The transferability of distribution models across regions: an amphibian case study

Flavio Zanini[1,2,3], Jérôme Pellet[4,5*] and Benedikt R. Schmidt[6,7]

[1]*Geographical Information Systems Laboratory, Swiss Federal Institute of Technology Lausanne (EPFL), CH-1015 Lausanne, Switzerland,* [2]*Restoration Ecology Group, Swiss Federal Research Institute for Forest, Snow and Landscape (WSL), CH-1015 Lausanne, Switzerland,* [3]*Drosera SA, Ch. de la Poudrière 36, CH-1950 Sion, Switzerland,* [4]*Division of Conservation Biology, Institute of Ecology, Balzerstrasse 6, University of Bern, CH-3012 Bern, Switzerland,* [5]*A. Maibach Sàrl, Ch. de la Poya 10, CP 99, CH-1610 Oron-la-Ville, Switzerland,* [6]*Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland,* [7]*KARCH, Passage Maximilien-de-Meuron 6, CH-2000 Neuchâtel, Switzerland*

ABSTRACT

Aim Predicting species distribution is of fundamental importance for ecology and conservation. However, distribution models are usually established for only one region and it is unknown whether they can be transferred to other geographical regions. We studied the distribution of six amphibian species in five regions to address the question of whether the effect of landscape variables varied among regions. We analysed the effect of 10 variables extracted in six concentric buffers (from 100 m to 3 km) describing landscape composition around breeding ponds at different spatial scales. We used data on the occurrence of amphibian species in a total of 655 breeding ponds. We accounted for proximity to neighbouring populations by including a connectivity index to our models. We used logistic regression and information-theoretic model selection to evaluate candidate models for each species.

Location Switzerland.

Results The explained deviance of each species' best models varied between 5% and 32%. Models that included interactions between a region and a landscape variable were always included in the most parsimonious models. For all species, models including region-by-landscape interactions had similar support (Akaike weights) as models that did not include interaction terms. The spatial scale at which landscape variables affected species distribution varied from 100 m to 1000 m, which was in agreement with several recent studies suggesting that land use far away from the ponds can affect pond occupancy.

Main conclusions Different species are affected by different landscape variables at different spatial scales and these effects may vary geographically, resulting in a generally low transferability of distribution models across regions. We also found that connectivity seems generally more important than landscape variables. This suggests that metapopulation processes may play a more important role in species distribution than habitat characteristics.

Keywords

Amphibian, anuran, *Bufo*, *Hyla*, *Rana*, *Triturus*, predictive distribution model, connectivity, spatial scale, presence/absence, model selection, newt, conservation, model transferability, occupancy.

*Correspondence: Jérôme Pellet, E-mail: jerome. pellet@amaibach.ch

INTRODUCTION

Distribution models play an important role in ecology, conservation and management (Guisan & Zimmermann, 2000; Lehmann *et al.*, 2002; Guisan & Thuiller, 2005). Models of the distribution of species (or habitat suitability models) can be used to learn which factors positively or 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. One desirable feature of such statistical models is

their generality (Johnson, 2002). Indeed, in the context of 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. There is evidence that regional differences in ecological characteristics can lead to apparent niche variation in distribution models (Murphy & Lovett-Doust, 2007). The issue of transferability of distribution models has been only recently addressed and the jury is still out on whether, how and under what conditions distribution models can be transferred (Graf *et al.*, 2006; Menendez & Thomas, 2006;

Randin *et al.*, 2006; McAlpine *et al.*, 2008; Rhodes *et al.*, 2008; Vernier *et al.*, 2008). We decided to comprehensively analyse the transferability of distribution models across regions by focusing on amphibian distribution models.

Amphibians are highly suitable for assessing the regional variability in the effects of landscape structure on distributions and transferability of distribution models across regions because conflicting results have been reported in the literature. The effects of habitat fragmentation and landscape scale predictors on amphibian distributions have been the subject of a large number of studies (Cushman, 2006). Depending on the study, 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. There are many similarly striking examples in the herpetological literature (e.g. Lehtinen *et al.*, 1999; Guerry & Hunter, 2002; Johansson *et al.*, 2005). Such differences among studies call into question the utility of predictive distribution models for species conservation and management. Two key elements usually included in such models were analysed.

The first key element in species distribution models are without doubt habitat variables. We asked whether the effects of descriptors were homogeneous across different regions or whether they varied geographically. We did so by asking whether there were interactions between study regions and descriptors. If there is a habitat factor by region interaction, then the effect of habitat factors vary among regions and consequently distribution models are not transferable across regions.

Secondly, 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 & Verboom, 1990; Sjögren, 1991; Vos & Stumpel, 1995). 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; Denoël & Lehmann, 2006). However, if connectivity determines the distribution of species, then distribution models are unlikely to be transferable across regions because the spatial arrangement of patches will vary from one region to another region.

We examined landscape-level habitat relationships and the geographical variation thereof for five anuran and one caudate amphibian species by measuring associations with their presence in 655 ponds in five different regions of Switzerland that varied strongly in landscape composition. Our goal was to investigate the following questions: (1) Is there geographical variation in the effects of landscape composition around the ponds on the distribution of species? (2) Does connectivity affect the distribution of amphibians and does the effect vary among regions? Taken together, the answers to these questions will provide a comprehensive assessment as to whether distribution models are transferable across regions.

METHODS

Study regions and species

Five regions were selected in intensively cultivated and densely inhabited regions of Switzerland (Zurich, Bern, Vaud, Valais and Ticino), all below 1000 m (Fig. 1). The regions differ in important aspects of land use (Table 1). 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 in Valais (VS). Ticino (TI) is, on the other hand, mainly forested (47%) and is the most urbanized region. General landscape statistics are presented in Table 1.
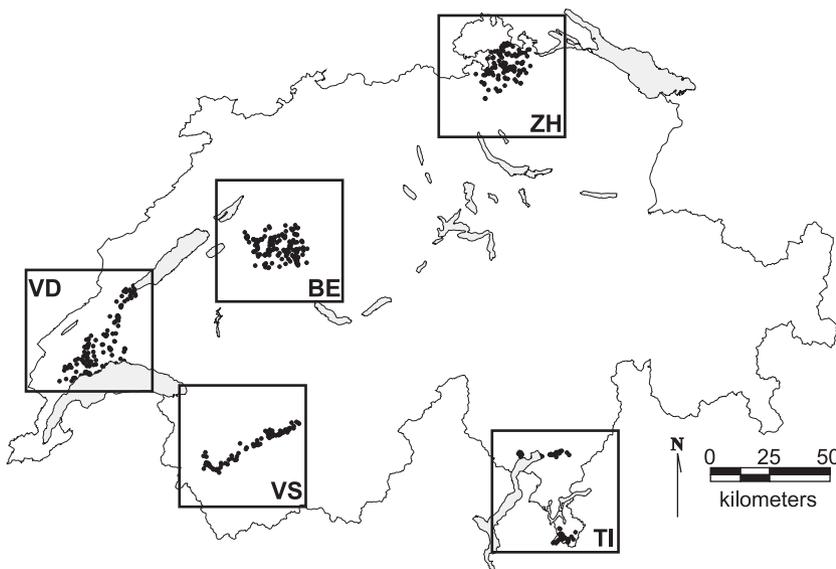
Figure 1 Location of the five study regions and the 655 amphibian breeding ponds in Switzerland (VD = Vaud, BE = Berne, ZH = Zurich, VS = Valais, TI = Ticino).

Table 1 Site occupancy, landscape composition and mean altitude of ponds in 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
Tree frog (*Hyla arborea*)	0.33	(–)	0.32	(–)	(–)
Agile Frog (*Rana dalmatina*)	0.35	(–)	(–)	0.71	(–)
Water frog (*Rana esculenta* complex)	0.59	0.29	(–)	0.51	(–)
Common frog (*Rana temporaria*)*	0.61	0.47	0.52	0.37	0.56
Alpine newt (*Triturus alpestris*)*	0.36	0.31	0.23	(–)	(–)
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
Average distance (m) between closest ponds	684	452	737	444	665
Mean pond altitude (m)	419	564	525	314	530

*Most common species in Switzerland (Schmidt & Zumbach, 2005).

(–) Species absent from region or proportion of sites occupied < 15% (see text for explanation).

The distribution of amphibians has been intensively monitored in 665 ponds in these regions. All sites were visited multiple times such that non-detection of species that were present is unlikely to be a problem (Pellet & Schmidt, 2005; Mazerolle *et al.*, 2005). Species occurrence data were collected by the Swiss Amphibian and Reptile Conservation Program (KARCH, http://www.karch.ch) and various experienced herpetologists (see Acknowledgements). In all regions, sites were visited at least three times between 1997 and 2003. In the survey of Schmidt & Zumbach (2005), per-visit detection probabilities of *Triturus alpestris*, *Bufo bufo*, *Hyla arborea*, *Rana dalmatina*, *Rana temporaria* and *Rana esculenta* were 67.6%, 57.7%, 89.9%, 58.6%, 70.5% and 64.4%, respectively. Hence, cumulative detection probabilities are high and absence can be inferred with 95% confidence after only 3, 4, 2, 4, 3 and 3 visits, respectively (Pellet & Schmidt, 2005). Because only presences were recorded, we could not use the MacKenzie *et al.* (2002) site occupancy models. 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 does not play a role (Schmidt & Pellet, 2005).

Because we wanted to explore species–habitat relationships with sufficient statistical power, we analysed species distribution only in regions where species occupancy was higher than 15%. Rarer species that also occurred were therefore excluded and not all species were included in all regions. 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 (*n* = 655), *R. esculenta* complex and *T. alpestris* in three regions (*n* = 417 and 497 respectively), and *R. dalmatina*

and *H. arborea* in two regions only (*n* = 202 and 282 respectively) (Table 1).

Landscape variables

Landscape variables were extracted from the VECTOR25 database, which is the vector format of the 1 : 25,000 topographical maps of Switzerland. Data precision is approximately 3–8 m in flat areas (SWISSTOPO, 2003). We selected 10 landscape variables (Table 2) representing different types of land cover that have been shown to affect amphibian distribution in Switzerland (e.g. Pellet *et al.*, 2004b; Zanini *et al.*, 2008). Landscape variables characterize the landscape composition (i.e. the type and amount of landscape components (Forman & Godron, 1986)) in the landscape surrounding the breeding ponds. The abundance of natural and semi-natural land uses around breeding ponds reflects the abundance of resource availability to species with amphibian life histories. Landscape variables can thus be considered as measures of resources availability (Austin, 2002).

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 six concentric buffers (disks) of different radius (100, 200, 500, 1000, 2000 and 3000 m) centred 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 & Findlay, 2003). Variables measured at different scales were labelled by adding the buffer radius to the name of the land use (i.e. FOREST100, FOREST200, . . .). Automated variable extraction was programmed in Mapbasic 7.5 software (MapInfo Corporation, Troy, NY, USA).

Table 2 The 10 landscape composition variables extracted in each of the 17 concentric buffers of radii from 100 m to 3000 m from ponds. A total of 60 variables (10 land uses × 6 radii) describe the landscape around each pond.

Variable	Description	Unit
AGRI	Proportion of arable lands and pastures*	%
FOREST	Proportion of forest	%
URBAN	Proportion of urban areas	%
MARSH	Proportion of marsh	%
BUSH	Proportion of bushes and hedgerows	%
MINERAL	Proportion of mineral extraction sites (gravel pits)	%
RIVER	Total length of rivers divided by the buffer area	m/m^2
ROAD12CLASS	Total length of first and second class roads divided by the buffer area	m/m^2
HIGHWAY	Total length of highway divided by the buffer area	m/m^2
HEDGE	Total length of hedgerows divided by the buffer area	m/m^2

*Vector 25 does not distinguish between pastures and other types of agriculture (e.g. fields).

Connectivity

To estimate the effect of connectivity on species occurrence we computed an additional variable (CONNECT) measuring the connectivity of each breeding pond or patch *i*. The formula for connectivity weighs the effect of distance on patch connectivity and is derived from metapopulation theory (Hanski, 1999).

$$\text{CONNECT}_i = \sum_{j \neq i} e^{(-d_{ij})} y_j \bigg/ \sum_{j \neq i} e^{(-d_{ij})} \tag{1}$$

In equation 1, d_{ij} is the distance between patch *i* and *j*. y_j is a binary variable that 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).

Spatial autocorrelation (SA) is often encountered in ecological data and may be source of problems if not properly addressed (Legendre, 1993). Indeed, if the presence of species in a breeding pond could be in part predicted by their presence in the neighbouring ponds (positive SA), then observations are not statistically independent and consequently the number of the degree of freedom in statistical analyses might be incorrect. In this case, the magnitude of habitat effect tends to be overestimated and the relative importance of different habitat variables can shift

(Klute *et al.*, 2002; Lichstein *et al.*, 2002). Here, we ensure the correct applicability of statistical tests because CONNECT 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, 2006).

Statistical analyses

We used binary logistic regression (GLM, presence/absence of the focal species being the response variable) to investigate the effect of various models on species occurrence (Hosmer & Lemeshow, 1989). We designed models starting with the simplest one (univariate) and finishing with the most complex (Table 3). The first three 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, and 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

Table 3 Structure of the 127 candidate models used for modelling the distribution of six amphibian species in five regions of Switzerland.

Model predictors	Number of models
REGION (R)	1
ALTITUDE (A)	1
CONNECT (C)	1
REGION+ALTITUDE (R+A)	1
REGION+CONNECT (R+C)	1
ALTITUDE+CONNECT (A+C)	1
REGION+ALTITUDE+CONNECT (R+A+C)	1
REGION+ALTITUDE+CONNECT (R+A+C)+Landscape (L)	60
REGION+ALTITUDE+CONNECT (R+A+C)+Landscape (L)+Interaction (R:L)*	60

Notes: For a description of landscape variables see Table 2.
*Region-by-landscape interaction.

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

Species	Model structure*	Landscape	D^2	AIC	*w*	K	β_1	β_2
Bufo bufo	R+A+C+L+R:L	HEDGE1000	4.94%	803.73	0.29	6	0.55	527.00
	R+A+C+L	HIGHWAY100	3.70%	805.97	0.10	5	1.30	−167.14
	R+A+C+L+R:L	RIVER200	4.67%	806.02	0.09	6	0.82	18.87
	R+A+C+L	FOREST500	3.65%	806.32	0.08	5	1.09	1.17
	R+A+C+L	FOREST1000	3.64%	806.44	0.08	5	1.02	1.45
	R+A+C+L	RIVER200	3.62%	806.57	0.07	5	1.05	−126.76
	C		1.61%	811.06	0.01	2	1.73	
	A+C		1.83%	811.30	0.01	3	1.58	
	R+C		2.45%	812.17	0.00	3	1.26	
	R+A+C		2.50%	813.76	0.00	4	1.24	
	R		1.74%	816.06	0.00	2		
	R+A		1.81%	817.42	0.00	3		
	A		0.56%	819.70	0.00	2		
Hyla arborea	R+A+C+L	FOREST100	22.88%	283.53	0.56	5	4.13	−2.04
	R+A+C+L+R:L	FOREST100	22.91%	285.42	0.22	6	4.11	−2.18
	R+A+C+L+R:L	MARSH100	22.24%	287.80	0.07	6	4.26	9.70
	R+A+C+L+R:L	MARSH200	22.09%	288.33	0.05	6	4.19	23.97
	C		17.81%	295.52	0.00	2	4.19	
	A+C		17.96%	296.98	0.00	3	4.10	
	R+C		17.86%	297.36	0.00	3	4.21	
	R+A+C		18.24%	298.01	0.00	4	4.10	
	R+A		2.59%	351.49	0.00	3		
	A		1.87%	352.07	0.00	2		
	R		0.00%	358.68	0.00	2		
Rana dalmatina	R+A+C+L	MARSH200	31.52%	201.42	0.19	5	4.81	28.12
	R+A+C+L	MARSH100	30.94%	203.04	0.08	5	4.79	8.29
	R+A+C+L	BUSH100	30.91%	203.14	0.08	5	4.85	45.22
	R+A+C+L+R:L	MARSH200	31.53%	203.39	0.07	6	4.80	29.34
	R+A+C+L	ROAD12CLASS500	30.62%	203.94	0.05	5	5.05	−506.56
	A+C		27.95%	207.40	0.01	3	4.66	
	C		27.16%	207.63	0.01	2	4.91	
	R+C		27.27%	209.32	0.00	3	4.73	
	R+A+C		27.98%	209.33	0.00	4	4.73	
	R+A		10.09%	257.34	0.00	3		
	R		8.98%	258.43	0.00	2		
	A		6.75%	264.67	0.00	2		
Rana esculenta complex	R+A+C+L	MARSH100	24.11%	442.99	0.65	5	2.77	6.86
	R+A+C+L+R:L	MARSH100	24.23%	446.33	0.12	6	2.75	8.37
	R+A+C+L	MARSH200	23.35%	447.28	0.08	5	2.68	12.81
	R+A+C		21.56%	455.47	0.00	4	2.80	
	A+C		20.04%	460.09	0.00	3	3.14	
	C		18.01%	469.62	0.00	2	3.91	
	R+C		18.26%	472.21	0.00	3	3.70	
	R+A		16.19%	483.96	0.00	2		
	A		11.95%	504.04	0.00	2		
	R		5.99%	539.88	0.00	2		
Rana temporaria	R+A+C+L	HIGHWAY100	9.24%	839.86	0.30	5	2.76	−167.63
	R+A+C+L	HIGHWAY200	9.13%	840.88	0.18	5	2.75	−220.22
	R+A+C+L+R:L	MINERAL200	9.88%	842.09	0.10	6	2.48	−5.28
	R+A+C+L	FOREST200	8.90%	842.96	0.06	5	2.49	0.97
	R+A+C+L+R:L	MINERAL100	9.71%	843.62	0.05	6	2.53	−3.01
	A+C		7.45%	846.16	0.01	3	2.79	
	C		7.14%	846.95	0.01	3	2.85	
	R+A+C		7.81%	850.89	0.00	4	2.63	
	R+C		7.23%	854.13	0.00	3	2.73	
	R+A		2.60%	896.18	0.00	3		
	R		1.51%	904.04	0.00	2		
	A		0.68%	905.61	0.00	2		

Table 4 *Continued*

Species	Model structure*	Landscape	D²	AIC	w	K	β₁	β₂
Triturus alpestris	R+A+C+L	RIVER200	5.81%	582.15	0.32	5	1.84	−182.75
	R+A+C+L+R:L	RIVER200	6.32%	583.05	0.20	6	1.84	−344.03
	R+A+C+L+R:L	RIVER100	6.16%	584.02	0.13	6	1.95	−192.30
	C		3.09%	590.62	0.00	2	2.34	
	R+A+C		3.90%	591.71	0.00	4	1.90	
	A+C		3.23%	591.76	0.00	3	2.31	
	R+C		3.42%	592.62	0.00	3	2.14	
	R+A		2.15%	600.33	0.00	3		
	R		1.08%	604.78	0.00	2		
	A		0.24%	607.89	0.00	2		

*Variable abbreviations are R = REGION, A = ALTITUDE, C = CONNECT, L = Landscape variable (see Table 2), R:L = Region-by-landscape interaction included.

K: Number of parameters (intercept parameter included).

β₁: Regression coefficient for connectivity.

β₂: Regression coefficient the focal landscape variable.

D²: explained deviance.

AIC: Akaike Information Criterion.

the same way in all regions. We fitted 127 models to each of the six amphibian species.

We used an information-theoretic model selection approach to identify the models that were best supported by data (Burnham & 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 evidence for each model. The sum of the Akaike weight of all models is 1. w can be interpreted as the probability that model i is the best model for the observed data, given the candidate set of models. Evidence ratios were computed as the ratio of the sum of Akaike weights of the models considered (Burnham & Anderson, 2002).

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

RESULTS

Landscape variables and geographical variation

Model selection results are shown in Table 4. The models best supported by the data always included a landscape variable, and in about half of the cases an interaction between region and a landscape variable. The explained deviance of the best models ranged between 5% (*B. bufo*) to 32% (*R. dalmatina*). Models including region-by-landscape interactions were always among the best three models and less than three AIC units away from the best model.

For the three widely distributed species (*B. bufo*, *R. temporaria* and *T. alpestris*), the explained deviance (D²) was low (between 5% and 9%), indicating a generally weak predictive ability of the models. For the three rare species (*R. esculenta* complex, *R. dalmatina* and *H. arborea*), explained deviance was much higher (between 23% and 32%). The landscape variables retained in the best models were MARSH100, MARSH200 and FOREST100,

respectively. For these three species, the best model including a landscape variable was accompanied by the same model including a region-by-landscape interaction. Even if there were no interactions between the landscape variable and region in the best models, different regions had different mean probabilities of occupancy for the same value of the landscape variable (i.e. there is an effect of the region on pond occupancies; Fig. 2). For example, no matter how much marsh was present, the predicted occupancy of the *Rana esculenta* complex was always highest in Bern and lowest in Ticino (Fig. 2).

In general, the evidence ratios for region-by-landscape interactions ranged between 0.25 and 1.18 (Table 5) which indicates that models without interactions are only weakly better than models with interactions.

Connectivity

For all species, connectivity alone explained about half of the deviance that was explained by the best models (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 effect of connectivity is positive for all the species and regions, but the amplitude is different and varied across regions (Fig. 3; [Correction added on 19 February 2009, after first online publications: reference to Fig. 2 corrected to Fig. 3]).

DISCUSSION

The effect of landscape composition

Our results demonstrate the general variability of distribution models in amphibian species. For the three most common study species, average explained deviance was very low (< 10%),
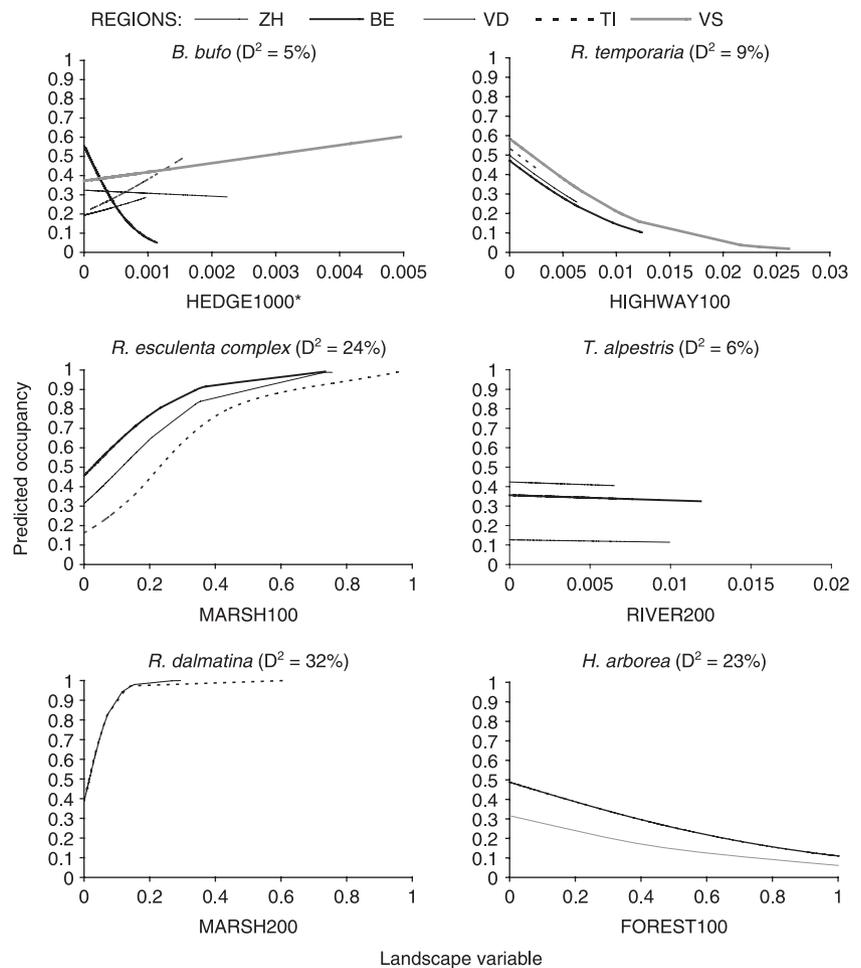
Figure 2 Prediction of the probability that breeding ponds will be occupied depending on landscape variables. Predictions are based on the best model (Table 4) and use the mean value of ALTITUDE and CONNECT across regions. [Correction added on 19 February 2009, after first online publications: Fig. 2 legend previously published with Fig. 3]

Table 5 Summary of model selection for all three groups of models. D^2 is the average explained deviance of all models in the category.

Sum of Akaike weights (average D^2)

Model structure	Models without landscape variables R, A, C, R+A, R+C, A+C, and R+A+C 7 models		Models with landscape variables R+A+C+L 60 models		Models with landscape variables and interactions R+A+C+L+R:L 60 models		Landscape interaction evidence ratio
Species							
Bufo bufo	0.02	(2%)	0.45	(3%)	0.53	(4%)	1.18 : 1
Hyla arborea	0.01	(11%)	0.62	(19%)	0.37	(19%)	0.60 : 1
Rana dalmatina	0.02	(19%)	0.68	(29%)	0.30	(29%)	0.44 : 1
Rana esculenta complex	0.01	(16%)	0.79	(22%)	0.20	(22%)	0.25 : 1
Rana temporaria	0.02	(5%)	0.74	(8%)	0.24	(9%)	0.32 : 1
Triturus alpestris	0.01	(2%)	0.54	(4%)	0.45	(5%)	0.93 : 1

indicating that we had weak support for all models considered. For the three rarest species, our models were better supported by the data than the models for the common species and reached moderately high explained deviances (between 23% and 32%). These results could be explained by a broad landscape-level niche for the most common species in Switzerland. On the other hand,

rare, threatened or species at the edge of their distribution range might have a narrow landscape-level niche that was easier to discriminate with our modelling approach.

For all species, top-ranking models always included a landscape variable. Natural elements such marshes and forests affected the distribution of the three species with the highest

REGIONS: ——— ZH ——— BE ——— VD - - - - TI ——— VS
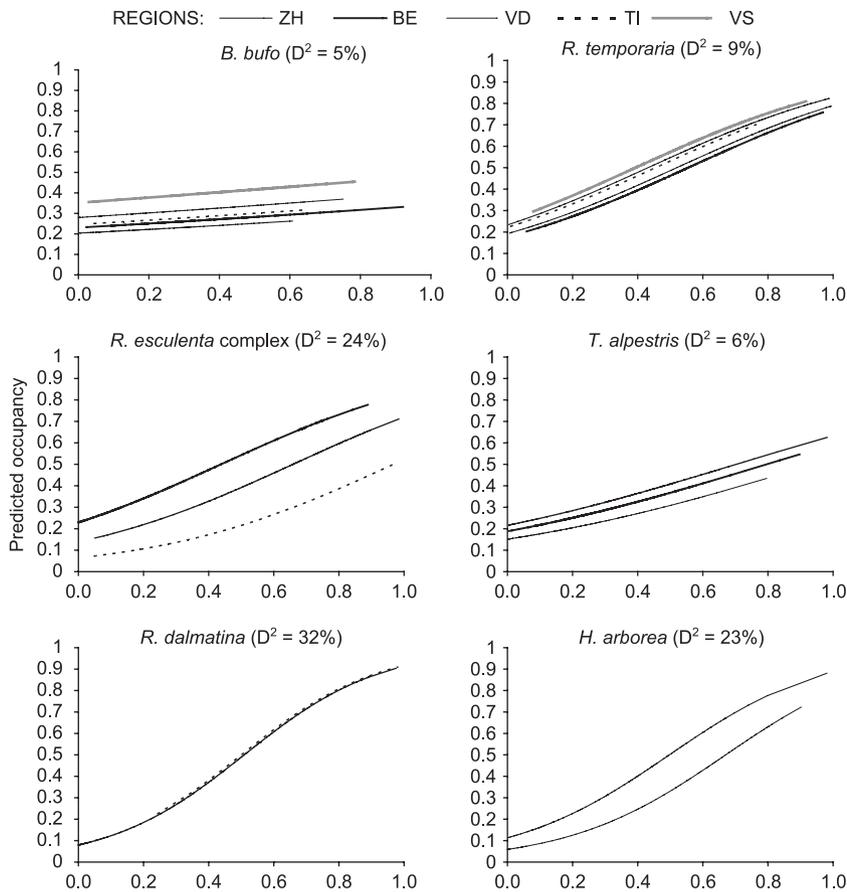
Figure 3 The effect of connectivity in breeding pond occupancy for six amphibian species in five Swiss regions. [Correction added on 19 February 2009, after first online publications: Fig. 3 legend previously published with Fig. 2]

explained deviance ($D^2 > 20\%$). Although our study regions 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 & Chardon, 1998; Knutson *et al.*, 1999; Pellet *et al.*, 2004b). Rather, we found that the (remaining) natural landscape elements such as marshes and forests positively affect species presence. One explanation may be that the variability of urban and road density across ponds is too low to induce a detectable effect. An alternative and more likely reason could be that these predictors have no direct effect on amphibian distribution and that more proximal variables (e.g. traffic density rather than road density) should be used in order to define causal relationships (Fahrig *et al.*, 1995; Pellet *et al.*, 2004b). Also, because we found that the most important variables represented relatively natural land covers, our results suggest the presence of a sufficient amount of suitable habitat is more important for species persistence than land-use types that negatively affect species. If this is true, then the areas with low anthropogenic stressors are not necessarily more favourable for species persistence than the areas with higher anthropogenic stressors when they have the same amount of suitable habitats. Put generally, it appears that the amount of available suitable habitat is more important than the surrounding matrix. These considerations deserve additional investigation, in order to completely understand the contribution of suitable and unsuitable habitats to species distribution.

Geographic variation in the effects of landscape variables

Although models including region-by-landscape interactions were always included among the best models, they performed best only once (*B. bufo*). However, region-by-landscape interactions had a weaker support (evidence ratio between 0.25 and 0.60) from the data for species where the overall explanatory power (i.e. proportion of deviance explained) was high. These results are in accordance to the results predicted by Murphy & Lovett-Doust (2007) who expect apparent regional niche variation (i.e. region-landscape interaction in our case) mostly for widely distributed species. The fact that we found a generally weak support for region-by-landscape interactions indicates that results (slope of a given landscape variable) obtained in one of our study regions can be transferred to other regions. However, models including interaction terms include different intercepts for different regions, indicating that absolute levels of occupancy are not correctly predicted by transferring models form one region to another (Figs 2 and 3). One patch could thus be predicted as unsuitable in one region while another patch with similar landscape features but situated in another region might be predicted as suitable because of different intercept terms. Multi-model inference techniques might provide a solution to this problem (Burnham & Anderson, 2002).

It is difficult to provide a biological explanation of how such region-by-landscape variable interactions arise. We believe that

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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 & 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 & Kiesecker, 2002). Region-by-landscape 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 or competitors, 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. Because many authors have questioned the transferability of model predictions to other regions (Graf *et al.*, 2006; Randin *et al.*, 2006; Murphy & Lovett-Doust, 2007; McAlpine *et al.*, 2008), we suggest a cautionary use of predictive distribution models in conservation.

Transferability across regions, landscape-by-region interactions and the biological mechanisms that prevent transfer of models ought to be added to the predictive distribution model research agenda (Araujo & Guisan, 2006). Several studies have started to elucidate factors that may affect transferability (e.g. the type of predictor variables: Austin, 2002; the kind of statistical model used: Peterson *et al.*, 2007; selection bias: Phillips, 2008). The incorporation of proximal predictor variables into distribution models (variables that directly relate to the species response) are thought to enhance the transferability of distribution models. In our case, the landscape variables can be considered to be intermediate resource predictors (Austin, 2002), thus diminishing the potential transferability of our models.

We believe that factors that relate to data collection are fundamental, may be particularly important and therefore should be assessed first. First, a common concern is sample selection bias (Reese *et al.*, 2005; Phillips, 2008; Sánchez-Fernández *et al.*, 2008). Selection bias means that the data are a non-random sample. If a sample is not a random sample then it is not representative and inference not reliable. Unfortunately, there are very few distribution models that are based on a spatial random sample (e.g. Royle *et al.*, 2005). Second, the case of false absences (overlooked species) (Pellet & Schmidt, 2005) can also lead to strong biases in species response curves (Mazerolle *et al.*, 2005; Royle *et al.*, 2005).

Transferability of models is inherently difficult outside the range they were constructed in. As illustrated in Figs 2 and 3, our models are defined in a restricted space of predictors, defined by the characteristics of the landscapes under scrutiny (Table 1). They are thus less likely to be transferable to other, drastically different landscapes, where their predictions are only extrapolated (Thuiller *et al.*, 2004).

The type of predictor variables, the issue of non-random sampling, false absences and the ranges of landscape variables may all lead to invalid inference and may impair transferability.

Several studies on amphibians and other wetland organisms have found that landscape features can be important up to several kilometres away from breeding ponds (e.g. Houlahan & Findlay, 2003; Gibbs *et al.*, 2005; Price *et al.*, 2005; Houlahan *et al.*, 2006). However, in our study, we found better support for landscape effects at a relatively small spatial scale. The landscape effect ranges between hundred metres to 1 km (Fig. 2). This agreed with other work on amphibians which also found a landscape effect at less than 1 km (e.g. Pellet *et al.*, 2004b; Herrmann *et al.*, 2005; Mazerolle *et al.*, 2005).

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 that exhibit greater annual mobility are expected to be more sensitive to landscape composition at a greater distance from aquatic habitats (Weyrauch & 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). *Bufo bufo* is, on the contrary, affected by landscape composition up to larger distances from breeding ponds than other species (Fig. 2). This toad is known to be a highly mobile species, using terrestrial habitat at several kilometres from aquatic breeding site (Blab, 1986). In addition, we found that models for species with large annual home ranges (*B. bufo*, *R. temporaria* and secondarily *T. alpestris*) had low explained deviance, as predicted by and McPherson *et al.* (2004) and McPherson & Jetz (2007).

Our results showed that connectivity is strongly and positively associated with species occurrence, especially for the less common species (*Hyla arborea, Rana dalmatina* and *Rana esculenta*). This corroborates the result of Ficetola & De Bernardi (2004) who also found a strong effect of isolation on rare species. Connectivity can be a key to the regional viability of amphibian populations (Semlitsch & Bodie, 1998; Marsh & Trenham, 2001; Smith & Green, 2005), especially because amphibian populations experience relatively frequent local extinctions and recolonizations (Sjögren, 1991; Vos *et al.*, 2000; Trenham *et al.*, 2003; Schmidt & Pellet, 2005). The maintenance and improvement of interpopulation individual exchange are therefore a crucial requisite for regional amphibian population persistence.

For all species, models that included connectivity as a predictor of occupancy had an explained deviance of at least half that of the best model (Table 4, model structure C), indicating that our connectivity alone explains patch occupancy to a substantial degree. The general positive effects of increasing connectivity indicate that amphibians are spatially organized in clusters of occupied ponds. The positive effect of connectivity implies that dispersal processes within a metapopulation are important. The consequence of this fact for distribution modellers is that habitat characteristics alone cannot explain patterns of distribution (unless favourable habitats are spatially autocorrelated as well). Better predictive distribution models will not only require a better understanding of the ecological niche (e.g. fundamental versus realized niche, Araujo & Guisan, 2006), but also of metapopulation processes that probably should also include source/sink dynamics (Schmidt & Pellet, 2005).

CONCLUSION

The design 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 aquatic habitats that should be placed within suitable terrestrial habitat. We found strong regional variability of the effect of landscape on species occurrence, which implies that what constitutes suitable habitat or landscape composition and structure varies geographically. Thus, even though landscape variable-by-region interactions were often weak, distribution models cannot easily be transferred across regions (Graf *et al.*, 2006; Menendez & Thomas, 2006; Randin *et al.*, 2006; McAlpine *et al.*, 2008; Rhodes *et al.*, 2008; Vernier *et al.*, 2008). This is a central but poorly understood issue, which needs additional research in order to determine under which conditions predictive distribution models can be generalized and used outside the region in which they were developed (McAlpine *et al.*, 2008; McPherson & Jetz, 2007; Peterson *et al.*, 2007; Phillips, 2008; Rhodes *et al.*, 2008; Vernier *et al.*, 2008).

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