



Climate warming and the decline of amphibians and reptiles in Europe

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ABSTRACT

Aim We explore the relationship between current European distributions of amphibian and reptile species and observed climate, and project species potential distributions into the future. Potential impacts of climate warming are assessed by quantifying the magnitude and direction of modelled distributional shifts for every species. In particular we ask, first, what proportion of amphibian and reptile species are projected to lose and gain suitable climate space in the future? Secondly, do species projections vary according to taxonomic, spatial or environmental properties? And thirdly, what climate factors might be driving projections of loss or gain in suitable environments for species?

Location Europe.

Methods Distributions of species are modelled with four species–climate envelope techniques (artificial neural networks, generalized linear models, generalized additive models, and classification tree analyses) and distributions are projected into the future using five climate-change scenarios for 2050. Future projections are made considering two extreme assumptions: species have unlimited dispersal ability and species have no dispersal ability. A novel hybrid approach for combining ensembles of forecasts is then used to group linearly covarying projections into clusters with reduced inter-model variability.

Results We show that a great proportion of amphibian and reptile species are projected to expand distributions if dispersal is unlimited. This is because warming in the cooler northern ranges of species creates new opportunities for colonization. If species are unable to disperse, then most species are projected to lose range. Loss of suitable climate space for species is projected to occur mainly in the south-west of Europe, including the Iberian Peninsula, whilst species in the south-east are projected to gain suitable climate. This is because dry conditions in the south-west are projected to increase, approaching the levels found in North Africa, where few amphibian species are able to persist.

Main conclusions The impact of increasing temperatures on amphibian and reptile species may be less deleterious than previously postulated; indeed, climate cooling would be more deleterious for the persistence of amphibian and reptile species than warming. The ability of species to cope with climate warming may, however, be offset by projected decreases in the availability of water. This should be particularly true for amphibians. Limited dispersal ability may further increase the vulnerability of amphibians and reptiles to changes in climate.

Keywords

Amphibian decline, bioclimatic-envelope models, climate change, ensemble forecasting, Europe, reptile decline, uncertainty.

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INTRODUCTION

Over recent decades, declines and extirpations of amphibian populations have been reported in many parts of the World (e.g. Alford & Richards, 1999; Houlihan *et al.*, 2000). Furthermore, it has been suggested that reptiles may be declining on a similar scale to that experienced by amphibians in terms of taxonomic breadth, geographic scope and severity (Gibbons *et al.*, 2000). Climate change is amongst the many hypotheses postulated to explain these declines (Alford & Richards, 1999; Gibbons *et al.*, 2000; Kiesecker *et al.*, 2001; Carey & Alexander, 2003; Collins & Storfer, 2003; Corn, 2005). We investigate potential impacts of climate change by modelling potential distributions of European amphibian and reptile species in response to five climate-change scenarios for 2050. By comparing future vs. current potential distributions, we assess whether suitable climate space for amphibians and reptiles is projected to increase or decrease with projected climate change in Europe.

Testing the hypothesis that climate warming is causing amphibian and reptile declines is challenging because there are many possible interacting processes, and they are likely to operate at varying spatial scales. Therefore, it is difficult to design controlled experiments to falsify different hypotheses. For example, one of the possible consequences of climate change includes changes in breeding phenology. Most temperate amphibian species spend a large portion of the year inactive, avoiding either cold winters or hot summers. Subtle increases in temperature or moisture trigger them to emerge from hibernation. Immediately upon emergence, they migrate to nearby ponds or streams to breed. Thus, one affect of global warming on amphibians might be to create a trend towards early breeding as average temperatures increase (e.g. Terhivuo, 1988; Beebee, 1995; Blaustein *et al.*, 2001; Tryjanowski *et al.*, 2003), although it remains unclear what impact this pattern might have on amphibian population dynamics (for discussion see Corn, 2005). A number of studies also showed that increasing length of dry periods (e.g. Stewart, 1995; Pounds *et al.*, 1999) or overall decreases in annual precipitation (Pounds & Crump, 1994) may cause the decline and probable extinction of several species of amphibians.

Global climate change may also affect amphibian populations in more subtle and complex ways. Local changes in climate can decrease immune function and lead to pathogen outbreaks and elevated mortality (Daszak, 2003). This problem may be further exacerbated by interactions between two or more factors. For example, Kiesecker *et al.* (2001) found that in extreme dry years reduced pond depth increases exposure of amphibian embryos to ultraviolet (UV-B) radiation. This increased exposure to UV-B, increases their vulnerability to infectious diseases, which causes egg mortality. Despite evidence from field and laboratory experiments that increases in UV-B may cause mortality in amphibian species, the possibility of a link between UV-B and global amphibian declines remains controversial (e.g. Cummins, 2002; Kats *et al.*, 2002; Licht, 2003). Effects of warming on reptiles

remains relatively unexplored, but there is a suggestion that impacts may occur on those species that have temperature-dependent sex determination, such as crocodiles and some turtles (e.g. Janzen, 1994; Godfrey *et al.*, 1999).

In spite of such complexities, models may be informative when investigating the likelihood that particular change in climate might affect species distributions. A possible tool for research includes species–climate ‘envelope’ models (for review see Pearson & Dawson, 2003), whereby present-day distributions of species are combined with climate variables to assess species–climate relationships and project distributions of species under future climates. Examining projections from ‘envelope’ models may provide important insights, especially when modelling uncertainties are explicitly addressed (for discussion see Whittaker *et al.*, 2005) and interpretation of model outputs is made in the light of existing autoecological knowledge. A limited number of previous studies have used this analytical tool to examine distributions of herptile species in relation to current climate (e.g. Brito *et al.*, 1999; Guisan & Hofer, 2003; Segurado & Araújo, 2004), and some have used scenarios to project distributions under future climates (Teixeira & Arntzen, 2002). Here, we modelled the distributions of most amphibian and reptile species in Europe in response to five climate-change scenarios for 2050. Because projections from different modelling techniques differ (e.g. Thuiller *et al.*, 2004; Thuiller, 2004; Araújo *et al.*, 2005a; Pearson *et al.*, 2006), we used four different modelling techniques and examined patterns of central tendency among groups of linearly co-varying projections. Interpretation of results is made by considering different assumptions of species dispersal and by discussing additional evolutionary and ecological factors that may influence the results of models. In particular we ask: (1) what proportion of amphibian and reptile species are projected to lose and gain suitable environments in the future, (2) do species projections vary according to taxonomic, spatial, or environmental properties, and (3) what climate factors might be driving projections of loss or gain in suitable environments for species?

DATA AND METHODS

Species and climate data

Species locality data included records of occurrence for 143 amphibian and reptile species (Gasc *et al.*, 1997) within Europe. Because there are problems in modelling data with limited observations (Stockwell & Peterson, 2002), we excluded from the analysis 35 species that have < 20 records. Models were thus fitted for 42 amphibian and 66 reptile species. The geographic grid used is based on that of the *Atlas Florae Europaeae* (Lahti & Lampinen, 1999), with cell boundaries typically following the 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. Data were converted to the AFE grid system by identifying unique (although sometimes approximate) correspondence between cells in

these grids. The mapped area (2434 grid cells) includes western, northern and southern Europe, but excludes most of the eastern European countries (except for the Baltic States) where recording effort was less uniform and intensive (Williams *et al.*, 2000).

A set of aggregated climate parameters were derived from an updated version of climate data provided by New *et al.* (2000). The updated data provides monthly values for the years 1901–2000 in a 10' grid resolution (Mitchell *et al.*, 2004; Schroter *et al.*, 2005). Average monthly temperature and precipitation in grid cells covering the mapped area of Europe were used to calculate mean values of five different climate parameters for the period 1961–1991 (referred to as 'baseline data'). Variables included mean annual temperature (°C), mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), mean annual summed precipitation (mm), and mean sum of precipitation between July and September (mm). Choice of variables was made to reflect two primary properties of the climate – energy and water – that have known roles in imposing constraints upon amphibian species distributions as a result of widely shared physiological limitations (Gibbons *et al.*, 2000; Carey & Alexander, 2003). Climate-change scenarios from HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model) and CSIRO's (Australia's Commonwealth Scientific and Industrial Research Organisation) GCMs (Global Circulation Models) were then averaged for the period of 2020–2050 (referred to as the 2050 scenario). Five GCM runs (four from HadCM3 and one from CSIRO) were used so as to account for different IPCC SRES (Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios) outcomes, reflecting different assumptions about demographic changes, socio-economic and technological development (Nakicenovic & Swart, 2000). These scenarios include four storylines (A1, A2, B1 and B2), ranging from fossil-fuel intensive to alternative futures involving rapid adoption of new technologies. This range of scenarios gives some idea of the range of greenhouse gas emission pathways that might be taken during the 21st century.

Species–climate modelling

Amphibian and reptile species distributions in Europe were modelled using four techniques implemented in the climate envelope modelling implementation 'BIOMOD' (Thuiller, 2003): (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) classification tree analysis (CTA), and (4) feed-forward artificial neural networks (ANN). Details on model parameterization are provided in Thuiller (2003). Models were calibrated on a 70% random sample of the observed data and predictive accuracy evaluated on the remaining 30% of the data. We tested agreement between observed species presences and absences and projected distributions by calculating the area under curve (AUC) of the receiver operating characteristic (Roc) curve and Cohen's

Kappa statistic (K). We used the Kappa approach after maximizing the statistic over a range of thresholds above which model outputs are considered to represent species presence. We calculated AUC using the nonparametric method based on the derivation of the Wilcoxon statistic (Fielding & Bell, 1997). Overall, we obtained 40 range shift projections for each of the 108 species modelled, i.e. 4320 projections in total including four modelling techniques \times two rules for transforming probabilities into presence records \times five climate scenarios.

Potential distributional shifts were then measured for every species as the difference in the total number of grid cells predicted to be occupied within each one of the two time periods considered. In order to measure the sensitivity of our projections to dispersal and establishment assumptions, we considered two scenarios (Pitelka, 1997): either species are unable to disperse and establish in new areas in the time period considered (no dispersal), or have no constraints to dispersal and establishment in new areas (unlimited dispersal). The reality will fall necessarily between these two extremes, although dispersal of amphibian and reptile species is likely to be lower than that observed in other organisms (Araújo & Pearson, 2005).

Combining ensembles of forecasts

Projections of species-range shifts may vary significantly with different modelling techniques (e.g. Thuiller *et al.*, 2004; Araújo *et al.*, 2005b; Pearson *et al.*, 2006). Because we lack an objective basis for selecting the most realistic techniques (Segurado & Araújo, 2004) we can fit a number of models and explore the resulting range of projections. A 'majority-vote' criterion can then be applied to explore the central tendency of projections (for review see Clemen, 1989). This idea is based on the central limit theorem in statistics, where central limits of particular projections are expected to be more likely than extremes. There are a variety of approaches to explore central tendencies (or consensus) in projections and simple averages are often thought to be sensible (e.g. Palm & Zellner, 1992). However, when a large number of forecasts are made with different assumptions (e.g. projecting future climates with different emission scenarios or assessing climate impacts on species using different response curves) it is more appropriate to group covarying forecasts together first and only then proceed to their averaging. This procedure recognizes that consensus forecasts calculated from 'good' models are better than consensus forecasts calculated from 'bad' models (Araújo *et al.*, 2005b) and that averages calculated from projections with reduced inter-model variability allow the consequences of different assumptions to be isolated and discussed.

Here, patterns of consensus among 40 range-shift projections for every species were investigated in two steps. First, we grouped projections into clusters with covarying species range shift projections. Second, we calculated the median projected species range-shift for each one of the selected clusters. To identify the clusters we utilized Principal Components Analysis

(PCA) that reduces projections into orthogonal components of linearly covarying projections (e.g. Sengupta & Boyle, 1998; Thuiller, 2004). Because the first PCA combined many projections together in the first axis (80% of the variation), excluding only projections with CTA that were grouped in the second axis (8% of the variation), we ran PCA a second time excluding CTA projections. With this analysis we sought to further discriminate projections that were initially grouped in the first axis. With this new PCA, projections with ANN (first axis, 88% of the variation) were grouped separately from projections with GAM and GLM (second axis, 5% of the variation). These analyses led to the construction of three groups of projections: ANN (maximum consensus); GLM/GAM (medium consensus); and CTA (no consensus). Projections using different climate scenarios were not sufficiently different to justify discrimination of projections by scenario.

To explore the consistency of this exploratory procedure for grouping covarying projections we used an agglomerative hierarchical classification (single linkage clustering) based on a Euclidean-distance matrix calculated for all pairs of model projections (Fig. 1). Two potential classifications were identified. The first included the same three major groups of

projections identified with PCA, i.e. ANN, GLM/GAM and CTA. The second kept ANN and CTA as distinct groups but identified two additional groups: one including projections with GAM and the two GLM projections using A2. CSIRO climate scenarios; and the other including the remaining GLM projections (Fig. 1). Projections with CTA could have been subdivided in two groups, but we chose not to split them as our aim was to explore group variation within consensus axes rather than further subdividing non-consensus projections. The magnitude of differences between clusters and the significance of these differences were tested with nonparametric analysis of similarity (ANOSIM, Clarke & Warwick, 1994). This test operates directly on a pairwise distance (or dissimilarity) matrix. The principle is that if two groups are significantly different, then differences between groups are greater than within groups. The ANOSIM global R statistic is based on the difference of mean ranks of distance between groups (r_B) and within groups (r_W):

$$R = \frac{r_B - r_W}{N(N - 1)/4}$$

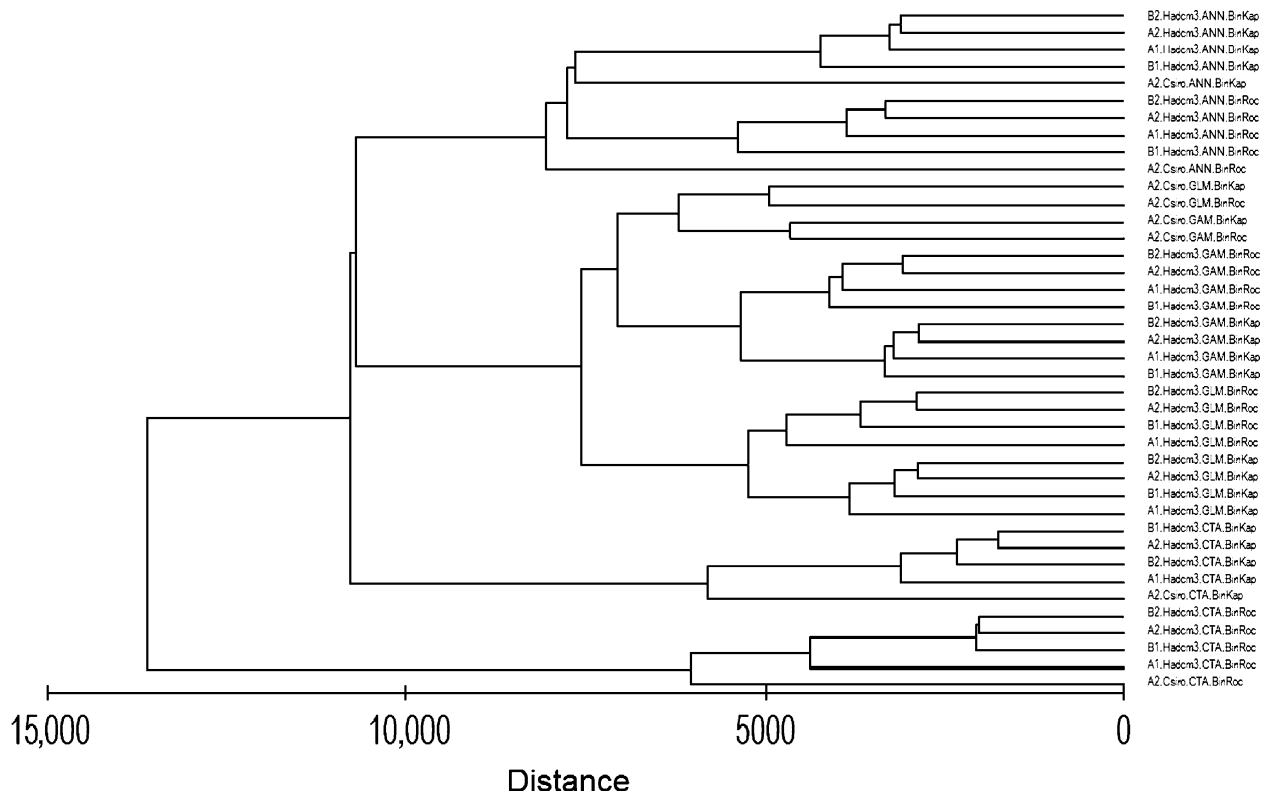


Figure 1 Single-linkage clustering based on Euclidean distances matrix. Three to four clusters were considered. When three clusters were considered groups included (1) projections made with artificial neural networks (ANN); (2) projections made with generalized additive and linear models (GAM and GLM); and (3) projections made with classification tree analysis (CTA). One-way analysis of similarity between groups (ANOSIM) with 999 permutations was performed to test for differences between clusters. The global R statistic was 0.84 ($P = 0.1\%$), whilst R statistics for pairwise tests were: 1,2 = 0.85; 1,3 = 0.84; 2,3 = 0.90 ($P = 0.1\%$). When four clusters were considered groups included (1) projections made with ANN, (2) projections made with GAM and GLM using A2.CSIRO scenarios, (3) projections made with the remaining GLM, and (4) projections made with CTA. The global R from ANOSIM was 0.72 ($P = 0.1\%$), whilst R statistics for pairwise tests were: 1,2 = 0.87; 1,3 = 0.90; 1,4 = 0.84; 2,3 = 0.45; 2,4 = 0.81; 3,4 = 0.82 ($P = 0.1\%$).

The divisor is chosen so that R will be in the interval $[-1; +1]$, value 0 indicating completely random grouping. The statistical significance of observed R is assessed by permutating (999 times) the grouping vector to obtain the empirical distribution of R under a null model. In this study, all clusters identified were significantly different from each other ($P = 0.1\%$), but the split between GAM/GLM.A2.CSIRO and GLM projections was the weaker ($R = 45$, see legend in Fig. 1). Consequently, we clustered projections into the three initial groups, i.e. ANN, GAM/GLM and CTA.

Taxonomic, spatial and environmental dependencies

We investigated if species projected responses to climate change among clusters of model projections varied according to taxonomic, spatial or environmental properties. The underlying idea is that species are not independent points for comparative analyses because closely related species or species occurring nearby in geographical or environmental space may have more similar responses to climate change than more distant species (e.g. Harvey & Rambaut, 1998; Stuart *et al.*, 2004). Here the following hypotheses were tested:

Taxonomic dependencies: The null hypothesis (H_0) is that projected range shifts among species of the same lineage are no different from projected range shifts among species of different lineages. If H_0 is falsified we then accept the alternative hypothesis (H_1) that projected range shifts among species of the same lineage are different from projected range shifts among species of different lineages. If H_1 is accepted the consequence is that there are taxonomic dependencies in projected responses of species to climate change. Kruskal–Wallis rank-sum tests (nonparametric independent group comparison method) were performed to test differences in patterns of range shift among species of different taxonomic lineages. Dun tests were also performed for *post hoc* multiple comparisons (Klockars & Sax, 1986). To explore this hypothesis we used reconstructed phylogenies of amphibians to identify monophyletic groups of species. These groupings were coincident with taxonomic classifications at the level of order and family (Arnold & Ovenden, 2002). Therefore we grouped species into: (1) orders Urodela (salamanders) and Anura (frogs and toads), and (2) families Proteidae, Salamandridae, Discoglossidae, Pelobatidae, Bufonidae, Hylidae and Ranidae. Phylogenies of salamanders and newts were taken from Titus & Larson (1995), whilst phylogenies of frogs and toads were taken from Hoegg *et al.* (2004). Phylogenies for reptiles were unavailable to us, hence we used the taxonomic classification from Arnold & Ovenden (2002). For reptiles we explored patterns of range shift at the level of order and family. The following groups were identified: (1) orders Ophidia (snakes), Sauria (lizards) and Testunide (turtles), and (2) families Cheloniidae, Emydidae, Bataguridae, Testudinade, Anguidae, Chamaeleonidae, Gekkota, Lacertidae, Scincidae, Amphisbaenide, Boidae, Colubridae, Typhlopidae and Viperidae.

Spatial dependencies: H_0 is that projected species range shifts are no different for species with different geographical

distributions. If H_0 is falsified we then accept H_1 that projected species range shifts are different for species with different geographical distributions. To investigate these hypotheses we first determined the geographical position (GP) of the centroids of each species in latitude (x) and longitude (y) coordinate system. We calculated GP by matrix multiplication: $GP = AB$, where A was a transposed matrix of species presence and absence within each grid cell and B was a matrix with latitude and longitude coordinates for grid cells. Secondly, we calculated a pairwise Euclidean distance matrix of GP. Thirdly, we classified species in two categories (contracting and expanding) for each cluster of projections. Finally, we used nonparametric analysis of similarity (ANOSIM, Clarke & Green, 1988) to test for differences in the GP of contracting and expanding species. These differences were further explored visually by plotting species distributional centroids in an x and y coordinate diagram.

Environmental dependencies: H_0 is that projected species range shifts are no different for species with different environmental distributions. If H_0 is falsified we then accept H_1 that projected species range shifts are different for species with different environmental distributions. To investigate these hypotheses we calculated species niche positions (NP) along environmental gradients. As for GP we used matrix multiplication to identify the centroids (i.e. mean niche position) of species ranges within environmental space. Matrix A was the transposed species presence and absence matrix, whilst matrix B was obtained by fitting a centred PCA on the five baseline climate parameters used in this study. The first two axes of PCA were retained (91% explained variation) and the component scores were used to define environmental space. As for GP, we used nonparametric analysis of similarity (ANOSIM) to test for differences in the NP of contracting and expanding species.

Range-shift correlates

To make inferences about potential factors causing changes in the occupancy of species within grid cells, we calculated and mapped two aggregated measures of range shift for amphibians and reptile species at a $10'$ grid resolution. The first was species loss (L) and was calculated as: $L = R(ND)_{t_2} - R_{t_1}$, where $R(ND)_{t_2}$ is projected species richness for 2020–2050 (t_2) assuming no dispersal and R_{t_1} is projected species richness for 1961–2000 (t_1). The second measure was species gain (G) and was calculated as: $G = R(UD)_{t_2} - R_{t_1}$, where $R(UD)_{t_2}$ is the projected species richness for future t_2 assuming unlimited dispersal. Values of $G < 0$ (i.e. indicating losses with the unlimited dispersal scenario) were set to zero.

Regression tree analysis (Breiman *et al.*, 1984) with tenfold cross-validation and a Gaussian response model was used to analyse relationships between losses, gains and climate for all three clusters of projections. Trees are built by recursive binary partitioning of data with rules applied to single predictor variables. Data are partitioned using a greedy algorithm that splits the response in groups that are as homogeneous as possible in terms of their deviance (e.g. sum

of squares). The advantages of regression trees are twofold. First, they allow investigation of complex nonlinear interactions between response and predictor variables (often better than with generalized linear or additive models). Second, results are easily interpretable (more so than with, for example, artificial neural networks). Both present climate and climate anomalies (i.e. climate in t_2 – climate in t_1) were used as predictor variables. This is because anomalies are bound to have different consequences depending on where they occur in environmental space. Because variation in climate scenarios for this particular time period did not affect significantly model outputs (see consensus forecasting section) we explored range-shift correlates for one climate scenario alone (A1FI.HadCM3). The RPART library in SPLUS (Therneau & Atkinson, 1997) was used to calculate regression trees.

RESULTS

What proportion of amphibian and reptile species are projected to lose and gain suitable environments in the future?

Model projections assuming unlimited dispersal were extremely variable with most species being projected both to expand and contract depending on the model (See Appendices S1 and S2 in Supplementary Material): 26% of the amphibian species were consistently projected to expand across models, whilst 5% were consistently projected to contract (see Appendix S1); 44% of reptile species were consistently projected to expand, whilst 5% were consistently projected to contract (see Appendix S2). When all individual-species projections were averaged (using the median range shift value across projections), then 31% of amphibians and 35% of reptiles were estimated to contract their potential ranges, whilst 69% of amphibians and 65% of reptiles were estimated to expand (Table 1). Cluster 1 (maximum consensus) was generally more conservative, providing greater estimates of contracting species than any of the remaining clusters. This was also the only cluster of projections where a greater proportion of amphibian species was projected to contract than expand. In the remaining two clusters of model projections amphibian species were projected to expand more often than contract. Consistent to almost all projections was the trend towards greater expansion of potential ranges for reptile species than for amphibian species. Only in one set of projections (cluster 2, unlimited dispersal) was there a greater proportion of contracting climate spaces for amphibians than for reptiles (Table 1).

Model projections assuming no dispersal were less variable (see Appendices S1 and S2) with most species being predicted to contract (Table 1). Nevertheless 2–3% reptile species were projected to keep their climate envelope stable in the studied region, with the exception of projections made with CTA where all species were projected to contract.

Table 1 Median percentage of contracting and expanding amphibian and reptile species in Europe among different clusters of model projections: cluster 1 includes projections with artificial neural networks (ANN); cluster 2 includes projections with generalized additive and linear models (GAM and GLM); cluster 3 includes projections with classification tree analysis (CTA). The ‘all’ projections includes the values obtained from averaging results of all 40 projections

	Amphibians		Reptiles	
	Contracting	Expanding	Contracting	Expanding
Unlimited dispersal				
Cluster 1 (ANN)	55	45	39	61
Cluster 2 (GAM/GLM)	33	67	38	62
Cluster 3 (CTA)	21	79	11	89
All	31	69	35	65
No dispersal				
Cluster 1 (ANN)	100	0	97	0
Cluster 2 (GAM/GLM)	100	0	98	0
Cluster 3 (CTA)	100	0	100	0
All	100	0	98	0

Table 2 Kruskal–Wallis rank sum tests used to test for global differences in patterns of range shift amongst independent taxonomic groups. The null hypothesis is that observed range shifts are no different among species of different taxonomic groups. We identified 21 families (Proteidae $n = 1$, Salamandridae $n = 14$, Discoglossidae $n = 6$, Pelobatidae $n = 4$, Bufonidae $n = 3$, Hylidae $n = 2$, Ranidae $n = 12$, Cheloniidae $n = 1$, Emydidae $n = 1$, Bataguridae $n = 2$, Testudinade $n = 3$, Anguidae $n = 2$, Chamaeleonidae $n = 1$, Gekkota $n = 4$, Lacertidae $n = 21$, Scincidae $n = 5$, Amphisbaenidae $n = 1$, Boidae $n = 1$, Colubridae $n = 17$, Typhlopidae $n = 1$ and Viperidae $n = 6$) with a median number of species per group $n = 3$ (SD = 5.83) and 5 orders (Urodela, Anura, Testunides, Sauria and Ophidia) with a median number of species per group $n = 25$ (SD = 10.62)

	Chi-square	d.f.	P-value
Species grouped by family			
Cluster 1 (ANN)	22.25	21	0.39
Cluster 2 (GAM/GLM)	20.41	21	0.50
Cluster 3 (CTA)	20.40	21	0.50
All	20.98	21	0.46
Species grouped by order			
Cluster 1 (ANN)	10.67	4	0.03*
Cluster 2 (GAM/GLM)	6.76	4	0.15
Cluster 3 (CTA)	7.83	4	0.10
All	8.09	4	0.09

* $P < 0.05$.

Species projections vary according to taxonomic, spatial or environmental properties?

When species were aggregated at the family level, no family was distinguished as having significantly different patterns of range shift from other families (Table 2), although the small sample sizes of family-based groupings (median $n = 3$, $SD = 5.83$) are likely to have had an influence on this result. When species were aggregated into orders (median $n = 25$, $SD = 10.62$), significantly different patterns between orders were detected in cluster 1 (Kruskal–Wallis, $P < 0.05$; Table 2). Multiple comparison (Dunn) tests (Table 3) reveal that differences were mainly due to contrasting patterns of range shift among species of Order Urodela ($P < 0.05$). This group has species whose range shifts are significantly different (trend towards contraction) from Anura, Ophidia and Sauria (Fig. 2). Patterns of range shift between Urodela and Testudines were not significantly different, most likely because of the small sample size of the latter group ($n = 3$). However, visual inspection of data in Fig. 2a shows that species of this order have a tendency for expansion, whereas species of the order Urodela have a tendency for contraction.

The spatial distribution of species projected to contract and expand was significantly different among amphibians (clusters 1 and 2) and reptiles (all clusters) (Table 4). Visual inspection of species–geographical centroids reveals a longitudinal pattern in the distribution of contracting and expanding amphibian species (Fig. 3). This pattern is similar for reptile species, but for cluster 3 there is a north (contracting) to south (expanding) gradient that was not recorded for amphibians. More generally and for most clusters, there was a tendency for contracting species to occur in Western Europe, particularly in the Iberian Peninsula, France and the northernmost areas of

Table 3 Dunn multiple comparison tests ($*P < 0.05$; n.s. $P > 0.05$) used to test for pairwise differences in patterns of range shift amongst independent taxonomic groups

	Urodela	Anura	Testunides	Sauria	Ophidia
Cluster 1					
Urodela					
Anura	*				
Testunides	n.s.	n.s.			
Sauria	*	n.s.	n.s.		
Ophidia	*	n.s.	n.s.	n.s.	
Cluster 2					
Urodela					
Anura	n.s.				
Testunides	n.s.	n.s.			
Sauria	n.s.	n.s.	n.s.		
Ophidia	n.s.	n.s.	n.s.	n.s.	
Cluster 3					
Urodela					
Anura	n.s.				
Testunides	n.s.	n.s.			
Sauria	n.s.	n.s.	n.s.		
Ophidia	n.s.	n.s.	n.s.	n.s.	

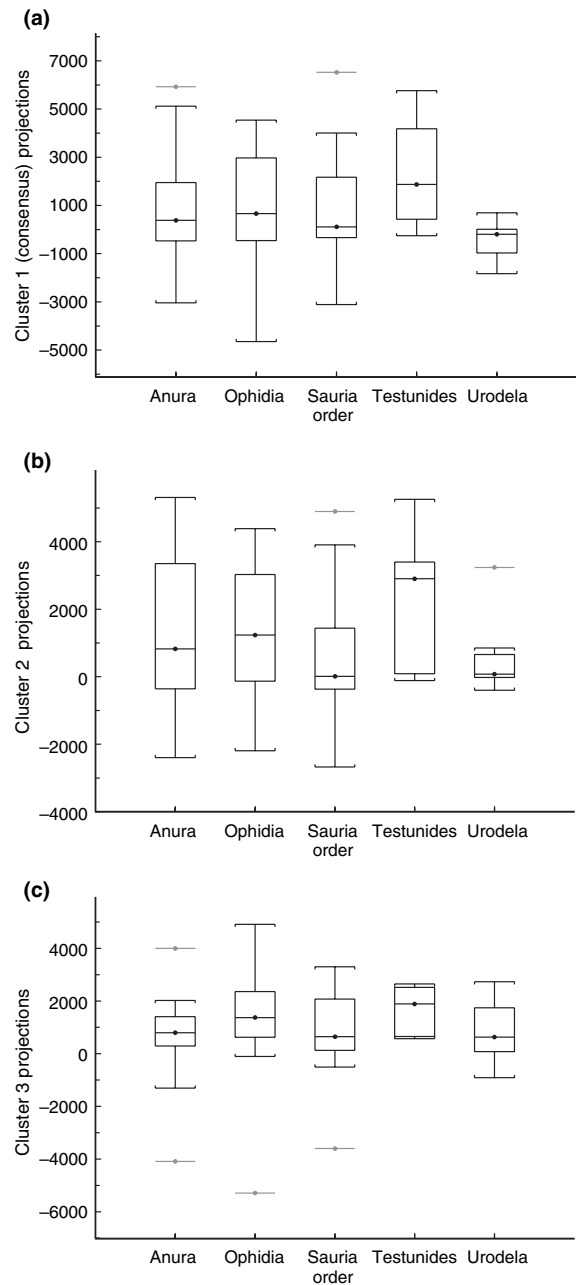


Figure 2 Frequency distribution of projected range shifts among three groups models in relation to the taxonomic order of modelled species: Anura (frogs and toads, $n = 27$); Ophidia (snakes, $n = 25$); Sauria (lizards $n = 34$); Testunides (tortoises and terrapins, $n = 7$); Urodela (salamanders and newts, $n = 15$). The shaded bar represents the interquartile range and the median is marked within this; the line extensions from each box are the largest and smallest values. Grey bars represent outliers (points more than 1.5 times the interquartile range distant from the box edges).

Scandinavia. Conversely, there was a tendency for expanding species to occur in Eastern Europe, particularly in the Anatolian peninsula. Central European countries represented a transition zone where ranges of many expanding and contracting species met. An example of such spatially struc-

Table 4 Results of one-way analysis of similarity (ANOSIM) with 999 permutations. This analysis tests for differences between the geographical (a) or environmental (b) position of contracting and expanding species for three different clusters of projections (see Methods)

	Amphibians		Reptiles	
	Global R	P-value (%)	Global R	P-value (%)
(a) Geographical dependencies				
Cluster 1 (ANN)	0.442	0.1	0.617	0.1
Cluster 2 (GAM/GLM)	0.350	0.2	0.471	0.1
Cluster 3 (CTA)	0.046	22.1	0.201	0.1
All	0.127	2.6	0.457	0.1
(b) Environmental dependencies				
Cluster 1 (ANN)	0.056	9.9	0.005	34.6
Cluster 2 (GAM/GLM)	0.075	9.6	0.013	29.4
Cluster 3 (CTA)	0.176	2.1	0.551	0.1
All	0.062	13.1	0.003	40.8

tured pattern is provided for three species (Fig. 4) of the same genus (i.e. *Pelobates*, order Anura) with allopatric distributions. For example, south-western *Pelobates cultripes* is forecasted to contract both with unlimited and no dispersal assumptions, whilst south-eastern *Pelobates syriacus* is forecast to expand northwards with unlimited dispersal and to remain almost stable with no dispersal. An eastern species with a central European distribution, *Pelobates fuscus*, is forecast to expand northwards (with unlimited dispersal) and to contract in the southern and western parts of its range.

In contrast with the spatial structure in species-range shift projections, there was no clear environmental structure in the distribution of modelled contracting and expanding species (Table 4; Fig. 5). One exception was the projected range contraction for reptiles in cluster 3 (Table 4), along the cold-dry edge of the European climate gradient.

What climate factors drive projections of losses or gains in suitable environments for species?

The geographical distribution of species range losses and gains by grid cell (Figs 6 & 7) was comparable to the distribution of species centroids among contracting and expanding species (Fig. 3). Major losses were projected to occur in the Iberian Peninsula, southern France, Italy and eastern European countries. Gains were projected to occur mainly in the northern fringes of central Europe for amphibians and southern and eastern fringes of central Europe for reptiles.

Regression tree analysis shows that losses of amphibian and reptile species predominated in areas with high annual temperatures (left branches, Fig. 8). Further discriminations in the intensity of species losses within grid cells were associated with anomalies in precipitation. For example, within cluster 1 (max consensus), greater losses of amphibian

species were projected to occur in the warm (Fig. 8a, annual temperature > 9.2 °C, first split) and dry (Fig. 8a, below -81 mm, second split,) areas more often than elsewhere. A further discrimination is made for areas with current annual precipitations below 1077.7 mm (third split). These areas are projected to lose between five and eight species, with greater losses associated with the most severe reductions, where annual precipitation deficits are greater than -124 mm. Greater declines for reptile species are also projected to occur in areas with high annual temperatures (Fig. 8b, first split, annual temperature > 6.5 °C) that are subject to important reductions in annual precipitation (second split, delta annual precipitation < 78.7 mm). Areas with warm climate and increased drought are projected become unsuitable for 10–20 species per grid cell (Fig. 8b).

In contrast to species range losses, colonizations were projected to occur mainly in cooler areas that were subject to slight increases in maximum temperatures of the coldest month and winter or summer precipitation. For example, major colonizations among amphibians (Fig. 8c, right branches) were projected in areas with mean annual temperatures between 3.7 and 7.1 °C and which were subject to reductions in summer precipitation that did not exceed -13.9 mm and had current winter precipitation above 224.5 mm (see Fig. 8c for further splits). Colonizations in warmer areas (Fig. 8c, left branches) were also projected for areas with mild annual temperatures between 8.9 and 10.7 °C (Fig. 8c, left branches, third and fourth splits) and subject to increases in maximum temperatures of the coldest month from up to levels above 1.2 °C. Colonizations of reptile species appeared to be mainly determined by changes in precipitation (Fig. 8d). For example, major increases in reptile species richness were projected to occur in areas where summer precipitation was reduced by -35.9 mm, and in cool areas (annual temperature < 9.4 °C) where annual precipitation declined less 56.3 mm, or were warmer (annual temperature > 9.4 °C) but were subject to little change in annual temperature (delta temperature > 1.8 °C). The selection of response variables, order of branching and cut-off values varied among clusters of projections (see Appendix S3), but the ecological interpretations remain relatively constant as patterns of contraction and expansion follow similar trends in temperature and precipitation.

DISCUSSION

Being ectothermic (i.e. 'cold-blooded'), reptiles and amphibians rely on external warmth to raise their body temperature and become active. Their ability to cope with lower temperatures is limited (most species are unable to live at temperatures below -4 °C), whilst their upper lethal temperature range is much wider (see Fig. 2 in Snyder & Weathers, 1975). Consequently, these species are likely to be more sensitive to climate cooling than warming and this is one reason why suitable climate spaces were projected to increase for a great proportion of herptiles with climate warming. During past glacial periods amphibian and reptiles have contracted

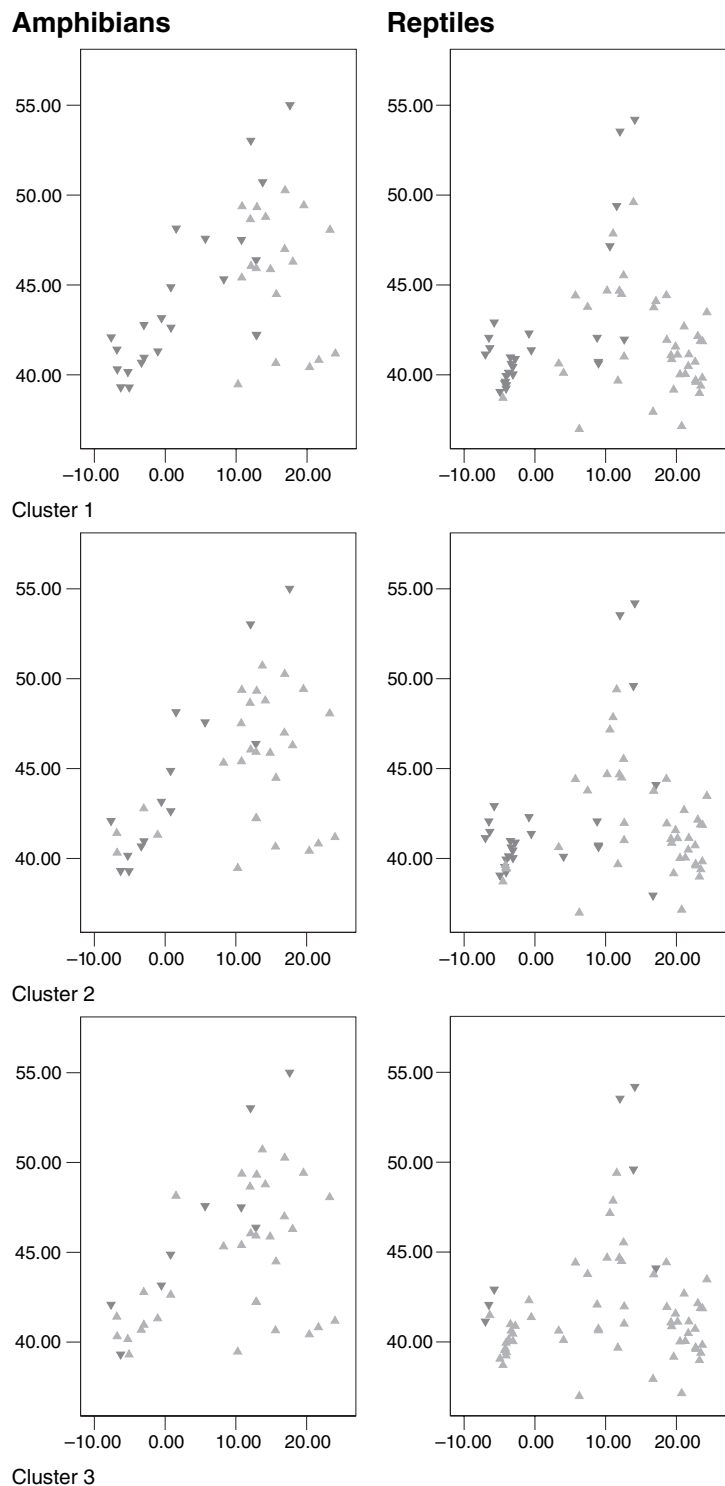


Figure 3 Distribution of centroids of contracting (▼) and expanding (▲) species within geographical x (longitude) and y (latitude) coordinate system.

distributions throughout most of central and northern Europe, whereas inter-glacial periods provided conditions for range expansions (see Gasc *et al.*, 1997, and references therein). The modern composition of herptile assemblages still reflects the location of past glacial refugia more than current climates (Araújo & Pearson, 2005). These observations cast some doubt as to whether current climate warming *per se* would cause major declines among amphibian and reptile species (Stuart

et al., 2004, provides evidence that habitat degradation might rank among the major determinants of amphibian declines in Europe). However, the alternative hypothesis that warming would drive range expansions among reptile and amphibian species is not supported by empirical evidence either (e.g. Alford & Richards, 1999; Gibbons *et al.*, 2000; Houlihan *et al.*, 2000). These apparently conflicting observations merit some discussion.

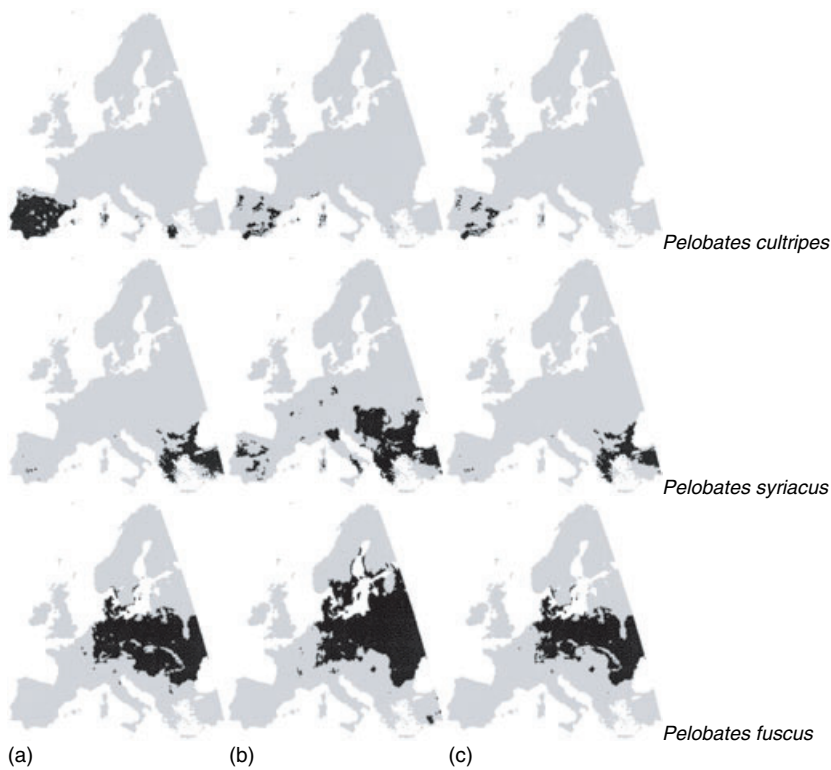


Figure 4 Examples of projected potential ranges of three species of the order Urodela (*Pelobates cultripes*, *Pelobates syriacus* and *Pelobates fuscus*) at a 10' grid resolution using artificial neural networks and kappa statistic procedure (see Methods): (a) current, (b) projected future with unlimited dispersal, and (c) projected future without dispersal. Potential (not actual) ranges indicate that areas have suitable climate conditions for the species.

First, it is important to acknowledge that despite an overall trend towards an increase in suitable climate space for amphibians and reptiles, these taxa are generally poor dispersers and highly philopatric (e.g. Sinsch, 1991; Blaustein *et al.*, 1994). Therefore, assumptions of unlimited dispersal under changing climate are unrealistic. A more realistic assumption would be that of no dispersal, especially in a study such as ours where a 10' resolution grid is used (10 and 16-km grid cells) and projections are made for a relatively short period of time (20–50 years). If no dispersal is assumed, virtually all species in our study would be projected to lose range (Table 1). Although in the past a number of species might have been able to track climate changes through dispersal, herptile ability to undertake rapid large-scale migrations remains controversial (e.g. Araújo & Pearson, 2005; Smith & Green, 2005) but would be further inhibited by current levels of habitat fragmentation in Europe. Indeed, past migrations among amphibian and aquatic reptile species might have relied upon a large number of ponds and aquatic environments that have since been drained or profoundly altered. Furthermore, projected rates of climate change are such that they might impose an additional level of difficulty for species migration; indeed, over the next century climate is projected to change more rapidly and with greater magnitude than has been experienced at least during the past 1000 years (Houghton *et al.*, 2001).

Secondly, even if climate warming does not entail a major threat to amphibian and reptile species, increasing drought may well represent an important threat for species persistence in many regions. Our results support previous observations that reductions in precipitation, more than increases in temperature, may cause decline and local extinctions of

amphibian species (e.g. Pounds & Crump, 1994; Stewart, 1995; Pounds *et al.*, 1999). The impact of reduced water availability is particularly important in areas that are already under hydrological stress, as verified in many parts of the Iberian Peninsula (Fig. 3). As previously acknowledged, 'water availability, rather than temperature, is the key determinant for life in semi-arid regions...and the major environmental factor determining amphibian distribution' (Carey & Alexander, 2003, p. 114). Indeed, amphibians are amongst the most vulnerable terrestrial vertebrates to changes in precipitation regimes as they require standing water for survival of eggs and larvae (Carey & Alexander, 2003; Corn, 2005, and references therein). Slight changes in water level in breeding ponds can trigger reproductive failure and, in a single year, cause a severe drop in the population size of short-lived species; persistent changes can lead to extinctions of species.

The observation that the Iberian Peninsula is a hotspot for species diversity and endemism for herptiles (Williams *et al.*, 2000) could be seen as providing evidence of wide tolerance of amphibian and reptile species to aridity. However, high diversity and endemism in the Iberian Peninsula (as well as within the Italian and Anatolian peninsulas) most likely reflect the fact that these areas remained relatively ice-free during glacial periods, thus acting as refugia for many European species (e.g. Hewitt, 2000). In addition, the relatively small thermal fluctuations and oscillations of rainfall within particular areas of southern peninsulas may have triggered speciation events or at least promoted the completion of speciation events that were inaugurated in earlier geological times (e.g. Willis & Whittaker, 2000). The observation that northern Africa (northern Sahara) has very low numbers of amphibian families

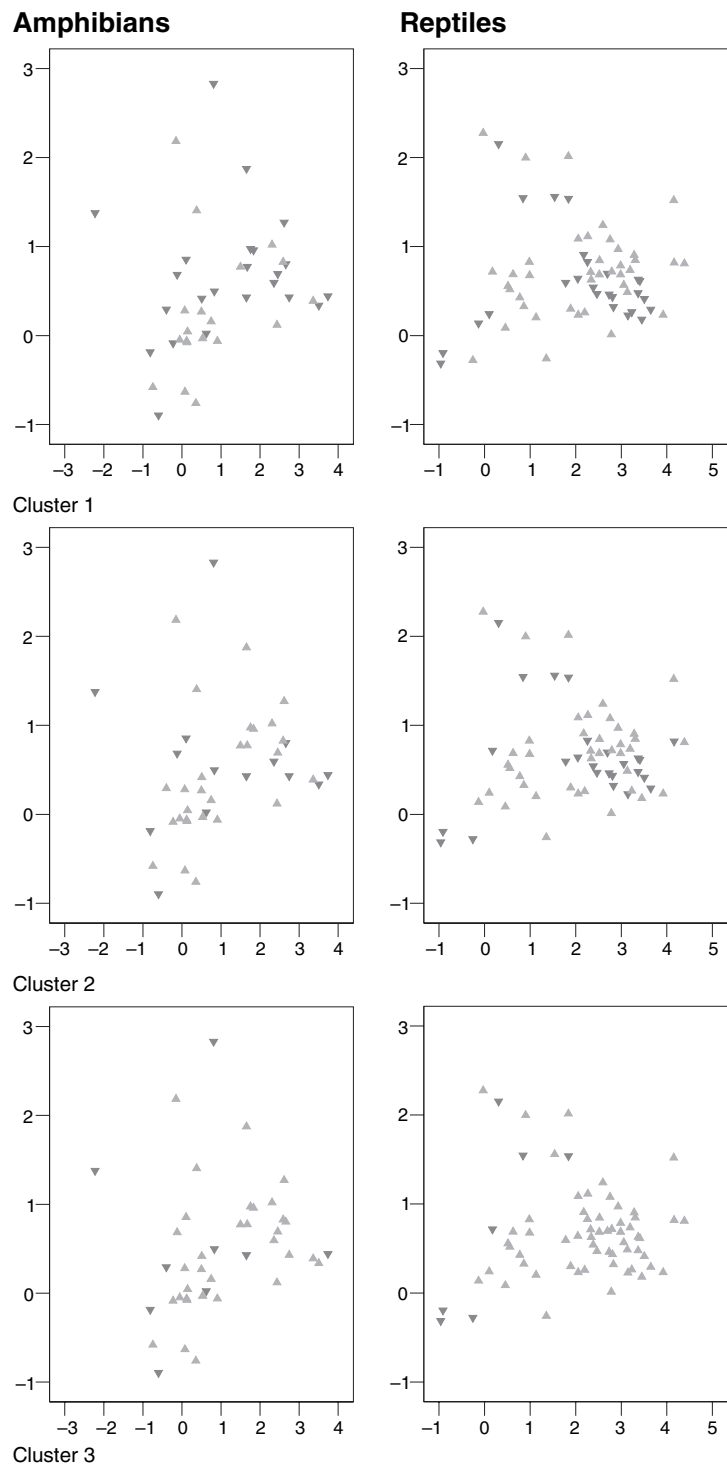


Figure 5 Distribution of centroids of contracting (▼) and expanding (▲) species within environmental space. Environmental axes represent component scores from PCA: axis 1 (x) is correlated with temperature (high scores represent high temperature), whilst axis 2 (y) is correlated with water precipitation (high scores represent high precipitation).

(unpublished maps from Groombridge & Jenkins, 2002) further supports the idea that semi-arid regions in the south-west of Europe might be at the limit of tolerance for many amphibian species. The existing physiological stress explains why amphibian species in these areas would be so vulnerable to increased aridity. In contrast to amphibians, tolerance of reptile species to aridity is likely to be great. This resilience is illustrated by excesses in observed numbers of reptile families occurring in northern Africa over the numbers of amphibian

families (based on unpublished maps from Groombridge & Jenkins, 2002). For reptiles, there is indeed a possibility that at least some of the projected contractions in south-western Europe might be a consequence of limited filling of the fundamental niche at the warm-dry edge of the European climate gradient. If the hypothesis of unfilled niches for southern European species were true, then European reptiles would be able to cope with increased warmth and drying climate conditions even more than already projected by our

Losses (no dispersal)

Gains (unlimited dispersal)



Cluster 1



Cluster 2



Cluster 3

Figure 6 Projected amphibian species losses (with no dispersal) and gains (with unlimited dispersal) by 2050 in 10' grid-cell resolution across Europe. Projections are made for three clusters of projections: cluster 1 includes projections with ANN; cluster 2 includes projections with GLM and GAM; and cluster 3 includes projections with CTA. We used a six class scale, where increasing intensities of grey represent increasing losses or gains.

models (see Table 1). This possibility would challenge the assertion that climate warming (including interactions with changes in precipitation regimes) would cause reptile declines similar to those expected for amphibians (Gibbons *et al.*, 2000).

The modelling approach adopted in this study is cutting-edge in the field of bioclimatic 'envelope' modelling (Thuiller, 2004; Araújo *et al.*, 2005b). However there are still important model uncertainties and cautious interpretation of model

results is required (for discussion see Araújo *et al.*, 2005a; Maggini *et al.*, 2006; Pearson *et al.*, 2006; Randin *et al.*, 2006). Our view is that empirical models provide potentially useful information for formulating hypotheses and exploring 'what if' questions, thereby illuminating which aspects of a problem are most in need of further investigation and where more empirical data are needed. The models may also be useful to support or contradict empirical evidence. In the first case, consistent model projections would increase confidence that

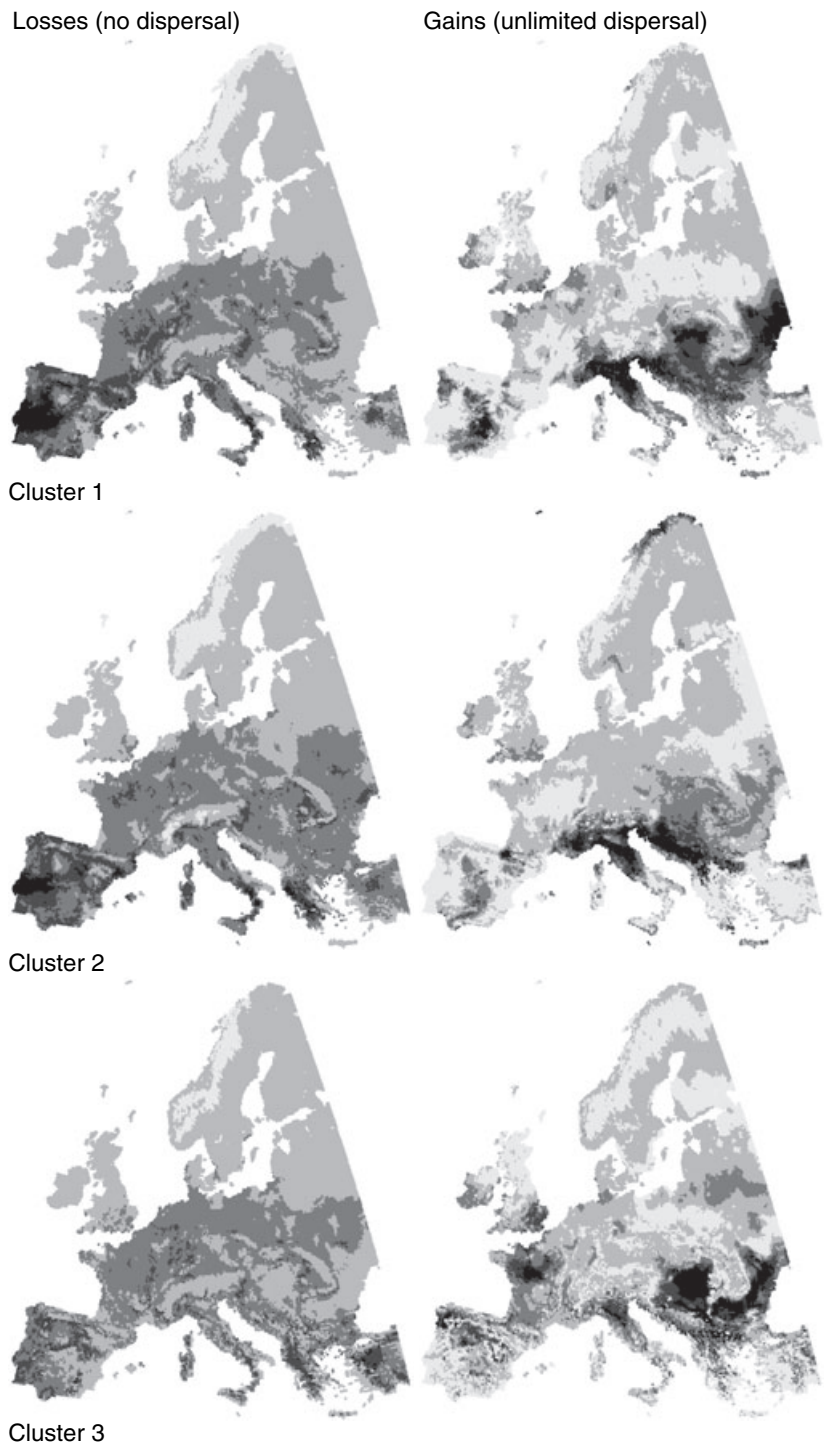


Figure 7 Projected reptile species losses (with no dispersal) and gains (with unlimited dispersal) by 2050 in 10' grid cell resolution across Europe. Projections are made for three clusters of projections: cluster 1 includes projections with ANN; cluster 2 includes projections with GLM and GAM; and cluster 3 includes projections with CTA. We used a six class scale, where increasing intensities of grey represent increasing losses or gains.

proposed mechanisms for observed patterns are realistic; in the second case, models would challenge accepted wisdom and call for more stringent evidence. In our study, empirical evidence regarding the importance of water deficit as a cause for amphibian decline was supported, whereas evidence that reptiles should decline at a similar rate as amphibians was provisionally challenged.

Other aspects of our results would also require further investigation. For example, there was a signal that species of

the order Urodela (salamanders and newts) might be more vulnerable to projected climate changes than other amphibian groups; this result contrasts with that of Stuart *et al.* (2004) who found that that four families of frogs would contribute overwhelmingly to the total global number of rapidly declining species, although climate change did not rank among the main drivers of decline for these taxa. Nevertheless, the prediction that species of the Urodela would be vulnerable to climate change was only recorded for maximum-consensus models

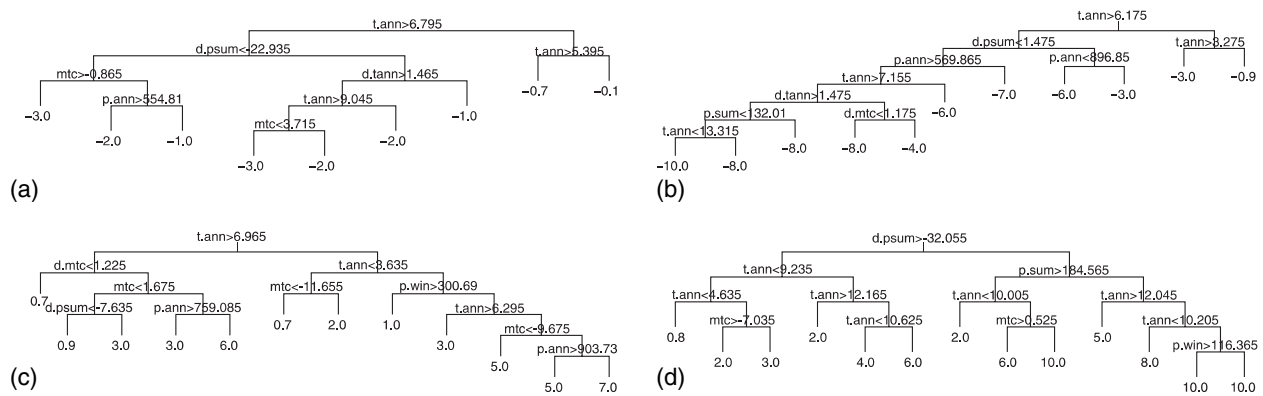


Figure 8 Regression trees for cluster 1: (a) range losses for amphibians; (b) range losses for reptiles; (c) range gains for amphibians; and (d) range gains for reptiles. Acronyms have the following meaning: T.ann = annual temperature of the coldest month; Mtc = minimum temperature of the coldest month; P.ann = annual precipitation; P.win = winter precipitation; P.sum = summer precipitation. The prefix ‘d’ refers to delta, i.e. climate anomalies.

(with ANN) and this invites the interpretation of a need for further enquiry.

The modelling approach adopted in this study does not account for complex interactions with additional factors possibly causing herptile declines, such as chemical and heavy metal contamination, increased UV-B radiation, habitat destruction and fragmentation, disease and parasitism, and predation by invasive species (e.g. Alford & Richards, 1999; Gibbons *et al.*, 2000; Bosch *et al.*, 2001; Kiesecker *et al.*, 2001; Collins & Storfer, 2003). Non-climatic factors have been shown to be important for modelling distributions of other taxa (e.g. Coudun *et al.*, 2006; Luoto *et al.*, 2006) and their appropriate incorporation within models along with feed-back mechanisms among variables is likely to magnify estimates of decline or extinction of species in the future. Multi-factorial studies would be required to address these complex interactions (Storfer, 2003). The development of hybrid-models that bring together the best of empirical modelling with the best of mechanistic and theoretical models is an important challenge for modellers.

CONCLUSIONS

Climate space for amphibians and reptiles was projected to expand for the majority of species. Exceptions (i.e. contractions) were projected to occur mainly in the Iberian Peninsula. Range contractions were associated with increased aridity in areas that are already under hydrological stress. A similar pattern was observed for reptiles, but consideration of their tolerance to drought in northern Africa raises the possibility that projected contractions at the warm-dry edge of the European gradient are due to incomplete niche descriptions within models. Our results concern changes in the availability of climate space for species and this implies perfectly covarying changes in the distributions of species. The ability of species to occupy future climate spaces will depend on their ability to disperse, as well on the existence of suitable pathways for dispersal. However, evidence that

current distributions of amphibians and reptiles display high levels of non-equilibrium with current climate raise the possibility that dispersal might indeed be lower for herptiles – particularly for amphibians – than for other groups of terrestrial vertebrates and plants. Furthermore, current levels of habitat fragmentation and degradation, especially among aquatic environments, might reduce the inherently low dispersal ability of these taxa. This being true, i.e., the ‘no dispersal’ assumption being more realistic, then most European species of amphibian and reptiles modelled in this study would be projected to lose suitable climate space by 2050. This would conditionally support the hypothesis that climate change might have caused or – more rigorously – cause further declines of herptile species (particularly amphibians) in the future.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>

Appendix S1 Projected range shift for amphibian species.

Appendix S2 Projected range shifts for reptile species.

Appendix S3 Regression trees for clusters 2 and 3.

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