches, while least-cost distance takes into account the landscape features between patches. The patch occupancy computed with the least-cost distance is lower than with Euclidean distance, with a difference varying among patches. Some of them are very sensitive to the distance algorithm, while other are almost unaffected by it. This provides useful clues about the characteristics of the surrounding landscape. Indeed, a large difference in occupancy highlights the fact that the landscape surrounding the patch is not favorable to species dispersal and that the patch is isolated by some important barrier. For instance, patch 7 in metapopulation M1 (Figure 4, A) has an "Euclidean" occupancy of 0.99, while its "least-cost" occupancy equals 0.01. Indeed, patch 7 is geographically close to seven patches (20, 21, 22, 23, 24, 28 and 32), but is separated from six of them by the nearly-impassable Rhone river (Figure 1), which explains the high discrepancy between Euclidean and least-cost occupancy. Thus, the higher the difference between Euclidean and least-cost occupancies, the more the landscape structure separating this patch from the metapopulation is expected to hinder species movement.

In our study, three of the impassable or nearly-impassable barriers were linear landscape features which separate the Rhone plain longitudinally: the highway, the railway and the Rhone river (Table 1). Because most patches are distributed along the Rhone river, on its right or left side, these barriers separate patches that are often geographically close (Figure 1). Therefore, it appeared that Euclidean inter-patch distance is an extremely unrealistic measure of the ecologically relevant distance. This underlines the need to take landscape structure into account when measuring inter-patch distance, especially when the fragmentation of the study area suggests a potentially important effect of movement upon.

Of course, occupancy depends on the values assigned to the resistance coefficients. Here, because no quantitative, empirical information was available for *B.variegata* movement, we had to rely on expert estimates. Although some methods have been developed to estimate resistance coefficients from field data (e.g Vos 1999, Schabetsberger et al. 2004, Leskovar and Sinsch 2005, Pellet et al. 2006) or arena experiments (Stevens et al. 2004) they are time-consuming and difficult to applicable to large study areas. Analyzing the sensitivity of our results to the resistance coefficients values was not feasible because of the time needed to compute the least-cost distances. However, we partly compensated for this by performing a sensitivity analysis to mean dispersal distance. In addition, we were not taking the patch occupancy rates we found as absolute values (which needed accurate parameters validation and sensitivity analyses) but we rather considered the discrepancies between the occupancy computed with Euclidean and least-cost distance. This makes our results qualitatively robust to parameter changes. Indeed, the occupancy patterns (Figure 4) mainly arise from the impassable or nearly-impassable landscape features (cf. Table 1), which cause some patches to be isolated. These resistance estimates cannot be completely wrong and even considerable changes would not affect our qualitative results. The landscape features with intermediate resistance have a smaller effect on dispersal, and thus, even some changes in their coefficients should not drastically alter our conclusions.

Effect of colonization rate, extinction rate and mean dispersal distance

The mean dispersal distance is often recognized as a key component of most spatially explicit population models (but see Etienne et al. 2005, p. 130) to predict species persistence (Moilanen and Hanski 1998, Hanski 1999, With 2005). For example, dispersal distance has been found as the most important factor in metapopulation models for the tree frog in western Switzerland (Pellet et al. submitted). This study, confirmed these results, showing that mean dispersal distance was the principal factor affecting patch occupancy for *B. variegata*, while extinction (*e*) and colonization rates (*c*) had only a marginal effect (Figure 5). This is likely due to the fact that the average dispersal distance has an exponential effect on the patch colonization (equation 2). By contrast, *c* and *e* have only a linear effect on the occupancy dynamics (equation 2 and 3).

The importance of mean dispersal distance for patch occupancy suggests that studies improving our knowledge of dispersal capacity should be encouraged, e.g. mark-recapture methods (e.g., Vos et al. 2000), radiotracking (Schabetsberger et al. 2004) or harmonic direction (e.g., Pellet et al. 2006).

Conservation and management implications

Model parameterization represents the major issue for conservation managers and often limits practical application of metapopulation models (Moilanen 1999, Etienne et al. 2005). Our method, in spite of having several parameters, provides robust results in two ways: 1) Sensitivity analyses of the metapopulation parameters provide confidence intervals around the expected patch occupancies. 2) The Euclidean and least-cost distances characterize two extremes of the system, with the reality bound to lie in between. The point is not to consider the patch occupancy values they provide, which are probably inexact, but to look at those patches where both estimates agree and those where they disagree. Here we presented practical implication of our method for the management and conservation of *B. variegata* in the Rhone plain.

In the context of conservation and metapopulation dynamics, it is obvious that large and well-connected habitat patches should generally be favored. However, decision-making is difficult when comparing small, well-connected patches with large, isolated patches, or when dealing with habitat patch networks with an aggregated distribution of patches. Metapopulation theory, with recent spatially-explicit models (Hanski 1999, Hanski and Ovaskainen 2000), provide methods to answer this central question in conservation biology. But an additional and central factor in this context is the estimation of the distance among patches: geographically closer patches are not necessarily well connected because inter-patch landscape resistance to species movement may be important (Petit and Burel 1998, Chardon et al. 2003, Verbeylen et al. 2003).

Our approach has considerable implications in conservation because it allows us to test whether patch occupancy is affected by inter-patch landscape structure. We consider that the conservation goal is to obtain the highest patch occupancy possible within the time, money and socio-politic constraints (e.g., Cabeza and Moilanen 2003). Our approach provides a graphical tool (Figure 4) for the manager to identify those patches where landscape management would be worth the effort, either by improving their connectivity (e.g. building forested corridors or removing barriers to dispersal) or by creating new habitat patches (e.g. digging out new ponds). On Figure 4, we distinguish three sets of patches: (1) The patches where both “Euclidean” and “least-cost” occupancy estimates are both high (0.95, Figure 4, I) require little management as they are already highly viable. (2) The patches where “Euclidean” occupancy is high but the “least-cost” occupancy is lower (<0.95, Figure 4, II) offer the highest potential for connectivity improvement. Indeed, in spite of being geographically close to other patches, some landscape features are maintaining their ecological isolation. (3) For patches where both occupancy estimates are low (<0.95, Figure 4, III), geographical distance is the main isolating mechanism. In such cases, improving inter-patch landscape connectivity would be worthless, and it would better to create new habitat patches to link the isolated patch to the metapopulation core.

Of course, this approach only provides demographic criterion. Other criteria, based on time and money, must be considered to define the actual feasibility of the connectivity improvement. For example, to increase significantly the occupancy of patches 7 and 20 would require the creation of a green-bridge over the Rhone river in order to link them with the metapopulation core on the opposite side of the river (Figure 1). For patch 11, while no major barrier (such as the highway, the railway or the Rhone river) isolates it from other patches, improving its connectivity might require vegetated corridors through agricultural fields. In both cases the costs would probably be high, but the types of interventions are completely different. In such cases, public acceptance is another feasibility criterion (Maystre and Bolliger 1999).

In conclusion, our study provides the first assessment of the effect of inter-patch distance measurement method (Euclidean *versus* least-cost) on patch-occupancy metapopulation analyses. By comparing patch occupancies estimated with least-cost and with Euclidean distance, it is possible to identify which patches are the most sensitive to inter-patch landscape structure. From a management standpoint, this allows decision-makers to determine those patches for which conservation measures would be worth considering. Moreover, our method could also be used to test scenarios, for example to identify the best location for the creation of a new pond. We have applied successfully this practical approach to the case of the threatened Yellow-bellied Toad and it can doubtlessly be extended to any species structured as a metapopulation and affected by landscape structure during dispersal.

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Chapter 8

Synthesis and conclusions

The effectiveness of conservation actions is strongly dependent on the quality and the amount of ecological knowledge regarding the focal species or ecosystem under study. This also requires a better understanding of the threats and the most effective measures for addressing those threats. Limited knowledge almost certainly provides approximate and inefficient conservation measures. Therefore, **it is of prime importance that ecologists, conservation biologists and landscape managers use accurate methodological approaches to collect the information required for the design of conservation strategies.** In this research we have addressed this issue in order to improve various methodological approaches and to offer practical ecological knowledge in the context of landscape management and amphibian conservation in fragmented landscapes.

Using historical data in the landscape restoration context

In **Chapter 3**, we used data from past landscape features in order to provide recommendations in the context of landscape restoration. We proposed a methodological GIS-based approach to determine and locate the rehabilitation potential of the landscape. The method enabled a rapid, ecologically relevant and spatially complete evaluation of a large and heterogeneous landscape. In addition, it could constitute an important tool for communication, decision-making and biological conservation management in landscape planning. The approach was based on land cover maps digitalized from topographic maps and on experts' estimates of the conservation value of each land cover. Obviously, the results were dependent on the subjectivity of the experts' opinion, but we considered each expert separately and analyzed where the results were consensual. This allowed us to (i) respect the specificity of the opinion of each expert and (ii) provide a way of finding common solutions, which is very important for the communication and acceptance of the results. Worldwide, landscapes are becoming more and more different from their pristine state. Therefore, **the use of historical data in the constitution of a reference state as a target to locate hot-spots for landscape restoration will become a useful practice which merits further investigation.**

Methodological improvements of species-habitat models

In order to propose useful conservation measures, it is important to understand species-habitat relationships. This is especially true since the main cause of decline is habitat alteration. **Concerning amphibians' autoecology, several methodological approaches exist, but they generally suffer from two limitations, which have been analyzed in this research.** First of all, the autocorrelation in the residuals (errors) of the regression analyses may cause under- or over-estimation of the predictor effect (**Chapter 4**). We found an over-estimation of the positive effect of marsh area and the negative effect of road density on the distribution of the agile frog in north-eastern Switzerland, when a logistic model (with autocorrelation in regression residuals) is used. However, we found that autologistic models allowed autocorrelation in regression residuals to be removed. An autologistic model is a logistic model including a measure of the spatial arrangement of the response variables as a predictor (i.e. autocovariate). Since regression residuals of autologistic models are independent, while residuals for logistic models are autocorrelated, we conclude that a logistic model was not a statistically valid option. We observed that autologistic regression is an appropriate technique for analyzing dependent data because (i) its application is simple and well adapted for presence/absence data, (ii) these models can effectively avoid spatial autocorrelation in regression residuals and (iii) the autocovariates may represent spatial ecological processes, such as dispersion, which can be explicitly represented in the models. Autologistic regression analysis is a practical tool providing estimation of both the effect of species-habitat relationship and the effect of spatially structured species distribution. Therefore, **we suggest to always testing whether spatial autocorrelation occurred in data (e.g. using Moran's I test) and avoiding it by using, for example, the approach presented in Chapter 4 for presence/absence data**. This is an important prerequisite for a valid species-habitat relationships assessment.

Secondly, the effect of landscape on amphibian occurrence in ponds is unlikely to be equal in every direction (as often assumed) since barriers or inhospitable surfaces may reduce movement patterns (**Chapter 6**). Consequently, the ideal circular surface, where landscape is usually studied, has to be reshaped into a non-circular form reflecting the actual use of the terrestrial landscape by amphibians. In this research, we demonstrated that reducing the boundaries of circular buffers, according to barriers of species movement, allowed landscape predictors to be computed which better explained species distribution (**Chapter 6**). These results suggest that the proposed approach is ecologically more pertinent than the traditional circular buffer analysis. In addition, our approach is potentially applicable for any species functioning on a geographically defined patch basis (e.g. pond site for reproduction or nesting place). Many applications may be found in conservation biology: (i) to identify critical land use in realistically accessible zones, (ii) to test hypotheses on the effect of barriers on species movement and (iii) to analyze the response time of species to environmental stressors at a landscape scale (**Chapter 6**). **We suggest that predictive distribution models should consider barriers and corridors to species movement in order to obtain more accurate results.**

The effect of landscape structure on species movement is fundamental for the persistence of species. Patch colonization and resource accessibility strongly depend on the presence of a favorable habitat for species movement. Accordingly, understanding how much a given landscape element (i.e. forest, canals, ditches, roads, urban areas, agricultural fields etc.) favors or hinders the movement of individuals is very important in the design of valuable conservation measures. **We suggest that efforts be made to assess landscape resistance of species movement** using field methods (e.g. radiotracking, harmonic direction), experimental designs (e.g. arena) coupled with simulation models based on Geographic Information System technologies (e.g. cost-distance surface algorithms: **Chapter 7**).

Spatial generalization of species-habitat models

An additional and central issue in conservation biology is the spatial generalization of species distribution models (**Chapter 5**). Distribution models are usually established for only a single region and it is unknown whether the identified relationships between the distribution of a species and environmental variables can be transferred to another geographic area. The question is whether the effects of predictor variables are homogeneous across different regions or whether they vary geographically. In other words, can we use the conclusion from a study in region A to suggest management strategies for the same species in region B? To answer the question, we studied the distribution of amphibian species in geographically distinct areas of Switzerland. For instance, we found that the occurrence of *Bufo bufo* was 1) positively, 2) negatively or 3) not affected by the density of hedgerows in the surroundings of ponds, as a function of the region. However, the occurrence of *Rana dalmatina* was positively affected by the proportion of marsh cover within 200 m from ponds in all the studied regions. Thus, **our results suggest that caution is needed when predicting species occurrence in separate geographic regions (Chapter 5)**. **Spatial generalization of species distribution models is an issue which is rarely addressed, and this merits further investigations, not only in amphibian distribution studies.**

Spatial scale of the landscape effect on species distribution

A further line of research into the landscape ecology of amphibians investigated the spatial scale (i.e. the distance from ponds) at which the landscape affects the presence of amphibians in ponds. In this study, we found that this spatial scale varied from one hundred to several km (**Chapter 4, 5** and **6**), which was in agreement with several recent studies suggesting multi-scale effects of habitat variables. Not only are pond-scale variables (e.g. pH, hydroperiod) important, but also landscape-scale variables (e.g. road density, forest area, connectivity to surrounding populations) have to be measured and assessed in order to improve the effectiveness of conservation practices. In addition, we found a species-specific response to landscape scale (**Chapter 5**). This has important implications for species conservation and management. Indeed, because variables measured at only one landscape scale did not adequately predict occurrences of all species, the conservation measures at only one spatial scale are unlikely to affect all species similarly. **Our results join the growing body of evidence that management strategies for amphibian habitats should be conducted at multiple scales.**

The study of the effect of landscape-scale predictors on species distribution is of particular interest in conservation. Such results may permit, for example, locating the areas where the landscape is the most suitable for the creation of new ponds. Restricting the pond creation effort to these areas would enable conservation managers to focus on a limited surface, maximizing the probability of species presence.

Both aquatic and terrestrial buffer zones have to be preserved. However, the location and extent of the upland surfaces used by most pond and stream-breeding amphibians remains unknown, due to the difficulties in tracking post-breeding movements in amphibians. Some techniques exist (radiotracking, harmonic direction) and have to be more frequently used even if they are time- and cost-consuming methods. Such results may be extremely helpful for the identification of crucial terrestrial resources and for the design of terrestrial conservation areas. In Switzerland, for example, the conservation of amphibians is based on a federal law which protects (at national level) 772 breeding ponds and the surrounding terrestrial area. Unfortunately, the boundaries of the terrestrial habitat are often based on presumption and are not evidence-based.

Connectivity and metapopulation structure

Not only do terrestrial and habitat quality determine species distribution, but also the demographic dynamics of local populations (**Chapter 5** and **7**). We found that the spatial proximity to neighboring populations (i.e. connectivity) is often an important determinant of species distribution (**Chapter 5**). In some cases, connectivity seems to be more important than habitat quality. This increases the difficulty of accurately predicting species distribution with habitat variables only. **Our results suggest that connectivity between local populations has to be included in distribution models.**

During recent decades, metapopulation theories and models have been carried out in order to estimate the probability that the metapopulation will persist in the future, considering a number of parameters. Among them, dispersal capacity of the species, colonization rate, extinction rate, and the distance separating suitable habitat (patches) are factors which may influence the viability of a metapopulation. Most metapopulation dynamics models assume that the landscape between patches can be neglected, basing dispersal on the Euclidean (shortest) distance between patches. However, inter-patch distance should take into account the resistance of landscape features to movement, as with the least-cost algorithms implemented in Geographic Information Systems (GIS). In this study, we explored how patch occupancy was sensitive to Euclidean versus landscape-based distance (least-cost algorithm) (**Chapter 7**). We derived two main conclusions: 1) from a theoretical standpoint, we showed that inter-patch landscape affected patch occupancy and we identified which patches were the most sensitive; 2) from a conservation standpoint, we proposed a method to identify which patches should be considered as the highest priority for landscape management. The approach was illustrated in the case of two metapopulations of the yellow-bellied toad in the Rhone plain (Switzerland). **Our**

results emphasize the importance of considering landscape structure in connection with metapopulation models in order to avoid incorrect conclusions about population viability analyses.

Final considerations

The definition of efficient conservation strategies to reverse amphibian declines will be a great challenge for the coming years and will largely focus on the restoration and creation of suitable breeding habitats. The additional problem is that human pressure, in terms of land demand for urbanization, recreation, agricultural and livestock practice, will probably increase. Conflicts between nature conservation and human requirements are expected to become more and more important in the coming years. The availability of land for nature will be rarer and the design of optimal conservation strategies will clearly be fundamental for the persistence of species. In this context, our research provides rigorous methodological tools for ecological knowledge acquisition. Our results highlight the necessity to move from site-specific to landscape-level analyses in amphibian autoecology studies. We also underline the need to base conservation planning on the demographic dynamics of local populations, considering the effect of landscape structure. We applied successfully the developed practical approach to the case of several amphibian species, but it can doubtlessly be extended to any species functioning on a spatially defined patch basis (e.g. pond site for reproduction or nesting place), structured as a metapopulation and affected by landscape structure during dispersal. **A vast improvement in our understanding of the factors that influence the distribution and persistence of species is necessary in order to improve the effectiveness of conservation actions.**

The yellow-bellied toad (*Bombina variegata*), threatened with extinction in Switzerland

Appendix 1

Review of 27 recent papers investigating determinants (predictors) of amphibian distribution

The result of our review is summarized in the following table and structured in three parts: **A) predictors of species occurrence and abundance**, **B) predictors of species richness** and **C) predictors of other indices describing amphibian communities.** **“Resp”** stands for the type of response variable (o=occupation, ab=abundance, amr=amphibians richness, anr=anurans richness, car=caudate richness), **“Sign”** the positive (+) or negative (-) effect of the predictor (for clarity, negative effect is also represented with grey colour), **“Scale”** the distance from ponds at which the predictor has a significant effect and **“Scale range”** the min and max scale at which predictors have bees studied. **“S”** stands to a re-classification of the predictors according to two spatial scales: p = pond scale and l = landscape scale (i.e. distance >30 m from pond). **“V”** indicates a re-classification of the predictors according with the type of land cover analysed at landscape scale (r = road and traffic, u = urban area, f = forest area, a = agriculture area) and the effect of surrounding ponds (c = amount and occupancy of ponds in the area surrounding the focal pond).This review considered a total of **46 species** and recorded **267 predictor effects**.

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
A) Occurrence and abundance									
Ambystoma jeffersonianum	o	Wetland area in woodlot	+	woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Ambystoma laterale	o	Hydroperiod	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Ambystoma laterale	o	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r
Ambystoma laterale/ A. jeffersonianum	o	Pond-forest adjacency	+		300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Ambystoma laterale/ A. jeffersonianum	o	Forest area	+	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Ambystoma maculatum	o	pond-forest adjacency	+		300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Ambystoma maculatum	o	Forest area	+	100	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Ambystoma maculatum	o	Forest area	+	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Ambystoma maculatum	o	Wetland area	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Ambystoma texanum	o	Presence of stream	+	30	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Ambystoma texanum	o	Water permanency	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Ambystoma tigrinum tigrinum	o	Woodlot edge-to-area ratio	+	1000	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	l	c
Ambystoma tigrinum tigrinum	o	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Ambystoma tigrinum tigrinum	o	Forest proximity	-		1000	Indiana (USA)	Kolozsvary and Swihart (1999)	l	f
Aschaphus truei	o	Large and mixed sawtimber core area density	-	Forest Patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Bufo americanus	o	Forest proportion	+	1000	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	f
Bufo americanus	o	Forest proportion	+	2500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	p	
Bufo americanus	o	Forest proportion	+	500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	f
Bufo americanus	ab	Sum of abundance indices for invertebrate (backswimmer)	+	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	c
Bufo americanus	o	Forest area	-	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Bufo americanus	ab	Wetland area	-	500	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	f
Bufo americanus	ab	Mean Pond depth	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Bufo americanus	ab	Mean turbidity	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Bufo americanus americanus	o	Number of ponds	+	woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Bufo americanus americanus	o	Proportion of wetland as marsh	+	woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Bufo bufo	o*	Density of canals	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Density of hedges	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Density of rivers	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Relief	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Soil drainage capability	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Woodland area proportion	+	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	f
Bufo bufo	o	Migration zone area	+	3000	1500 -3000	Geneva (Switzerland)	Ray et al. (2002)	l	c
Bufo bufo	o	Number of occupied ponds	+	3000	1500 -3000	Geneva (Switzerland)	Ray et al. (2002)	l	c
Bufo bufo	o	Sparse vegetation area	+	3000	1500 -3000	Geneva (Switzerland)	Ray et al. (2002)	l	
Bufo bufo	o*	Altitude	-		Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	
Bufo bufo	o*	Woodlot presence	-	100	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	f

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Bufo bufo	ab*	Density of ponds	-	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	c
Bufo bufo	o*	Proportion of rough pasture	-	1000	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	l	a
Bufo bufo	o	Cultivated field area	-	3000	1500 -3000	Geneva (Switzerland)	Ray et al. (2002)	l	a
Bufo bufo	o*	Fish presence	-	Pond	Ponds-1000	Leicestershire (Great Britain)	Scribner et al. (2001)	p	
Bufo punctatus	o	Hydroperiod	+	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Proportion of bedrock terrain	+	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Water area	+	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Altitude	-	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Vegetation cover over adjacent land	-	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Vegetation cover over water	-	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Bufo punctatus	o	Water conductivity	-	Pond	Pond	Mojave Desert (USA)	Bradford et al. (2003)	p	
Crinia parinsignifera	o	Annual mean temperature	+		Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	l	
Crinia parinsignifera	o	Area of waterbody during breeding season	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Crinia parinsignifera	o	Bank stability and livestock pugging index	+	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Crinia parinsignifera	o	Proportion of waterbody perimeter with emergent vegetation at edge	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Crinia parinsignifera	o	Wetland area	+	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Crinia parinsignifera	o	Presence of tussock in the riparian zone	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Dicamptodon tenebrosus	o	Large and mixed sawtimber core area	+	Forest Patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Hyla arborea	o	Distance from the nearest occupied pond	+		100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	l	c
Hyla arborea	o	Number of occupied ponds	+	100-2000	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	l	c
Hyla arborea	o	Number of ponds	+	100-2000	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	l	c
Hyla arborea	o	Area of high herbs	+	250-1500	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	l	
Hyla arborea	o	Area of shrubs	+	500-2000	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	l	
Hyla arborea	o	Hours of direct sunlight	+	Pond	Pond-2000	West Switzerland	Pellet et al (2004a)	p	
Hyla arborea	o	Ponds vegetation area	+	Pond	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	p	
Hyla arborea	o	Distance from nearest two-lane road	-		Pond-2000	West Switzerland	Pellet et al (2004a)	l	r
Hyla arborea	o	Urban area	-	100-1000	100-2000	West Switzerland	Pellet et al (2004b)	l	u
Hyla arborea	o	Traffic index	-	100-400	100-2000	West Switzerland	Pellet et al (2004b)	l	r
Hyla arborea	o	First class road length	-	200	100-2000	West Switzerland	Pellet et al (2004b)	l	r
Hyla arborea	o	Urban area	-	30	Pond-2000	West Switzerland	Pellet et al (2004a)	p	

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Hyla arborea	o	Conductivity	-	Pond	100-2000	Zealand Flanders (Netheralnds)	Vos and Stumpel (1995)	p	
Hyla arborea	o	Water conductivity	-	Pond	Pond-2000	West Switzerland	Pellet et al (2004a)	p	
Hyla spp.	o	Hydroperiod (unimodal)**	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Hyla spp.	o	Max water depth (unimodal)**	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Hyla spp.	o	Pond area	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Hyla versicolor	ab	Forest area	+	1000	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	f
Hyla versicolor	o	Wetland area	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Hyla versicolor	o	Forest area	+	3000-4000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Hyla versicolor	ab	Sum of abundance indices for invertebrate (backswimmer)	+	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Hyla versicolor	o	Woodlot area	+	woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Hyla versicolor	ab	Mean conductivity	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Hyla versicolor	ab	Total nitrogen concentration	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Hyla versicolor	o	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r
Limnodynastes fletcheri	o	Fringing vegetation index	+	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Limnodynastes tasmaniensis	o	Aquatic vegetation index	+	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Limnodynastes tasmaniensis	o	Area of waterbody during breeding season	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Limnodynastes tasmaniensis	o	Wetland area	-	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Litoria aurea	o	Distance to occupied ponds	+		Pond	Kooragang Island (Australia)	Hamer et al. (2002)	l	c
Litoria aurea	o	Banks vegetation diversity	+	Pond	Pond	Kooragang Island (Australia)	Hamer et al. (2002)	p	
Litoria aurea	o	Presence of Juncus kraussii, Schoenoplectus litoralis and	+	Pond	Pond	Kooragang Island (Australia)	Hamer et al. (2002)	p	
Litoria peronii	o	Area of native canopy cover	+	1000	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	l	f
Litoria peronii	o	Fringing vegetation index	+	Pond	Pond	Murray-Darling Basin (Australia)	Jansen and Healey (2003)	p	
Litoria peronii	o	Annual mean temperature	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Litoria peronii	o	Percentage of 2-m wide riparian zone with bare ground	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Litoria verreauxii	o	Annual mean temperature	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Litoria verreauxii	o	Percentage of 2-m wide riparian zone with bare ground	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Notopthalmus viridescens	o	Forest area	+	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Pelobates cultripes	o	Agriculture intensification index	-	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Pelobates cultripes	o	Ponds transformation in irrigation reservoirs	-	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Pelobates cultripes	o	Hydroperiod	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Pelobates cultripes	o	Maximum water depth	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pelodytes punctatus	o	Ploughing index	+	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Pelodytes punctatus	o	Ponds transformation in irrigation reservoirs	-	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Pelodytes punctatus	o	Hydroperiod	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pelodytes punctatus	o	Maximum water depth	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pelodytes punctatus	o	Presence of exotic predators	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pelodytes punctatus	o	Relative water depth	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Plethodon cinereus	o	Forest area	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	f
Plethodon dunni	o	Large sawtimber core area density	+	Forest patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Plethodon dunni	o	Large sawtimber area weighted mean patch fractal dimension	-	Forest patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Plethodon dunni	o	Large sawtimber edge density	-	Forest patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Plethodon dunni	o	Large sawtimber patch density	-	Forest patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Pleurodeles waltl	o	Agriculture intensification index	-	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Pleurodeles waltl	o	Hydroperiod (unimodal)**	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pleurodeles waltl	o	Ponds transformation in irrigation reservoirs	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Pseudacris crucifer	ab	Forest area	+	2500	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	f
Pseudacris crucifer	o	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Pseudacris crucifer	o	Hydroperiod	+	Pond	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Pseudacris crucifer	ab	Distance to the nearest forest	-		Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	f
Pseudacris crucifer	ab	Distance to the nearest wetland	-		Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	c
Pseudacris crucifer	o	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r
Pseudacris triseriata	ab	Grassland area	+	2500	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	l	
Pseudacris triseriata	o	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Pseudacris triseriata	ab	Index of percentage of shoreline composed of trees or shrubs	+	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Pseudacris triseriata	o	Perimeter of wetlands	+	woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Pseudacris triseriata	ab	Mean conductivity	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Pseudacris triseriata	ab	Mean Pond depth	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Pseudacris triseriata	o	Total phosphorus concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Ran temporaria	ab*	Agriculture intensity	+	500	500	Sweden	Johansson et al. (2005)	l	a
Ran temporaria	ab*	Agriculture intensity	-	500	500	Sweden	Johansson et al. (2005)	l	a
Rana arvalis	ab	Area of occupied pond	+	250, 750, 1000-2000	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	l	c
Rana arvalis	o	Area of occupied pond	+	250,500, 2000	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	l	c
Rana arvalis	o	Area of moorland	+	250-2000	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	l	

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Rana arvalis	ab	Area of moorland	+	250-2000	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	l	
Rana arvalis	o	Marsh vegetation area	+	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	p	
Rana arvalis	ab	Marsh vegetation area	+	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon. (1998)	p	
Rana arvalis	o	Traffic index	-	750	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	l	r
Rana arvalis	ab	Traffic index	-	750	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	l	r
Rana arvalis	o	PH	-	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	p	
Rana arvalis	ab	PH	-	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	p	
Rana arvalis	o	Water conductivity	-	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	p	
Rana arvalis	ab	Water conductivity	-	Pond	250-2000	Drenthe (Netheralnds)	Vos and Chardon (1998)	p	
Rana catesbeiana	o	Wetland proximity	+		1000	Indiana (USA)	Kolozsvary and Swihart (1999)	l	c
Rana catesbeiana	o	Hydroperiod	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana catesbeiana	o	Kjeldahl nitrogen concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana catesbeiana	o	Forest area	-	100	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Rana clamitans	o	Wetland proximity	+		1000	Indiana (USA)	Kolozsvary and Swihart (1999)	l	c
Rana clamitans	o	Forest area	+	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Rana clamitans	o	Pond area	+	100-1000	Pond-1000	New Brunswick (Canda)	Mazerolle et al. (2005)	l	c
Rana clamitans	ab	Lengths of stream	+	1500	250-5000	Ontario (USA)	Carr and Fahrig (2001)	l	
Rana clamitans	o	Forest area	+	3000-4000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Rana clamitans	o	Forest area	+	500-1000	Pond-1000	New Brunswick (Canda)	Mazerolle et al. (2005)	l	f
Rana clamitans	o	Area of herbs and floating vegetation	+	Pond	Pond-1000	New Brunswick (Canda)	Mazerolle et al. (2005)	p	
Rana clamitans	o	Hydroperiod	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana clamitans	o	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Rana clamitans	o	Wetland area	-	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Rana clamitans	o	Forest area	-	250	Pond-1000	New Brunswick (Canda)	Mazerolle et al. (2005)	l	f
Rana clamitans	o	Cover of floating and submerged vegetation	-	Pond	Pond-1000	New Brunswick (Canda)	Mazerolle et al. (2005)	p	
Rana clamitans	ab	Index of percentage of shoreline composed of trees or shrubs	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Rana clamitans	o	Kjeldahl nitrogen concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana clamitans	ab	Sum of abundance indices for invertebrate (crawling water beetle)	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Rana clamitans	ab	Total nitrogen concentration	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Rana clamitans	o	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r
Rana clamitans melanota	o	Hydroperiod	+	Pond	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Rana mucosa	o	Proportion of high quality lakes in drainage	+		Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	l	
Rana mucosa	o	Proportion of high quality lakes	+	1000	Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	l	
Rana mucosa	o	Number of inlets	+	Pond	Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	p	
Rana mucosa	o	Proportion of littoral zone slit	+	Pond	Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	p	
Rana mucosa	o	Water depth	+	Pond	Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	p	
Rana mucosa	o	Fish presence	-	Pond	Pond-1000	Sierra Nevada, California (USA)	Knapp et al. (2003)	p	
Rana palustris	o	Forest area	+	1000	1000	Ontario (USA)	Findlay et al. (2001)	l	f
Rana palustris	o	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Rana perezi	o	Agriculture intensification index	+	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Rana perezi	o	Hydroperiod	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Rana perezi	o	Maximum water depth (unimodal)**	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Rana perezi	o	Ponds transformation in irrigation reservoirs	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Rana perezi	o	Relative water depth	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Rana pipiens	o	Wetland proximity	+		1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Rana pipiens	o	Area of summer habitat	+	1000	Pond-1000	Ottawa (Canada)	Pope et al. (2000)	l	
Rana pipiens	ab	Length of spawning favourable habitat	+	1500	250-5000	Ontario (USA)	Carr and Fahrig (2001)	l	c
Rana pipiens	o	Number of occupied ponds	+	1500	pond-1500	Ottawa (Canada)	Pope et al. (2000)	p	
Rana pipiens	o	Hydroperiod	+	Pond	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	l	
Rana pipiens	o	Hydroperiod	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana pipiens	o	Perimeter of spawning habitat	+	Pond	Pond-1000	Ottawa (Canada)	Pope et al. (2000)	p	
Rana pipiens	o	Forest proximity	-		1000	Indiana (USA)	Kolozsvary and Swihart (1999)	l	f
Rana pipiens	o	Forest area	-	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Rana pipiens	ab	Traffic index	-	1500	250-5000	Ontario (USA)	Carr and Fahrig (2001)	l	c
Rana pipiens	o	PH	-	Pond	Pond-1000	Ottawa (Canada)	Pope et al. (2000)	l	r
Rana pipiens	ab	PH	-	Pond	250-5000	Ontario (USA)	Carr and Fahrig (2001)	p	
Rana septentrionalis	o	Wetland area	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Rana septentrionalis	o	Forest area	+	3000-4000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Rana septentrionalis	o	Hydroperiod	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana septentrionalis	o	Road density	-	1000	1000	Ontario (USA)	Findlay et al. (2001)	l	r
Rana septentrionalis	o	Kjeldahl nitrogen concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana septentrionalis	o	Total phosphorus concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rana septentrionalis	o	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Rana sylvatica	o	Forest area	+	100	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Rana sylvatica	o	Forest area	+	1000	300-500-1000	Maine (USA)	Guerry and Hunter (2002)	l	f
Rana sylvatica	o	Wetland area	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Rana sylvatica	o	Perimeter of wetlands	+	Woodlot	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Rana sylvatica	o	Road density	-	1000	1000	Ontario (USA)	Findlay et al. (2001)	l	r
Rana sylvatica	o	Total phosphorus concentration	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Rhyacotriton variegatus	o	Large and mixed sawtimber core area density	-	Forest Patch	Patch	Oregon (USA)	Martin and McComb (2003)	p	
Triturus alpestris	o*	Migration zone area	+	800	400-800	Geneva (Switzerland)	Ray et al. (2002)	l	c
Triturus alpestris	ab	uncultivated sector proportion	+	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus alpestris	ab	Arable ground proportion	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus alpestris	ab	Fish presence	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus alpestris	ab	Hedgerow length	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus alpestris	ab	Pond area	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus cristatus	ab	Floating vegetation proportion	+	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus cristatus	ab	Arable ground proportion	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus cristatus	ab	Fish presence	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus cristatus	ab	Pond area	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus helveticus	ab	Forest area	+	1260	Pond-1260	Southern Larzac, France	Denoel and Lehmann (2006)	l	f
Triturus helveticus	ab	Number of occupied ponds	+	1260	Pond-1260	Southern Larzac, France	Denoel and Lehmann (2006)	l	c
Triturus helveticus	ab	Floating vegetation proportion	+	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus helveticus	ab	uncultivated sector proportion	+	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus helveticus	ab	Vegetation area	+	Pond	Pond-1260	Southern Larzac, France	Denoel and Lehmann (2006)	p	
Triturus helveticus	ab	Water depth	+	Pond	Pond-1260	Southern Larzac, France	Denoel and Lehmann (2006)	p	
Triturus helveticus	ab	Arable ground proportion	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus helveticus	ab	Fish presence	-	Pond	Pond-1260	Southern Larzac, France	Denoel and Lehmann (2006)	p	
Triturus helveticus	ab	Fish presence	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus helveticus	ab	Hedgerow length	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Triturus helveticus	ab	Pond area	-	Pond	Pond-400	Bresse and Dombes (France)	Joly et al. (2001)	p	
Triturus marmoratus	o	Pond area	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Triturus marmoratus	o	Ploughing index	-	200	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	l	a
Triturus marmoratus	o	Hydroperiod (unimodal)**	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Triturus marmoratus	o	Relative water depth	-	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Uperoleia laevigata	o	Area of native canopy cover	+	1000	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	l	f
Uperoleia laevigata	o	Proportion of waterbody perimeter with emergent vegetation at edge	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
B) Species richness									
Amphibians	amr	Area of native canopy	+	1000	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	l	f
Amphibians	amr	Forest area	+	1000	1000	Ontario (USA)	Findlay et al. (2001)	l	f
Amphibians	amr	Forest area	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Amphibians	amr	Hydroperiod	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Amphibians	amr	Hydroperiod	+	Pond	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Amphibians	amr	Intermediate degrees of water permanency	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Amphibians	amr	Maximum abundance Index of tiger salamander larvae (predation)	+	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Amphibians	amr	Pond area	+	Pond	Pond-200	Southwest Portugal	Beja and Alcazer (2003)	p	
Amphibians	amr	Presence of tussock in the riparian zone	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Amphibians	amr	Proportion of waterbody perimeter with emergent vegetation at edge	+	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Amphibians	amr	Wetland area	+	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Amphibians	amr	wetlands proportion	+	2000-3000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Amphibians	amr	Ammonia concentration	-	Pond	Woodlts-1000	Ohio (USA)	Weyrauch and Grubb (2004)	p	
Amphibians	amr	Distance to nearest wetland	-		500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	
Amphibians	amr	Fish presence	-	Pond	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	p	
Amphibians	amr	Fish presence	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Amphibians	amr	Nitrogen levels.	-	Pond	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	p	
Amphibians	amr	Percentage of 2-m wide riparian zone with bare ground	-	Pond	Ponds-1000	Shoalhaven (Australia)	Hazell et al. (2001)	p	
Amphibians	amr	Pond area	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Amphibians	amr	Road density	-	1000	1000	Ontario (USA)	Findlay et al. (2001)	l	r
Amphibians	amr	Road density	-	500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	r
Amphibians	amr	Road density	-	1000	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	r

Species	Resp	Predictors	Sign	Scale (m)	Scale range (m)	Study area	Reference	S	V
Amphibians	amr	Road density	-	2500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	r
Amphibians	amr	Roads density	-	2000	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r
Amphibians	amr	Total nitrogen concentration	-	Pond	Pond-2500	Minnesota (USA)	Knutson et al. (2004)	p	
Amphibians	amr	Urban area	-	500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	u
Amphibians	amr	Urban area	-	1000	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	u
Amphibians	amr	Urban area	-	2500	500-1000-2500	Minnesota (USA)	Lehtinen et al. (1999)	l	u
Anurans	anr	Intermediate degrees of water permanency	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Caudates	car	Hydroperiod	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Caudates	car	PH	+	Pond	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
Caudates	car	Woodlot edge-to-area ratio	+	woodlot	1000	Indiana (USA)	Kolozsvary and Swihart (1999)	p	
C) Other indices									
Maximum abundance index	ab	Agriculture area	+	1000	1000	Wisconsin (USA)	Knutson et al (1999)	l	a
Maximum abundance index	ab	Forest area	+	1000	1000	Wisconsin (USA)	Knutson et al (1999)	l	f
Maximum abundance index	ab	Length of the edge between wetland and forest	+	Various distances	1000	Iowa (USA)	Knutson et al (1999)	l	
Maximum abundance index	ab	Urban area	-	1000	1000	Iowa (USA)	Knutson et al (1999)	l	u
Number of individuals see per hour	ab	Distance to the nearest wetland	+	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	c
Number of individuals see per hour	ab	Forest area	+	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	f
Number of individuals see per hour	ab	Marsh area	+	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	
Number of individuals see per hour	ab	Permanent pond	+	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	
Number of individuals see per hour	ab	Road density	-	Various distances	100-4000	Ontario (USA)	Houlahan and Findlay (2003)	l	r

* Including population estimates from genetic data

** unimodal refers to determinants with quadratic relationship (optimum)

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Appendix 2

Information-theoretic approach and model selection

An alternative to null hypothesis testing

As said by Johnson and Omland (2004) "*science is a process for learning about nature in which competing ideas about how the world works are evaluated against observations. These ideas are usually expressed first as verbal hypotheses, and then as mathematical equations, or models. Models represent biological processes in simplified and general ways that provide insight into factors that are responsible for observed patterns. Hence, the degree to which observed data support a model also reflects the relative support for the associated hypothesis.*"

To draw biological inferences, the dominant paradigm in literature is to generate a null hypothesis and ask whether the hypothesis can be rejected in light of observed data (Anderson et al. 2000, 2001). The hypothesis is rejected when a test statistic generated from observed data falls beyond an arbitrary probability threshold (usually $P<0.05$), which is interpreted as tacit support for a biologically more meaningful alternative hypothesis. Hence, the actual hypothesis of interest (the alternative hypothesis) is accepted only in the sense that the null hypothesis is rejected. However, there are a number of problems with the application of the null hypothesis testing. Anderson et al. (2000) presented a good review of these statistical problems and underlined that null hypothesis testing is uninformative in mostly case, and of relative little use in model or variable selection:

- The null hypothesis is often almost surely false ("false null hypothesis"). Thus, the rejection of this clearly false assumption hardly advances science.
- The α-level of statistical significance is without theoretical basis and it is therefore arbitrary.
- *P*-value depends on sample size. One can always reject null hypothesis with a large enough sample, even if the true difference is trivially small. This is the difference between statistical significance and biological importance.
- *P*-value cannot validly be taken as the probability that the null hypothesis is true, although this is often the interpretation given.

In this context, a practical alternative to null hypothesis testing is model selection, which offers a way to draw inferences from a set of multiple competing hypotheses. Johnson and Omland (2004) presented three main advantages. First, practitioners are not restricted to evaluating a single model where significance is measured against some arbitrary probability threshold. Instead, competing models are compared to one another by evaluating the relative support in the observed data for each model. Second, models can be ranked and weighted, thereby providing a quantitative measure of relative support for each competing hypothesis. Third, in cases where models have similar levels of support from the data, model averaging can be used to make robust parameter estimates and predictions.

Best model selection and ranking: the AIC

Conceptually, there is information in the observed data, and we want to express this information in a compact form via a “model”. Such model is then the basis for making inference about the process or system that generated the data. The goal is to achieve a translation such that minimal information is lost in going from the data to a model of the information.

Models are only approximation and we cannot hope to perfectly achieve this idealized goal. However, we can attempt to find a model of the data that is best in the sense that the model loses as little information as possible (Burnham and Anderson 2002). This thinking leads directly to Kullback-Leibler (*K-L*) information, *I*(*f*, *g*); the information lost when model *g* is used to approximate full reality, *f*. Thus, the goal is to select a model that minimizes *K-L information* loss. Because we must estimate model parameters from the data, the best we can do is to minimize (estimated) *K-L information* loss. This can be done using one of the information-theoretic criteria (e.g. *AIC*). We are not really trying to model the data; instead we are trying to model the information in the data (Burnham and Anderson 2002).

Akaike information criterion (*AIC*) (equation 1) is an estimate of the expected *Kullback–Leibler information* lost by using a model to approximate the process that generated observed data (full reality). *AIC* has two components: negative loglikelihood ($-2\ln\left[\mathrm{L}\left(\hat{\theta}\middle|y\right)\right]$), which measures lack of model fit to the observed data y, and a bias correction factor ($2k$), which increases as a function of the number of model parameters (k). $\mathrm{L}\left(\hat{\theta}\middle|y\right)$ is the likelihood of the model parameters given the data y, $\hat{\theta}$ is the parameters estimation.

$$AIC = -2\ln\left[\mathrm{L}\left(\hat{\theta}\middle|y\right)\right] + 2k \qquad \text{(eq. 1)}$$

A modified criterion (AIC_c) has to be used when K is large relative to sample size n (n/k<40, Burnham and Anderson 2004), equation (2):

$$AIC_c = -2\ln\left[\mathrm{L}(\hat{\theta}_p\middle|y)\right] + 2k + \frac{2k(k+1)}{(n-k-1)} \qquad \text{(eq. 2)}$$

Some authors suggest to use AIC_c in any case (Burnham and Anderson 2004). Indeed, when n is large, the correction factor ($\frac{2k(k+1)}{(n-k-1)}$) tends to zero and the AIC_c converges to AIC. In small samples correction factor for AIC_c is more severe regarding the number of parameters than for AIC. Therefore, in small samples AIC_c tend to select models with low parameters (simpler). AIC_c retains all of the advantages of AIC, while removing many of the disadvantages.

At some point, the addition of more parameters will have the opposite from desired effect and the relative *Kullback–Leibler* distance will increase because of “noise” in estimated parameters that are not really needed to achieve a good model (Burnham and Anderson 2002). In the case of *AIC*, the first term tends to decrease as more parameters are added to the model, while the second term gets larger as more parameters are added. This is the tradeoffs between bias and variance or the tradeoffs between under-fitting and over-fitting that is fundamental to the principle of parsimony (Figure 1). This principle should lead to a model with “ *… the smallest possible number of parameters for adequate representation of the data*” (Box and Jenkins 1970). In under fitted models bias in the parameters estimators is often important, and the sampling variance is underestimated, both factors resulting in poor confidence coverage. Under fitted models tend to miss important effects in experimental settings. Over fitted models, as judged against a best approximating model, are often free of bias in the parameter estimators, but have sampling variance that are needlessly large (the precision of estimators is poor, relative to what could have been accomplished with more parsimonious model)

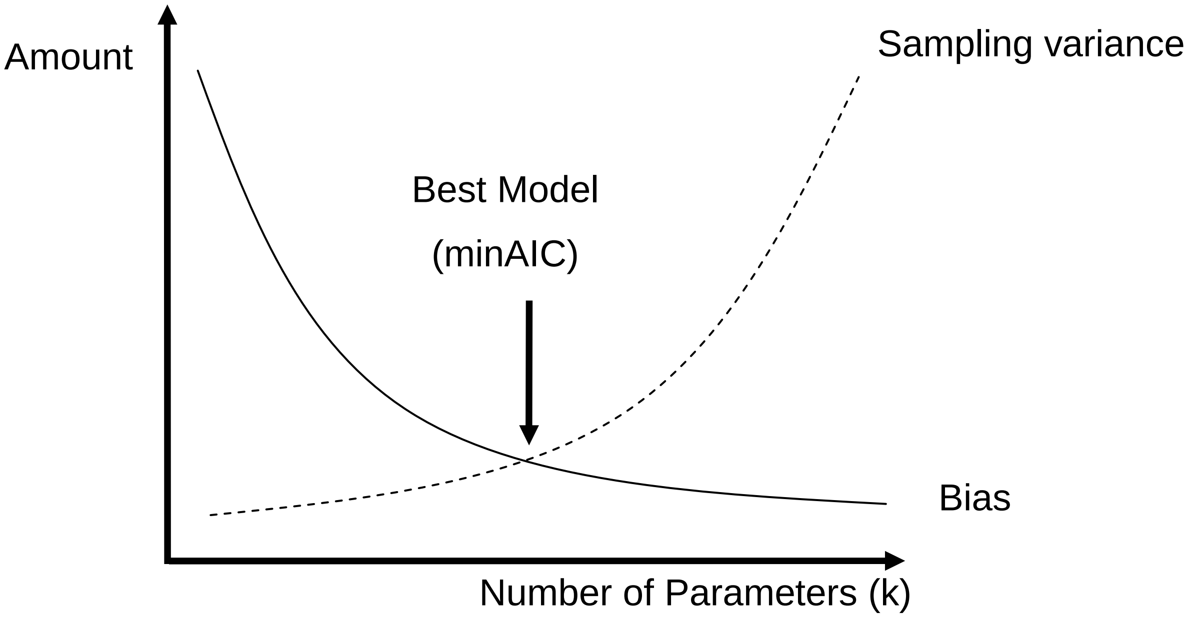

Figure 1. *Relationships between the number of parameters (K), the bias and the explained variance. Bias in the parameters estimation decreases and sampling variance (a measure of the precision of the estimators) increases as the number of parameters increases. According to the principle of parsimony, the best approximating model has the lower Akaike Information criterion (AIC) value. Best model however not occurs exactly where the two curves intersect. Full truth or reality is not attainable with finite sample and usually lies well to the right of the region in which the best approximating model lies (the tradeoff region) (modified from Burnham and Anderson 2002)*

Akaike weight and model averaging

The model selection approach can also be used to (i) compute the relative weight of a model in a set of models and (ii) to compute an average weight of parameter estimates. Here we present these statistical approaches accordingly with Johnson and Omland (2004), Box 4.

(i) Generate a confidence set of models: the Akaike weight.

The goal is to determine which models are well supported by data. This estimation is possible using AIC based calculations. We remind that the best model in the set of candidates has the minimum AIC value. Thus, once each model has been fitted to the data, the difference in AIC score between each model and the best model yields an estimation of the relative model support (equation 3):

$$\Delta i = AICi - AIC\,\mathrm{min} \qquad \text{(eq. 3)}$$

Models having $\Delta i < 2$ have substantial support (evidence), those in which 4 Δi 7 have considerably less support, and models having $\Delta i > 10$ have essentially no support (Burnham and Anderson 2004). The support or evidence refers to the relative capacity of a model to describe the information present in the data, i.e. how much data support the model. The likelihood of a model, gi, given the data, y, is then calculated as equation 4,

$$\mathrm{L}(g_i \mid y) = \exp(-1/2\Delta i) \qquad \text{(eq. 4)}$$

From equation 4, it is possible and useful to contrast the likelihood of pairs of models, using the evidence ratio (equation 5),

$$ER = \frac{\mathrm{L}(g_{best} \mid y)}{\mathrm{L}(g_i \mid y)} \qquad \text{(eq. 5)}$$

Finally, the model likelihood values can also be normalized across all R models (equation 6).

$$Wi = \frac{\exp(-1/2\Delta i)}{\sum_{j=i}^{R} \exp(-1/2\Delta i)} \qquad \text{(eq. 6)}$$

This value is termed Akaike weight and provides a relative “weight of evidence” for each model. The sum of all the Akaike weight across R models is 1 and thus the Akaike weights can be interpreted as *“the probability that model i is the best model for the observed data, given the candidate set of models*” Johnson and Omland (2004). The Akaike weights can be summed in order to estimate the relative importance of a predictor variable or a hypothesis associated to the models.

(ii) Compute an average weight of parameter estimates: model averaging.

From the model selection approach, it is also possible to estimate an average weight of parameters ($\hat{\theta}$) across a set of R candidate models (θ_i is the regression coefficient in the *i*th model) (equation 7).

$$\hat{\theta} = \sum_{i=1}^{R} w_i \theta_i \qquad \text{(eq. 7)}$$

This may be very interesting when the goal is parameter estimation or prediction, and no single model is clearly supported by the data (i.e. $w_{best} < 0.9$).

Conclusions

We underlined the advantages and potential applications of model selection using the *AIC* criterion. Other criteria can also be computed (e.g. *BIC*, Burnham and Anderson. 2004). However, this recent and developing statistical field go behind the subject of our research which has been limited to the use of *AIC* criterion. Model selection with *AIC* derived statistics has been recently used with success in some studies. Weyrauch and Grubb (2004) and Van Buskirk (2005) are both excellent example of the application of these methods in amphibian-habitat association analyses. Information-theoretic approach is also used in our research in **Chapter 5** and **6**.

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Appendix 3

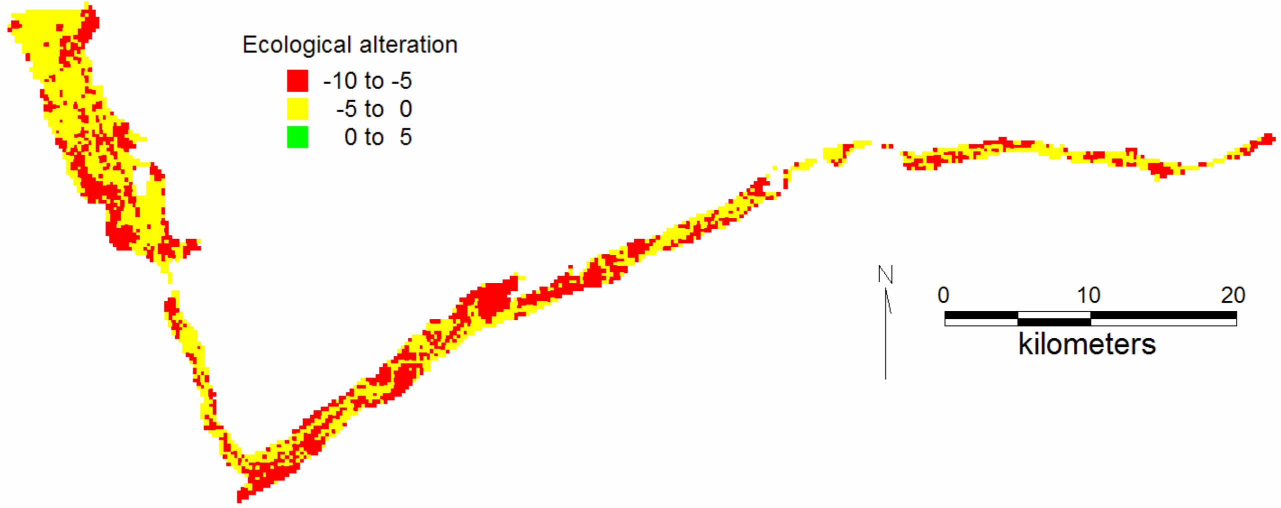
Data and cartographic complements to chapter 3

a) Nature conservation value scores estimated by experts for each land cover. Nature conservation value ranges from 0 (no conservation value) to 10 (maximum conservation value).

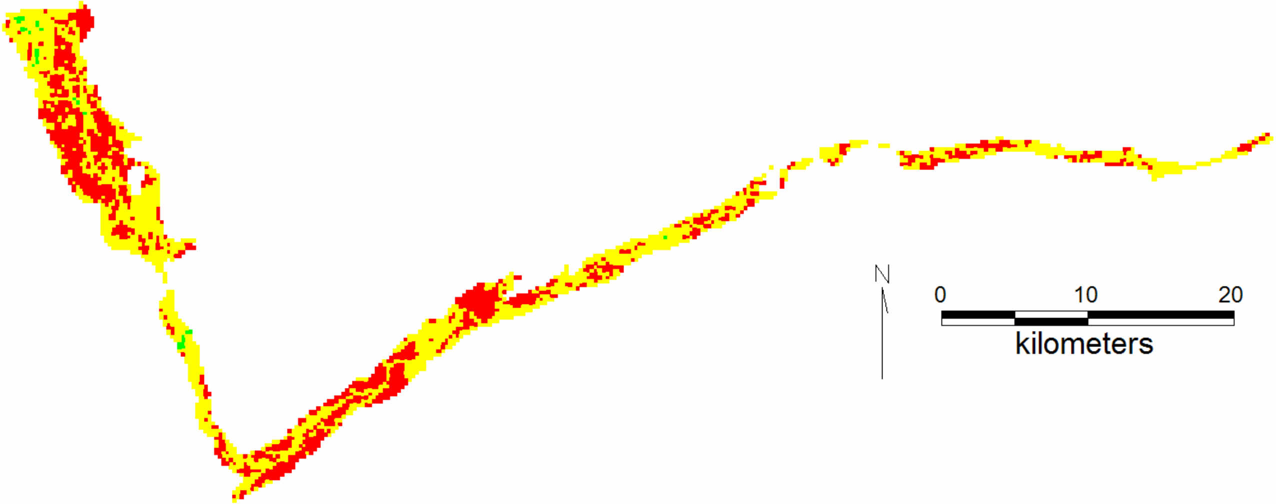
	1900				2003			
	EXP1	**EXP2**	**EXP3**	**Mean**	**EXP1**	**EXP2**	**EXP3**	**Mean**
Floodplain, river Rhone	10	10	9	9.67	7	7	9	7.67
Dune	8	10	10	9.33	-	-	-	-
Wetland	9	10	8	9.00	7	7	8	7.33
Hill	8	9	9	8.67	8	5	9	7.33
Floodplain tributary	7	10	7	8.00	6	5	7	6.00
Canal	5	10	7	7.33	2	2	5	3.00
Stagnant water	6	8	8	7.33	5	8	8	7.00
Forest	8	8	5	7.00	7	8	5	6.67
Agricultural zone	8	7	4	6.33	3	2	2	2.33
Tributary	5	6	7	6.00	4	2	7	4.33
Rhone, canalized	3	5	4	4.00	2	7	4	4.33
Urban Area	4	4	2	3.33	2	2	1	1.67
Railways	5	2	2	3.00	4	2	1	2.33
Roads	2	3	0	1.67	0	1	0	0.33
Highways	-	-	-	-	1	3	1	1.67

b) Maps of ecological alteration computed for each expert

Ecological alteration EXP1



Ecological alteration EXP2



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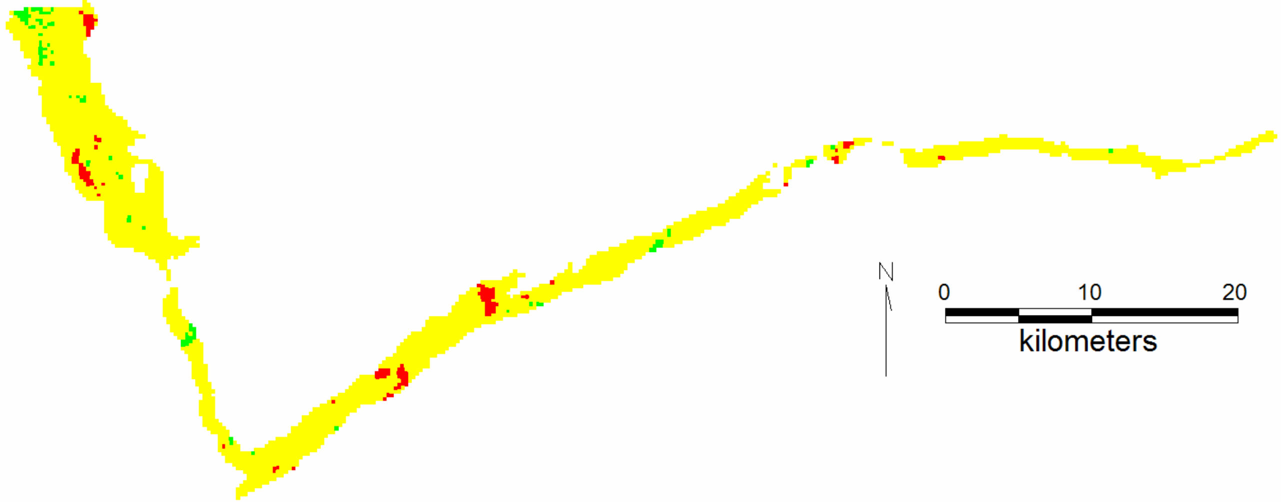
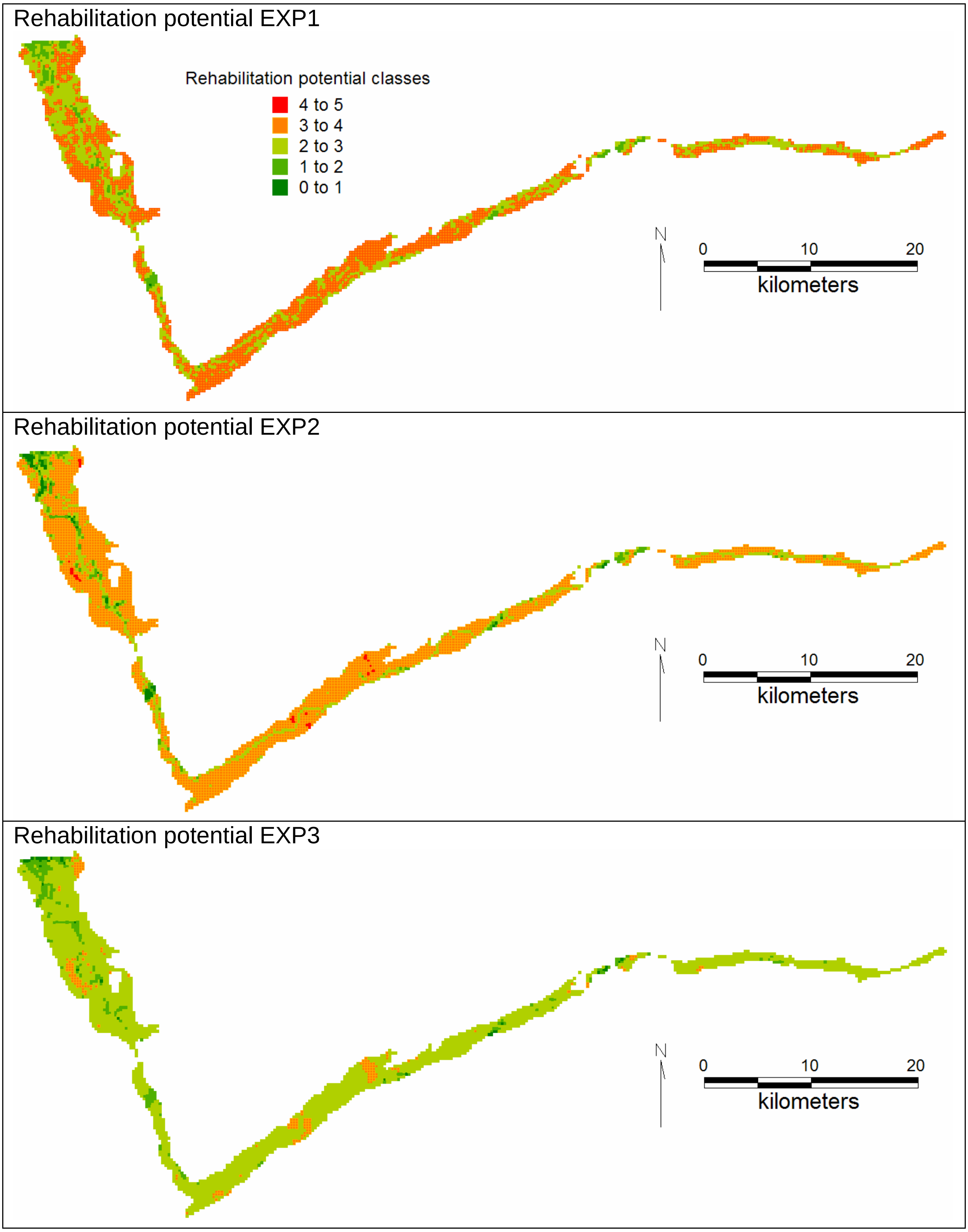
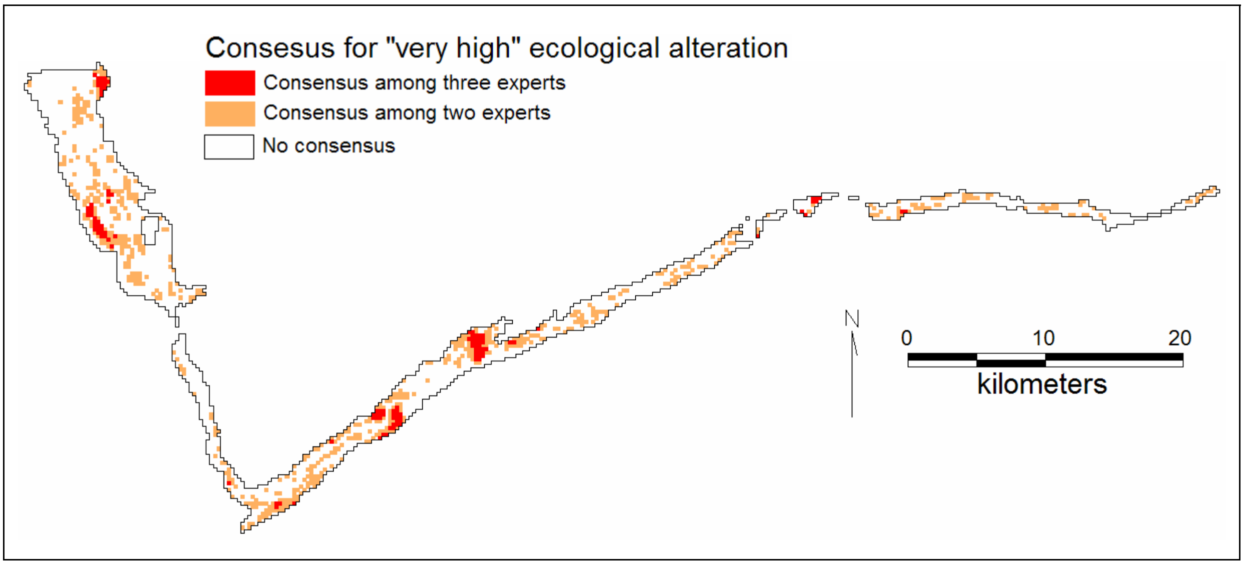


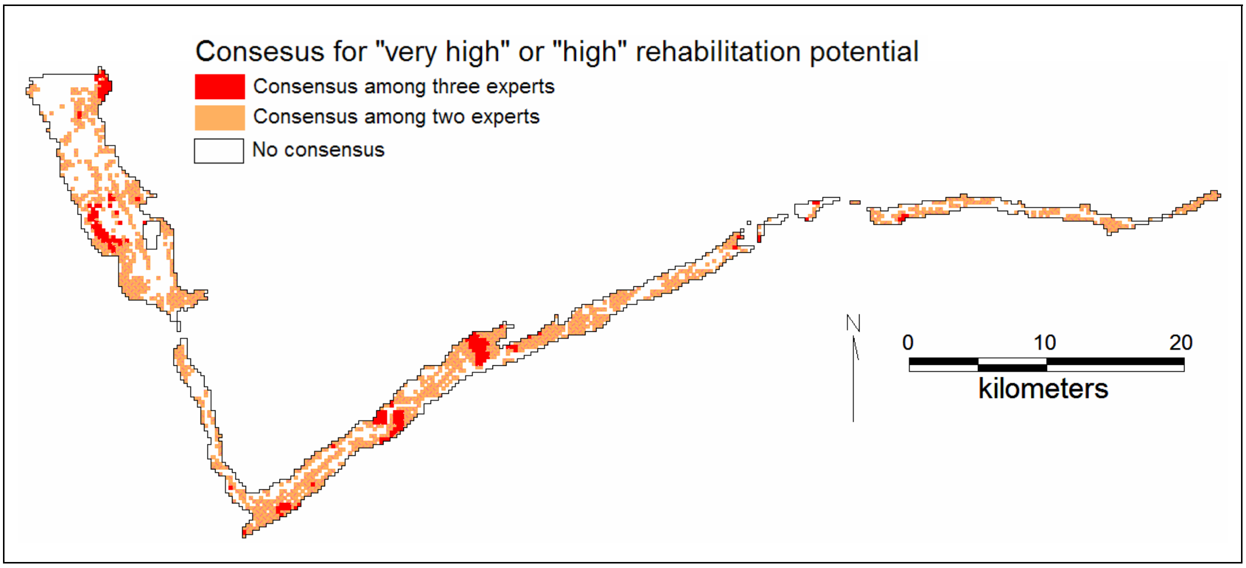
c) Maps of rehabilitation potential computed for each expert



d) Map of consensus among experts on ecological alteration



e) Map of consensus among experts on rehabilitation potential



Appendix 4

Three indices for the description of spatial autocorrelation

1) **The Moran's I** (Moran 1950) is based on Pearson's correlation and generally varying between [-1; 1]. Positives values correspond to positive correlation:

$$I(D) = \frac{\left(\frac{1}{W}\right)\sum_{i=1}^{p}\sum_{j=1}^{p} w_{ij}\left(y_i - \bar{y}\right)\left(y_j - \bar{y}\right)}{\frac{1}{p}\sum_{i=1}^{p}\left(y_i - \bar{y}\right)^2}, i \neq j$$

Where, y_i =observations, w_{ij} = distance weight (1 if pairs (*i,j*) included in distance D and 0 if they are outside), p =number of observations, D =classes of distance tested, W =Somme w_{ij} (number of pairs used for the $I(D)$ estimation).

2) **The Geary c** (Geary 1954) is based on distance measures and varies between [0; $+\infty$[, but usually <3. the formula is the following (see Moran's I for parameters description):

$$c(D) = \frac{(p-1)\sum_{i=1}^{p}\sum_{j=1}^{p} w_{ij}\left(y_i - y_j\right)^2}{2W\sum_{i=1}^{p}\left(y_i - \bar{y}\right)^2}, i \neq j$$

3) **Modified join-count statistics** (Sokal and Oden 1978, Mangel and Adler 1994) to quantify spatial patterns can also be used in case of presence/absence data. This approach is well adapted to appraise at spatial autocorrelation in breeding ponds occupancy by amphibian species. The structure function for the probability that a

pond *j* is occupied, given an occupied pond *i* as a starting point, δ units away, can be defined as follow:

$$\Pr_j\{1|1,\delta\} = \frac{\sum_{j \neq i} C(x_j) I(\delta, d(x_i, x_j))}{\sum_{j \neq i} I(\delta, d(x_i, x_j))}$$

Where $C(x_j)$ indicates the condition of the breeding pond x_j as follow:

$$C(x_j) = \begin{cases} 0 \text{ if pond } x_j \text{ is unoccupied} \\ 1 \text{ if pond } x_j \text{ is occupied} \end{cases}$$

and $I(\delta, d(x_i, x_j))$ is the indicator function for ponds x_i and x_j which are $d(x_i, x_j)$ units apart:

$$I(\delta, d(x_i, x_j)) = \begin{cases} 0 \text{ if } d(x_i, x_j) \neq \delta \\ 1 \text{ if } d(x_i, x_j) = \delta \end{cases}$$

Taking the average of this probability across each pond yields an overall probability of encountering an occupied pond at a given distance from another occupied pond. Note that by changing the conditions of $C(x_i)$ it is possible to look at the distribution of unoccupied ponds of δ units from one occupied. Randomization tests are used to generate distributions for the structure under the null assumption that the presence/absence of species is randomly distributed in space and constrained only by the locations of ponds. To create the distributions for each distance class, the number of species presences at the considered distance was randomly reassigned. By repeating this process 1000 times a probability distribution was generated given the observed ponds locations. For each random result at δ distance, the lower and the upper value of $\Pr_j\{1|1,\delta\}$ were kept. If the observed value is outside the range of its lower and upper randomized estimation, then the value of the probability is considered statistically significant at the 5% threshold. The $\Pr_j\{1|1,\delta\}$ can be computed for different distance steps to asses the sensibility of the results to the distance class δ.

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Appendix 5

Bombina variegata populations in the Rhone plain

A) Metapopulation M1

Population number	Coordinates (Swiss reference system)		Abundance classes[1]	Carrying capacity[2]
3	570200	109700	1	3
5	563430	123790	1	3
6	563300	121550	1	3
7	555750	137640	1	3
10	568770	109320	1	3
11	564500	121600	2	18
12	563100	121600	2	18
17	568700	114500	3	66
19	561400	122900	4	176
20	555250	136500	4	176
21	558000	137750	1	3
22	557700	137550	1	3
23	557080	137880	1	3
24	556450	138240	1	3
25	561280	134640	1	3
26	564900	122900	1	3
27	557630	136000	1	3
28	557100	137100	1	3
29	562820	126400	1	3
30	561900	132550	1	3
31	561850	131580	1	3
32	557700	137620	2	18
33	563000	126000	2	18
34	564040	125850	2	18
35	563500	124470	3	66
36	561350	137540	4	101

B) Metapopulation M2

Population number	Coordinates (Swiss reference system)		Abundance Classes[1]	Carrying Capacity[2]
1	595100	121000	1	3
2	585720	115840	1	3
4	594840	122270	1	3
8	605800	125300	1	3
9	592200	120200	1	3
13	600850	123000	2	18
14	599500	121600	2	18
15	596360	121570	2	18
16	600720	122900	2	18
18	604150	124530	3	66

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[1] Abundance classes: 1=1-5, 2=6-30, 3=31-100, 4=>100 (Grossenbacher K. 1988. Atlas de distribution des Amphibiens de Suisse. Documenta faunistica helvetiae 7:1-208)

[2] The carrying capacity used in patch occupancy metapopulation models (*Ni*, see §7)

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Objective

Biologist, with a Master in Engineering and Environmental management, I accumulated experiences in spatial ecology and biodiversity conservation. I would like to tack up new challenges with a dynamic team in the fields of nature protection and sustainable development.

Present job

2003-2006 **Biologist-PhD** at the Swiss Federal Institute of Technology Lausanne (EPFL), Geographical Information Systems Lab (LaSIG) and Swiss Federal Research Institute for Forest, Snow and Landscape (WSL)
Supervisor: Prof. Rodolphe Schlaepfer
PhD-Subject: landscape dynamics, distribution modelling, and metapopulation analyses for amphibian conservation in Switzerland
Activities: funds management (50000 CHFR.), honours projects supervising (4), collaboration with the Wallis state concerning the Ecological Network Concept of the Rhone plain, 6 month of civil service at KARCH (Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz, Bern), management of the PhD project.
Realisations: publications in preparation (5), conferences (4)

Professional experience

2001-2003 **Geographic Information Systems (GIS) expert** for the project GESORBE (Integrated management of the Orbe plain, Vaud, Switzerland) at the Laboratory of Hydrology and Land Improvement (HYDRAM-EPFL). The project involved 30 experts from several fields (hydrology, biology, economy, agriculture …) with a budget of 2 Mio of CHFR for two years.
Activities: management and analysis of spatial data, modelling of ecological network with raster approach, information and formation of the project actors in various fields (GIS, multi-criterion analyses, decision making processes)
Realisations: contribution to the evaluation of 15 scenarios of future landscape management, carrying out a system of data exchange, introductive report on decision making processes which has been distributed to the experts involved in the project.

2000-2001 **Geo-botanist** for the office of environmental consulting ECOCONTRAL SA, Locarno, Switzerland.
Realisations: phytosociological mapping of the Bosco Gurin region (TI) in order to assess and limit potential impact on flora diversity caused by the construction of a skiing resort.

1992-2001	**Various**: teaching assistant at the laboratory of botanic and systematic of the University of Lausanne, guide at the botanic garden of the island of Brissago (TI), various biology papers for divulgence revues.

Education

2000-2001	**Master of Sciences in «Engineering and Environmental Management »**, EPFL
1995-2000	**Majored of Biology** (Zoology, Ecology, Botanic) at the University of Lausanne, Diploma on Ants systematic (Myanmar, Burma).
1991-1995	**Degree in Sciences** (“Maturità scientifica tipo C”), Locarno, Switzerland.

Courses

2005	1 semester: Modelling species distribution, Prof. Antoine Guisan, University of Lausanne.
2001	1 week: MS Access, SIC-EPFL, Advanced level
1998	3 weeks: Tropical botany, Bryology and Alpine botany.

Languages

Italian	Mother Tongue
French	Mother Tongue equivalent
English	Fluent verbal and written (6 months in Australia)
Spanish	Good verbal and basic written
German	High School level

Computer skills

MS Office, **Data base** (FileMaker), **GIS** (Autocad, Idrisi32, Mapinfo, Manifold Arcview, Fragstats, ERDAS), **programming languages** (SQL, MapBasic, R), **Statistics** (S-Plus, R), **Web** (Dreamweaver)

Interests

Sport	Trekking, climbing, skating and running (20 km Lausanne, SOLA Zurich)
Travel	6 months in Australia, 6 weeks in Bolivia and Chili
Social	Civil service, scout coach (certificate G&S II Sport et Trekking), member of ProNatura, WWF, Alpinism Society of Vallemaggia (TI), co-redactor of the nature insert of the Ticino scout review, communal councillor in my village (Cavergno, TI).

Publications

Zanini, F., J. Pellet, and B. R. Schmidt. in preparation. Assessing geographic variation in the effects of landscape composition on the distribution of amphibians.

Zanini, F., J. Jaquiéry, R. Schlaepfer, P. Marchesi, and A. H. Hirzel. How does the landscape affect patch occupancy in metapopulation models? Comparing Euclidean vs landscape-based inter-patch distance. Submitted to Landscape Ecology.

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Oral presentations and posters

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Zanini F. 2005. Aires Prioritaires pour la Restauration du Paysage: approches basées sur la dynamique du paysage et la modélisation de l'habitat d'espèces focales. SFP, Etat du Valais. 7 févier 2005 (oral presentation).

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Zanini F. 2004. Selecting suitable area for rehabilitation and biodiversity conservation in human dominated landscape: historical and focal species approach. Seminary at the Spatial Ecology Laboratory, University of Queensland, Brisbane (Australia).

Zanini F., Paulmier E. et Weber C. 2004. Evolution de la qualité écologique des paysages de la plaine du Rhône sur la base d'une analyse spatiale de cartes historiques. Premier Colloque Mémoires du Rhône, Milieux et sociétés, 10 décembre 2004, Institut Universitaire Kurt Bösch, Bramois (présentation Orale de C.W.).

Zanini F., Pellet J., Schmidt B.R. 2004. Urbanization and its effects on amphibians: geographic variation and variation among species. 18th SCB Annual Meeting, “Conservation in an urbanizing world”, New York, USA, 30 July – 2 August 2004. (Invited symposium, oral presentation of B.R.S.).

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Reports

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Teaching and honours project supervised

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