

Ecological Niche Modeling Applications to Forecasting Status of European Species and Habitats

September 26, 2009

A. Townsend Peterson, Jorge Soberón, Alberto Jiménez-Valverde, and Andrés Lira-Noriega
Biodiversity Research Center, The University of Kansas, Lawrence, Kansas USA

Table of Contents

I. Introduction	1
II. Methodology	2
III. Results and Discussion	7
IV. Conclusions and Recommendations	13
V. Appendix	14
VI. Bibliography	35

I. Introduction

This document serves to present the results of a series of explorations of the distributions and conservation status of various species of the European biota. Specifically, responding to a call for tenders, the objective was to present a quantitative evaluation of the potential for alternative methodologies to provide information useful to the regional status assessment and conservation prioritization activities under the Article 17 effort of the European Environmental Agency. We used ecological niche modeling and various GIS operations to evaluate 20 species, including mammals, reptiles, amphibians, plants, and invertebrates, which were selected to provide diverse range sizes, ecological amplitudes, and regional localization. The result of these analyses is the view that several goals of the Article 17 effort can be either achieved or complemented substantially by means of such analyses, likely at substantial cost savings, and certainly with the benefit of significant scientific rigor.

II. Methodology

The purpose of this exercise is to assess to what degree ecological niche modeling (ENM) techniques can be used to obtain accurate distribution maps of species occurring in Europe. The exercise is particularly relevant under conditions of data scarcity, since for species in regions that see intensive monitoring, modeling is basically unnecessary. Once accurate distribution models are obtained, we will use them to assess effects of habitat modification and climate change on species' geographic distributions.

As per contract, our first objective is to use ENM techniques to test the Article 17 summaries of species' population status and current distributions. To that effect, we:

- 1) Selected 20 suitable species and obtained the necessary occurrence data
- 2) Selected relevant and appropriate environmental variables
- 3) Selected suitable ENM methods
- 4) Obtained predictions using a suitable calibration method and compared ENM-based distributions with current Article 17 range distributions (<http://biodiversity.eionet.europa.eu/article17/speciesreport>).
- 5) Estimate indices of loss of habitat under the Corine LU/LC scenarios and under a suite of IPCC scenarios for future climate conditions and scenarios of marine intrusion.

The following sections provide further detail on each of these points.

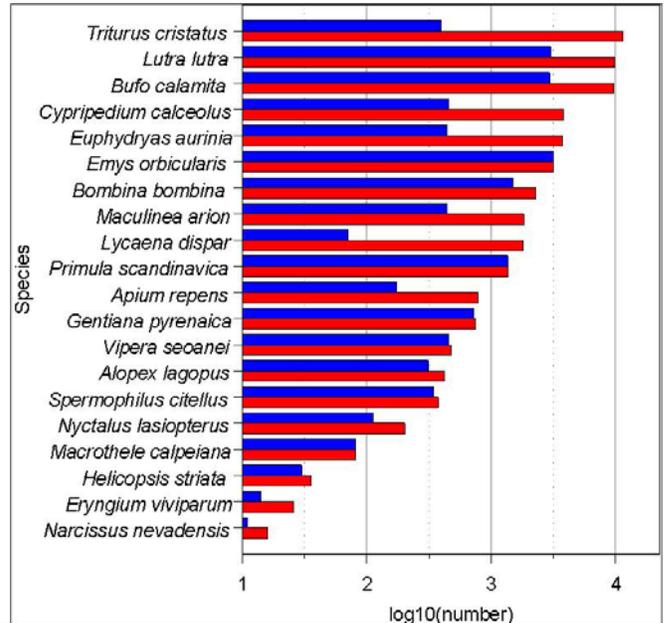
1) Species selection and data acquisition

Species were selected based on 4 main criteria: occurrence in EU countries with contrasting technical capacities; degree of biogeographic and habitat specialization; taxonomic coverage; and data availability. Selection of species was performed in direct discussions with EEA personnel, and are summarized in the table below.

Mammals	Reptiles and amphibians	Plants	Invertebrates
<i>Alopex lagopus</i>	<i>Bombina bombina</i>	<i>Primula scandinavica</i>	<i>Euphydryas aurinia</i>
<i>Spermophilus citellus</i>	<i>Vipera seoanei</i>	<i>Apium repens</i>	<i>Macrothele calpeiana</i>
<i>Lutra lutra</i>	<i>Bufo calamita</i>	<i>Narcissus nevadensis</i>	<i>Helicopsis striata</i>
<i>Nyctalus lasiopterus</i>	<i>Emys orbicularis</i>	<i>Cypripedium calceolus</i>	<i>Maculinea arion</i>
<i>Galemys pyrenaicus</i>	<i>Triturus cristatus</i>	<i>Eryngium viviparum</i>	<i>Lycaena dispar</i>

The largest existing source of records of species presence globally is the Global Biodiversity Information Facility (GBIF; www.gbif.org), which we supplemented with data from the MaNIS (<http://manisnet.org/>) and HerpNet data (<http://www.herpnet.org/>) portals. Numbers of records available to us via these sources for each species are shown in the bar graph at right, in the red bars. The blue bars represent the actual number of records that were used, after data cleaning, as described below.

We used data from these three sources, which require a process of data cleaning (Chapman 2005). In the present case, we removed records falling outside of the region of analysis or in marine environments, as well as records for which georeferencing precision was insufficient. Finally, we examined the distribution of occurrence records available with respect to the known (approximate) distribution of the species, to assure that occurrence data were reasonably representative of the species' distribution and ecology, and to detect any areas that were overrepresented in sampling — for the latter problem, we reduced data density in such areas to match the data density across the broader distributional area to avoid introducing bias in estimates of niche characteristics. Some of these problems are illustrated in the map above, which shows occurrence data for *Lycaena dispar*, and the numbers of occurrence points remaining for analysis after cleaning are shown in the blue bars in the bar graph shown above.



2) Selection of environmental variables

A suite of relevant and appropriate environmental data sets was chosen for analyses. Initially, we sought to base analyses on European sources (<http://dataservice.eea.europa.eu/dataservice>), such as the PRUDENCE climate data

archives. However, in light of serious problems with data formats (specifically the PRUDENCE data are stored in a netCDF format that was opaque to our best efforts!), we decided to use the WorldClim database (<http://www.worldclim.org>).

We selected a set of variables most appropriate for analysis of different sets of species, based on our prior experience. Specifically, in WorldClim, we used annual mean temperature, mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month, and precipitation of driest month. The highest resolution available in WorldClim is 30"; however, most openly available occurrence data are precise, at best, on the order of 1', so we used a 2.5' resolution data set from WorldClim resolution.

To provide a view into likely future potential distributions of each species, we projected niche models developed for the present onto modeled conditions for future, changed-climate conditions. In particular, we used 2020 and 2050 projections from the CCCMA A2a projection from the WorldClim data archive download site (<http://www.worldclim.org/futdown.htm>). Variables used paralleled those detailed for present climates above (in b).

To provide a view into likely effects of sea level rise and consequent marine intrusion into areas that are presently terrestrial, we used data products developed as part of recent global analyses (Li et al. In press). These data sets are at a 1 km resolution, and as such provide a relatively coarse view of coastline modification. Improvements to this data set are now under development that will improve resolution to 90 m, thus providing a much finer-scale view.

To provide a view of land cover, and its changes through time, we used two data sets drawn from the Corine Land Cover project (CLC1990 and CLC2000) and the associated PHARE data set for Eastern Europe.

3) ENM methods

To maintain consistency with the overall purpose of this exercise, we used background-pseudoabsence methods that operate based on presence-only data (Phillips et al. 2006). Specifically, we used Maxent (Phillips et al. 2006), program available at <http://www.cs.princeton.edu/~schapire/maxent/>, a maximum-entropy method that estimates a probability related to similarity of a given environment to those where a species has been observed, for model evaluation, taking advantage of automated routines for receiver operating characteristic (ROC) analyses. For final ENM generation, we used GARP (Stockwell and Peters

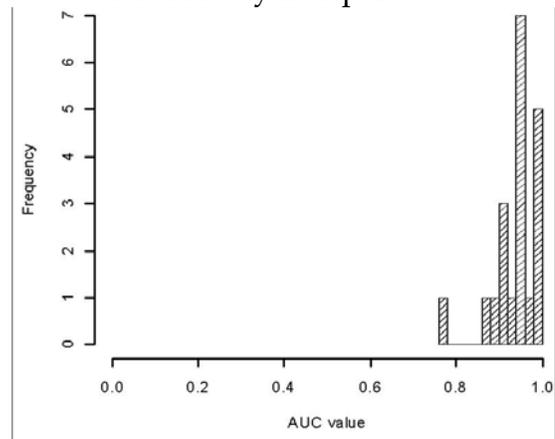
1999), program available at <http://www.nhm.ku.edu/desktopgarp/>, a genetic algorithm with a best-subsets (Anderson et al. 2003) implementation that estimates the degree of concordance by which independent simulations find similarities between observed environments and those in the region under consideration. Both methods have been used extensively for niche modeling purposes, and when used and evaluated properly, provide results with similar predictive power (Peterson et al. 2008a).

4) Niches to distributions

ENM models estimate potential distribution areas of species (Soberón and Peterson 2005). As a consequence, two steps were necessary. First, we used a lowest training presence thresholding approach (Pearson et al. 2007; modified to accommodate 5% georeferencing or identification error) to convert continuous raw ENM outputs to binary predictions. Second, we reduced potential distribution estimates that emerge directly from the ENM algorithms to actual distribution estimates by means of explicit hypothesis regarding dispersal capacities of the species since the end of the last glaciation (Svenning and Skov 2004) to trim potential distributions (Soberón 2007) to obtain estimates, expressed as maps, of actual distributions of each species.

5) Predictions and testing

We used random samples of 50% of available occurrence data to perform quantitative validations of model performance, based on relatively independent occurrence data. Models were calibrated based on half of the occurrence data, and tested using the other half. We used a traditional receiver operating characteristic technique implemented in Maxent, although improved and more appropriate implementations are available (Peterson et al. 2008a); in general, AUC values derived from these analyses that are >0.8 are considered to indicate excellent predictive ability. Results of the validation exercises are shown at right, and indicate excellent predictive ability for 19 of the 20 species that were analyzed.



The ENM-based maps were compared with the Range Distributions developed under Article 17 of the Habitat Initiative provided by the EEA by means of a hierarchical fuzzy pattern matching methodology (Power et al. 2001). In the

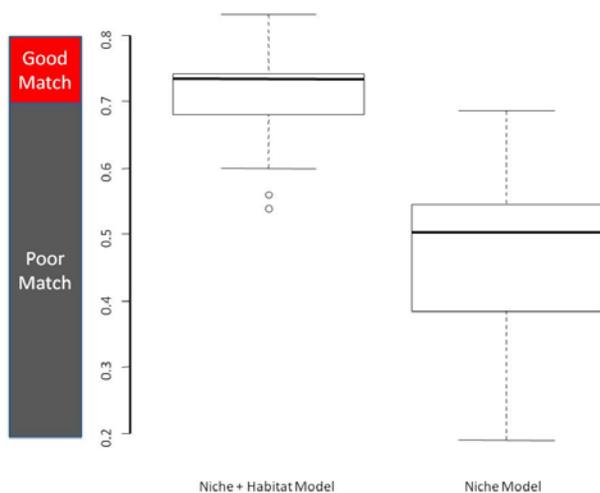


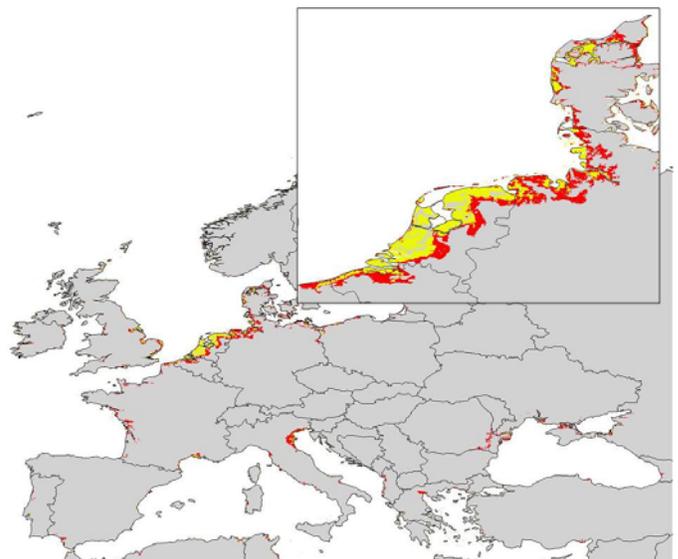
figure at left, we compare the Article 17-ENM matching for the raw niche model (i.e., not taking into account land cover) and for the niche model plus land cover scenarios described in the next section across the 20 species analyzed. In the latter case, matching was quite good, whereas in the former case, matching was not close (clearly because the raw niche model projections included many areas not holding appropriate land cover types).

6) Land cover effects

We next incorporated effects of land cover change by means of integrating the ENM-based maps with land cover information from the CORINE/PHARE projects. In general, we sought descriptions of critical habitats for each species, and chose land-cover categories based on these descriptions. However, we point out that this step was by far the most subjective that we took in the entire project—associations between land cover and species’ use of those land cover types are not well described, and this led to some ambiguity of distributional estimates. We signal this step as a point in which the regional/national expert networks that EEA has assembled as part of the Article 17 effort could aid considerably in the process of regional biodiversity assessment.

7) Marine intrusion

The effects of climate change on biodiversity (and human well-being as well!) take two forms: direct effects of changing climates (see next section), and indirect effects mediated by rising sea levels and consequent marine intrusion into terrestrial environments. The map and inset at right offer a view of marine intrusion implications under a scenario of 1 m of sea level rise (in yellow) and a scenario of 6 m of sea level rise (in red). We used these hypotheses of range attrition to cut estimates of species’ distributions under each of these scenarios.



8) Forecasts of future scenarios under climate change

Following current best practices (Thuiller et al. 2006; Peterson et al. 2008b) we estimated probable future impacts of climate change based on consensus among modeled future-climate scenarios to assess trends in range loss and change in conservation status. To incorporate aspects of changing climates, we assessed the CCCMA A2a scenario for 2020 and 2050. Because this type of predictions cannot be tested in the short term, except in rare circumstances (Araújo et al. 2005), we present these results principally to illustrate the potential. Further, and more in-depth, work will be necessary to provide the EEA with a fully developed and robust methodology.

9) Integration of effects of various factors on species' distributions

We provide our results in the form of Arc grids, which have an associated attributes table that offers considerable useful information about the different factors considered in our analyses. For example, one can easily query these data sets for any of the species to see distributional area likely lost as a consequence of marine inundation, or marine inundation X land cover change, etc.

III. Results and Discussion

1) Classification of Results

Throughout this exercise, we have emphasized practical methodologies and robust testing methods. We have used methods and approaches that are broadly available and accessible to investigators of diverse backgrounds, and with diverse levels of resources of time, data, and funding. As such, these explorations will help the EEA not only to fulfill better its mandate in some of the more unequal regions that comprise the European Union, but also potentially to transfer useful methods to countries of the developing world. Results of this study are divided into two parts, as follows:

2) First-level Cross-checking of EEA Article 17 Results

A first challenge for this effort was to ascertain whether presently available distributional information can be assembled and integrated quickly and efficiently by means of existing biodiversity data sets and quantitative analyses into a useful picture of biodiversity status and pattern. The answer is a qualified yes.

That the results of our analyses are useful is clear from the ease with which the products were assembled. That is, the environmental data sets that we used are all freely and openly available to the scientific community, and the biological occurrence data sets similarly are broadly available. In this sense, our results do not depend on expensive or difficult-to-access information—in fact, all data used for analysis of any given species can be assembled in a few minutes to a few hours of work. The distributional summaries that we developed were all validated by means of data-splitting approaches, and 95% were indicated to show ‘excellent’ levels of predictivity. What is more, our distributional summaries showed close correspondence to the Article 17 distributional information, indicating that the niche modeling approaches and the Article 17 information converge on the same content. The difference, we suspect, is in the time and expense involved in assembling the information (the niche modeling work is quite efficient), and the quantitative detail

The positive result is qualified only in the sense that the quality and richness of information that our approaches yields is dependent on the information that is available—that is, one does not get something for nothing, and the information products that result *do* get better as the input information gets denser, of better quality, and more detailed. In this sense, the success of our efforts should be a call for broad participation in efforts aimed at sharing primary, research-grade biodiversity data as has been the focus of the Global Biodiversity Information Facility and other distributed biodiversity information networks. Only by enriching those networks to the extent possible can information content and analytical insight be maximized with these new methods.

3) Looking into the Future

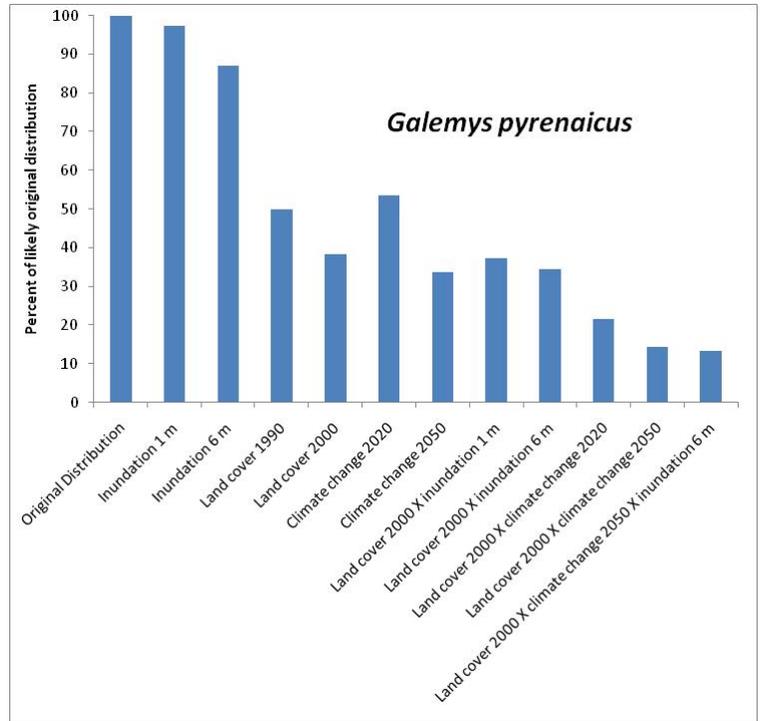
The second challenge for this effort was that of anticipating likely effects of future phenomena, such as climate change, marine intrusion, land use change, and their probable effects on the species’ distributional area. Such insights have considerable potential to provide a proactive perspective on the species’ distributional potential. These techniques can detect areas of loss or gain of distributional area for species.

Of course, validation of such predictions is not easy, as much of the phenomenon takes place in the future. As such, investigators have had to rely on special opportunities for model validation: e.g., retropredictions to the Last Glacial Maximum for species for which distributional information exists for the Pleistocene (Martínez-Meyer et al. 2004a; Martínez-Meyer et al. 2004b). Similarly, a few opportunities have permitted validation over shorter time periods (Araújo

et al. 2005; Foden et al. 2007). Regardless, although the preference would be for more validation, it is clear that useful information results from future projections of niche models.

4) Species Profiles

The data sets developed as part of this study lend themselves well to development of profiles, species by species, of likely threats. For example, the bar graph below shows such a profile for *Galemys pyrenaicus*. From the profile, it is quite clear that marine inundation poses little threat to this species, but that land cover change (even between 1990 and 2000) threatens the species' distributional status, and indeed that climate change further threatens the species' distributional integrity.



5) Specialists versus Generalists

The niche models developed in the course of this work can also be used to evaluate relative specialization *versus* generalization for species objectively and quantitatively. The estimates are of specialization *in terms of* climatic distribution, and are relative to the area of analysis, but such estimates can be developed for any set of environmental variables on which niche models might be based.

To provide an illustration of this functionality, we extracted niche breadth estimates for the 20 species analyzed in this study. Specifically, we followed this recipe:

1. Combine the grids summarizing the niche model prediction with the grids summarizing the 7 climate variables to produce a composite grid.
2. Export the attributes table associated with this composite grid, which summarizes all combinations of environments represented across the region of analysis.
3. Perform principal components analysis on the 7 climate variables in this table, and retain only components with eigenvalue >1.

4. Calculate the variance along each of the retained principal component axes for the sites that are within the distributional prediction for the species.
5. Average the variances across the principal component axes. This value can be taken as an estimate of niche breadth relative to the geographic region and set of environmental variables.

These estimates were derived for each of the 20 species that we examined, with results as shown in the table below. These niche breadth estimates are not broadly comparable among studies or among landscapes, as they are developed relative to a particular area and set of environmental variables. However, they could be standardized without too much trouble, or species can be analyzed over the same landscape, to produce more generally comparable indices of niche breadth to summarize generalization *versus* specialization of species.

6) Evolutionary Potential of Species under Changing Conditions

A common question is why one might have confidence in such forecasts of distributional potential under future climate conditions if species are able to evolve. That is, if climates are changing, for example, can't species just evolve to be able to take advantage of the new conditions? The answer, at least to the limit of present knowledge, appears negative.

The challenge for species under changing conditions is to broaden their ecological potential (i.e., the ecological niche) to include the new conditions. Three lines of evidence, however, suggest strongly that such adaptive evolution is unlikely. First, theoretical expectations are that ecological niche evolution will not occur easily or frequently (Brown and Pavlovic 1992; Holt and Gaines 1992; Kawecki and Stearns 1993; Kawecki 1995; Holt 1996; Holt 2003). The logic is that only individuals that reproduce can contribute genes to the next generation; however, because the ecological niche is *defined as* the set of conditions under which the species can maintain populations, populations occurring under novel conditions

Species	Niche breadth
<i>Alopex lagopus</i>	17845
<i>Apium repens</i>	6951
<i>Bombina bombina</i>	3095
<i>Cypripedium calceolus</i>	20230
<i>Bufo calamita</i>	9571
<i>Euphydryas aurinia</i>	11502
<i>Emys orbicularis</i>	12646
<i>Eryngium viviparum</i>	9506
<i>Galemys pyrenaicus</i>	22185
<i>Helicopsis striata</i>	1623
<i>Lycaena dispar</i>	6708
<i>Lutra lutra</i>	12178
<i>Maculinea arion</i>	8965
<i>Macrothele calpeiana</i>	6218
<i>Nyctalus lasiopterus</i>	11520
<i>Narcissus nevadensis</i>	2177
<i>Primula scandinavica</i>	59463
<i>Spermophilus citellus</i>	2222
<i>Triturus cristatus</i>	18396
<i>Vipera seoanei</i>	8220

will not generally contribute genes to the next generation. As a consequence, ecological niche dimensions will tend to remain stable.

Second, ample empirical evidence has accumulated that indicates that ecological niches are generally highly conserved across ecological and evolutionary time periods. After initial explorations indicated that niches are frequently conserved evolutionarily (Peterson et al. 1999; Peterson 2003), an impressive body of subsequent work has continued to support the hypothesis of ecological niche stability (e.g., Martínez-Meyer et al. 2004a; Araújo et al. 2005; Martínez-Meyer and Peterson 2006). What few examples have been cited as indicating nonconservatism (Fitzpatrick et al. 2007) have been refuted in the face of better-founded analyses (Peterson and Nakazawa 2008). Hence, the empirical evidence indicates that evolutionary change in ecological niche characteristics is at least quite uncommon.

Finally, actual experimental manipulations provide more direct tests of the potential of species to respond evolutionarily to changing climatic conditions. Among the best-developed examples is a study by Etterson and Shaw (2001), in which reciprocal translocations of plant populations placed each population under conditions that could be interpreted as representing 'future-climate' conditions. They observed strong selection pressures, which might be expected to produce evolutionary change. However, they found that antagonistic genetic correlations among characters would retard any adaptive response, to the point that evolutionary adaptation to conditions expected within the next century would not be adequate to permit population persistence.

7) Measures of Biodiversity Loss or Progress

A central challenge in regional biodiversity and natural resources planning is that of assessing where progress is being made, or where ground is being lost. In particular regarding biodiversity, the so-called "2010 Target" was that of reducing rates of biodiversity loss by 2010, as part of national commitments under the Convention on Biological Diversity. Although several indices have been proposed (Butchart et al. 2004; Butchart et al. 2005; Loh et al. 2005), they have been highly dependent on global status lists or complex indices, and as such have not been broadly applicable, scalable, or accessible to countries outside of Western Europe and North America.

A recent publication authored by two of the authors of this report (Soberón and Peterson 2009), however, offered a much more flexible and broadly applicable alternative. Niche modeling approaches were integrated with multitemporal

land cover estimates, and range loss or gain was tracked via this integration through time. The result is a simple, highly accessible approach that can track single species or customized sets of species, across particular regions or globally. The sort of analyses developed in the present study can easily be considered in this framework: the 1990 and 2000 CORINE land-cover evaluations provide two time steps over which range loss can be measured. Additional land-cover data sets can provide additional detail in tracking these biodiversity conservation status trajectories for European species.

8) Future Possibilities

The ideas explored and tested in this study indicate several intriguing 'next steps' that could be pursued towards the goal of a broadly comparable, quantitative assessment of European biodiversity status and trends. Of course, no substitute exists for high-quality field data on biodiversity status: this information will come only from enthusiastic participation by European countries, and the biodiversity specialists located in each.

In direct response to the work carried out in this study, however, ground-truthing the model predictions regarding possible population distributions. Specifically, the contrast between our hypotheses of 'actual distributions' and the EEA distributional information can be instructive. Areas signalled as present under EEA information but predicted as absent by our models would represent failure of some step in our modeling process (model predictions, thresholding, land cover classification). However, areas predicted as present by our models, but not included in EEA data sets, are of particular interest. Possible explanations are as follows:

1. The species is not and never was present at the site, because conditions are not, in truth, appropriate there (= model failure, producing an overly broad niche estimate).
2. The species is not and never was present at the site, but because its dispersal abilities have not permitted it to colonize the site (= incorrect assumptions regarding dispersal abilities of the species).
3. The species is not present, but was at one time, having been extirpated subsequently (= loss of a population of the species).
4. The species is indeed present, but has not been detected at the site. Such a situation represents an opportunity to add qualitatively to knowledge of the species.

Clearly, resolving among these possibilities requires on-ground field studies, which can be oriented and guided by analyses such as those we have developed.

IV. Conclusions and Recommendations

We distill the above explorations into a series of direct conclusions and recommendations for future steps on the part of the European Environmental Agency, as follows:

Conclusions

- We have emphasized practical methodologies and robust testing methods
- We have used data, methods, and approaches that are broadly available
- We achieved a first-level cross-checking of EEA Article 17 results
 - Sufficient distributional information could be assembled
 - Our results do not depend on expensive or difficult-to-access information
 - Our distributional summaries were all validated, and 95% showed 'excellent' predictivity
- Our distributional summaries coincided closely with the Article 17 distributional information

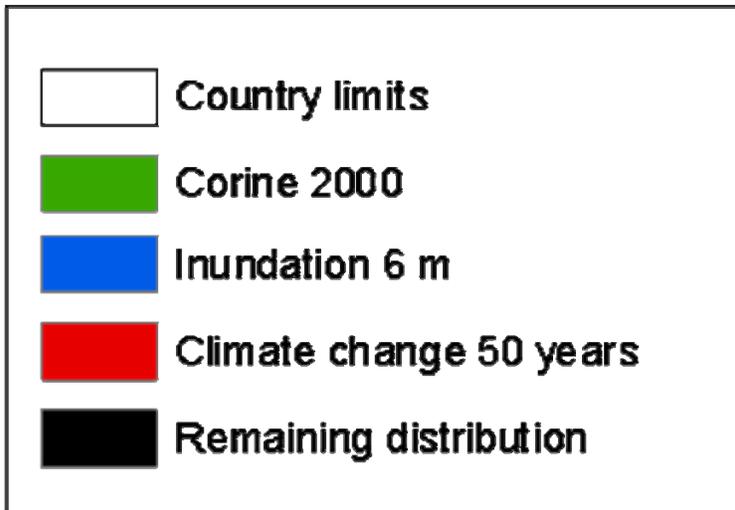
Recommendations to EEA

- Work with other agencies and institutions to build primary biodiversity information resources relevant to European biodiversity issues
- Enrich Article 17 data sets to link directly to CORINE land cover classes across species' geographic distributions
- Incorporate broad consideration of likely effects of future phenomena (e.g., climate change, marine intrusion, land use change) on species' distributional areas in decision-making
- Indices of specialization or generalization should be built from data, rather than from expert opinion.
- Ground-truthing of model predictions regarding possible population distributions may yield additional detections of populations of species of particular conservation interest.

V. Appendix

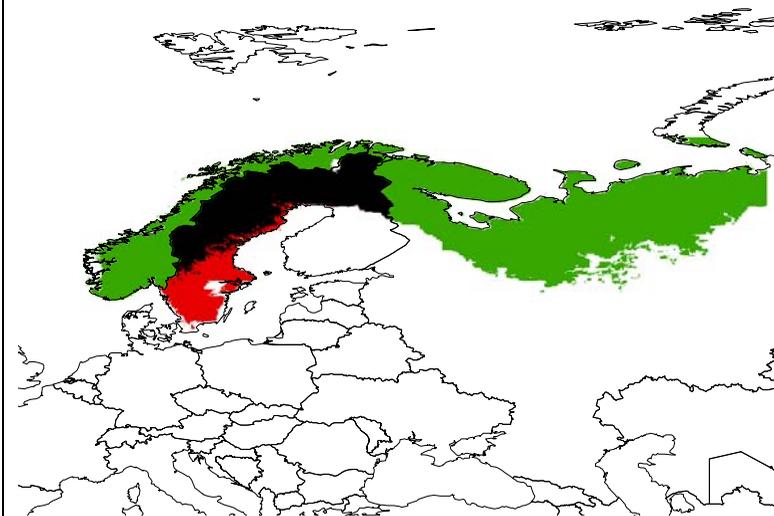
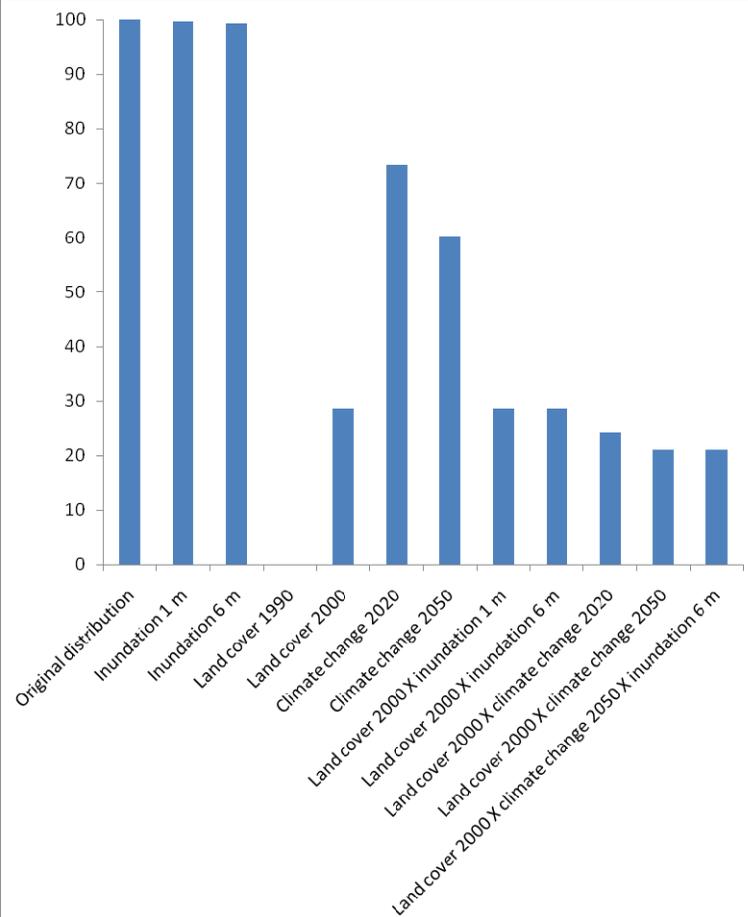
On the succeeding pages, we present a brief, species-by-species commentary treating the status of the species, and the relative magnitude of different threats that were identified as part of this exercise. The textual treatment is accompanied by a graphic summarizing areal loss to different factors, as well as a map of the spatial distribution of those losses.

Color Legend for Maps

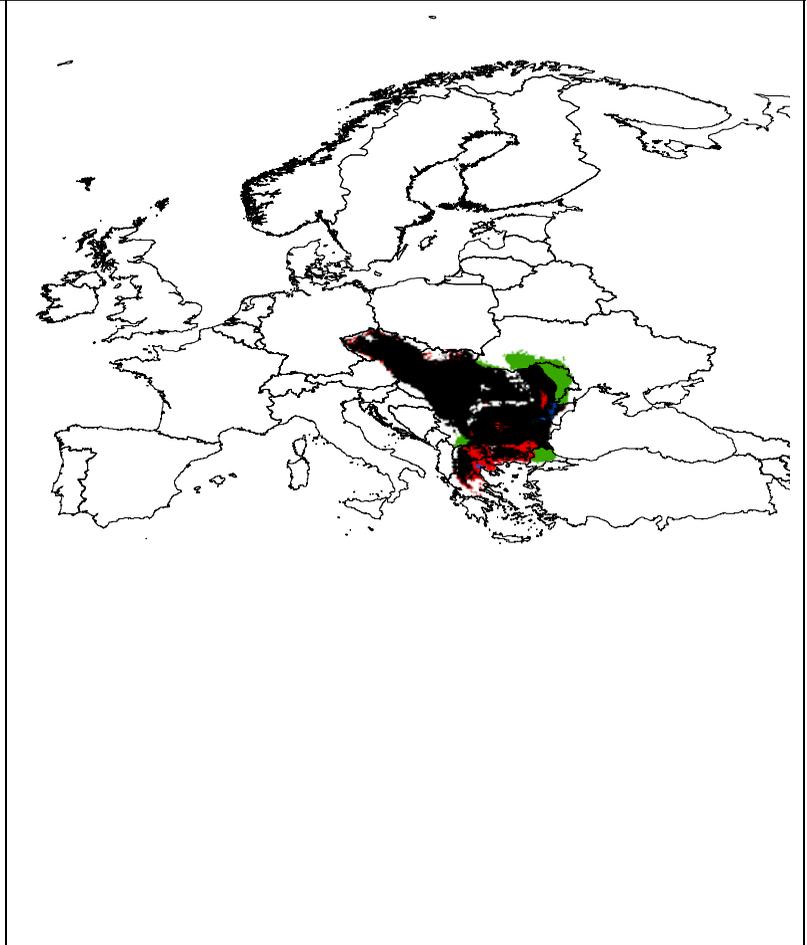
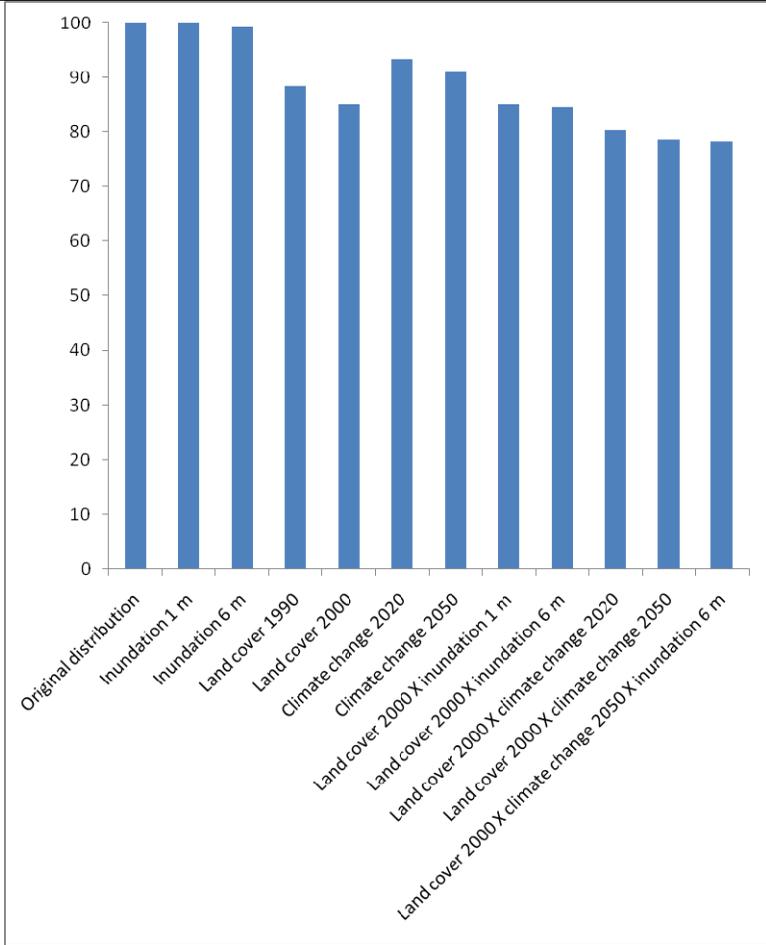


Mammals

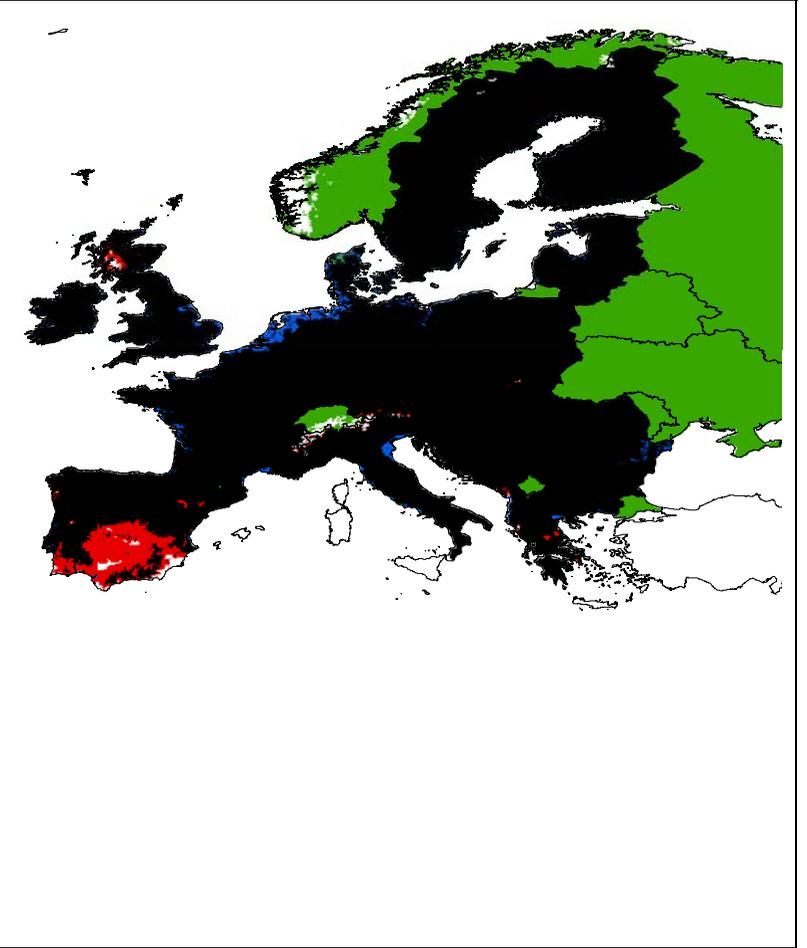
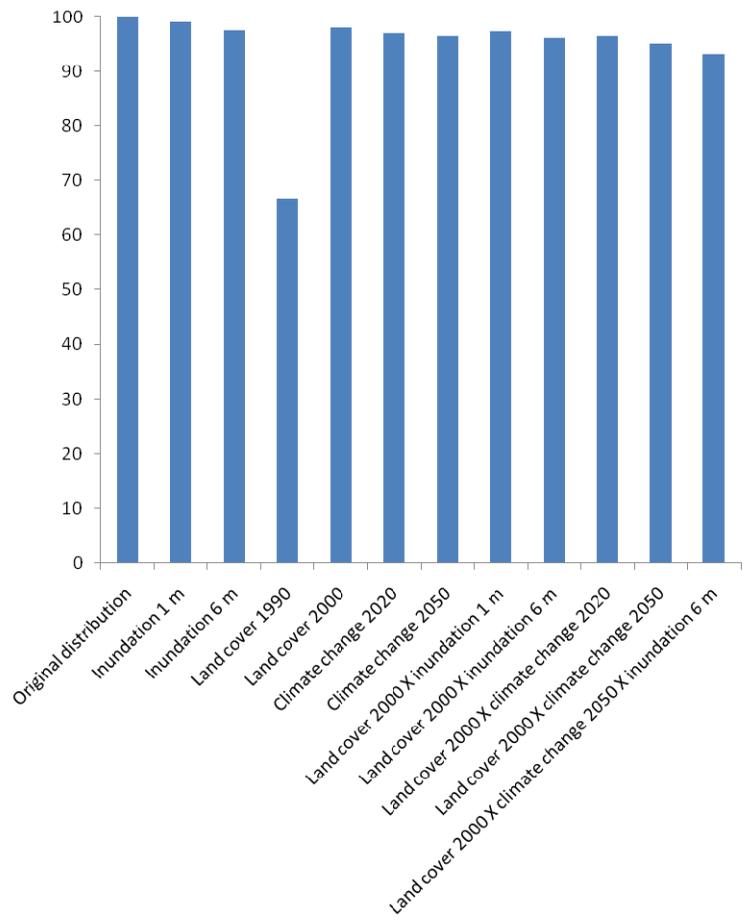
Alopex lagopus Circumpolar distribution in most Arctic tundra habitats. Not greatly affected by land use change (note that portions of its range are outside of the spatial extent of CORINE), nor projected to see much effects of marine inundation. Climate change processes, however, may move southern range limit northward, most notably in southern Sweden.



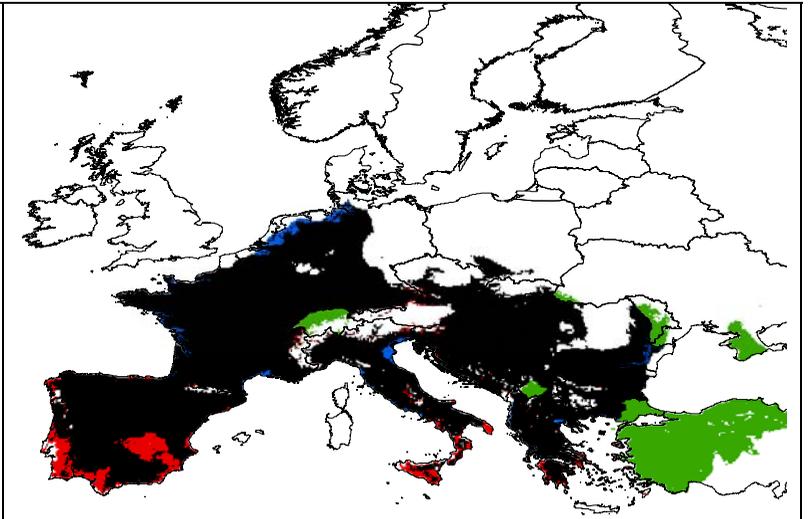
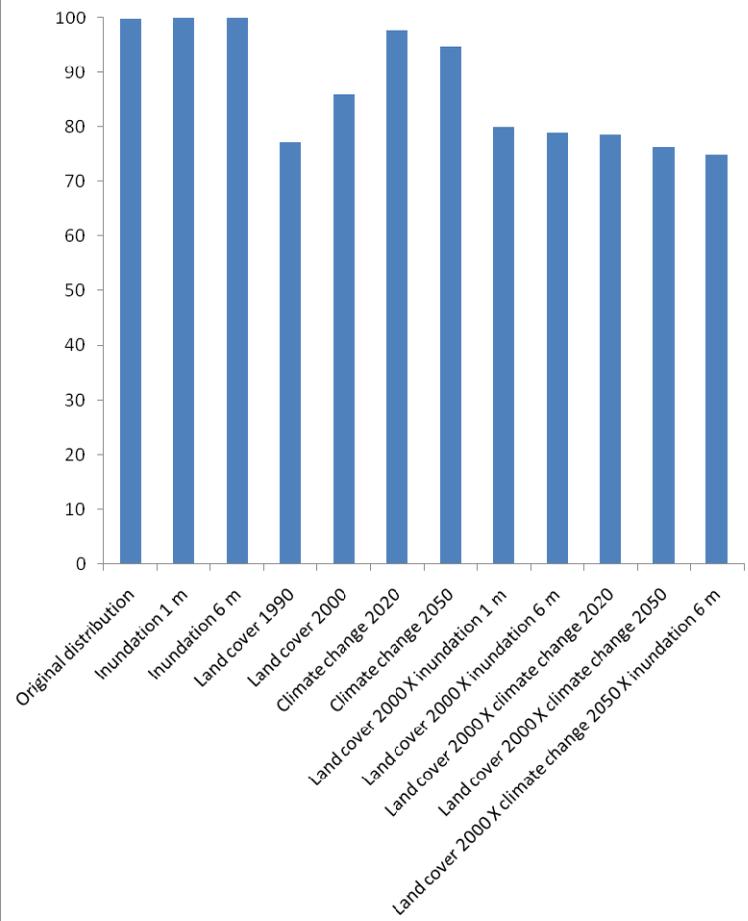
Spermophilus citellus Endemic to central and southeastern Europe. Affected most dramatically by land-use change; effects of climate change and marine intrusion appear negligible.



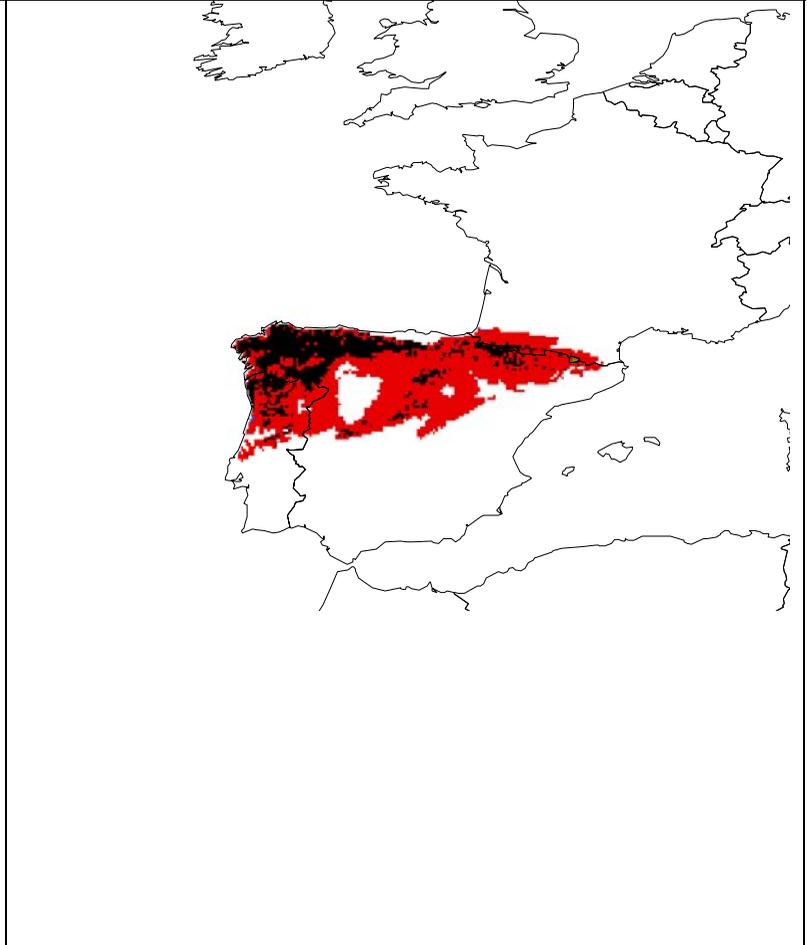
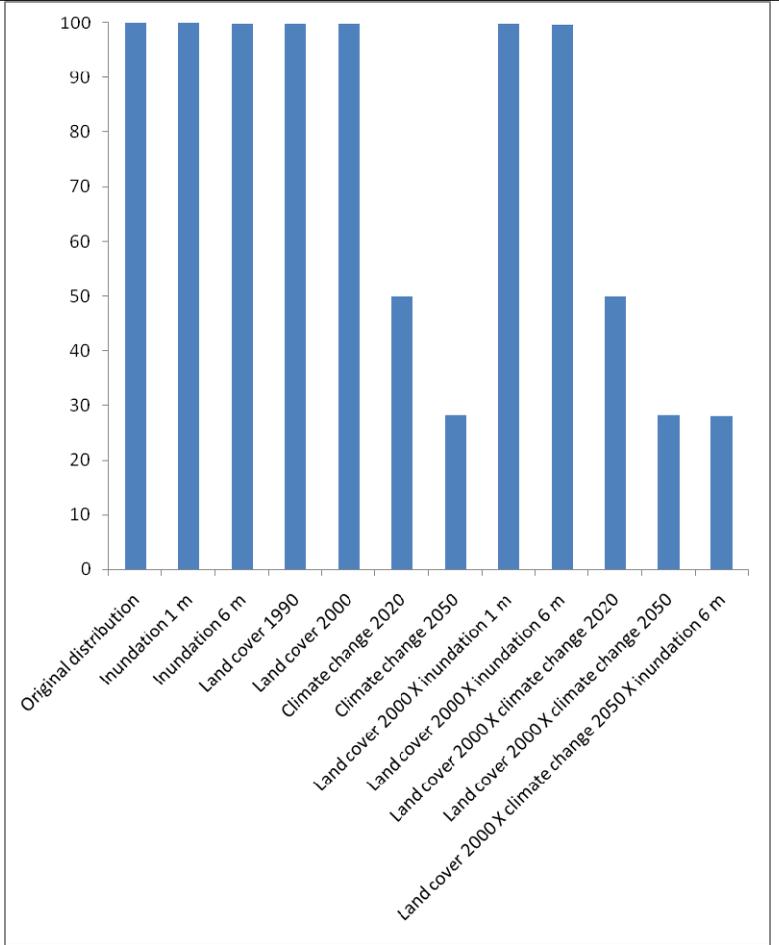
Lutra lutra One of the widest distributions of all Palearctic mammals. Projected to see some range loss owing to climate change in the Iberian Peninsula, and some range loss from marine inundation in northern Europe; however, probably most affected by land use change and habitat fragmentation.



Nyctalus lasiopterus Distributed locally through central and southern Europe and North Africa. Affected by land use change and habitat fragmentation; effects of climate change and marine intrusion are not dramatic, and some new areas to the north and east may become accessible to the species, at least climatically.

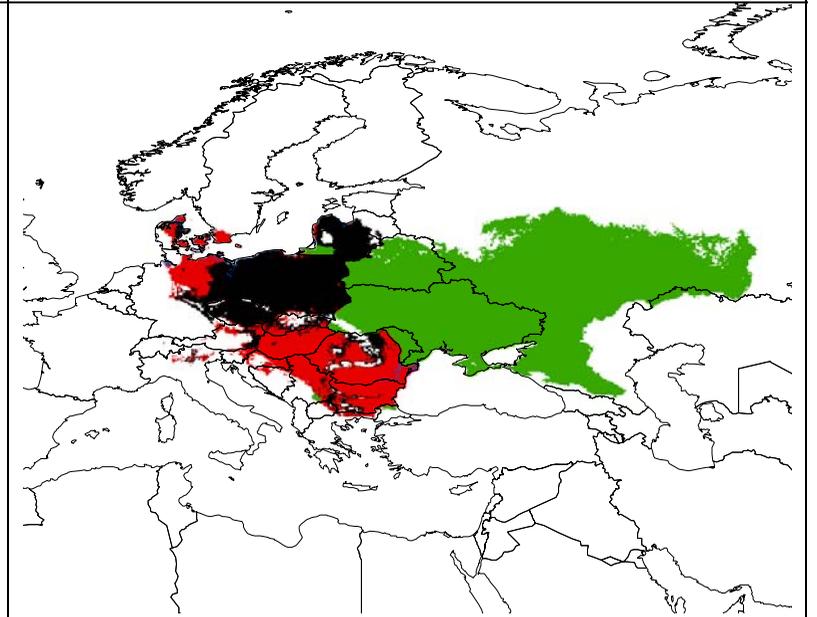
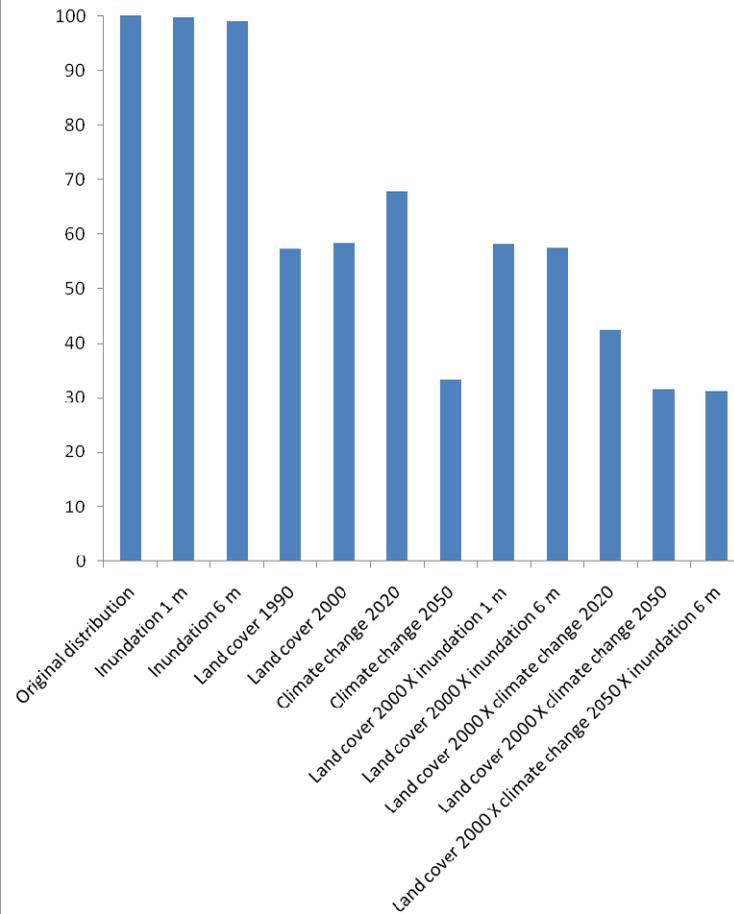


Galemys pyrenaicus Endemic to Pyrenees Mountains, parts of northern and central Spain, and northern Portugal. Affected by land use change and habitat fragmentation; however, climate change may affect the species' distributional potential massively. Marine intrusion effects will be nil.

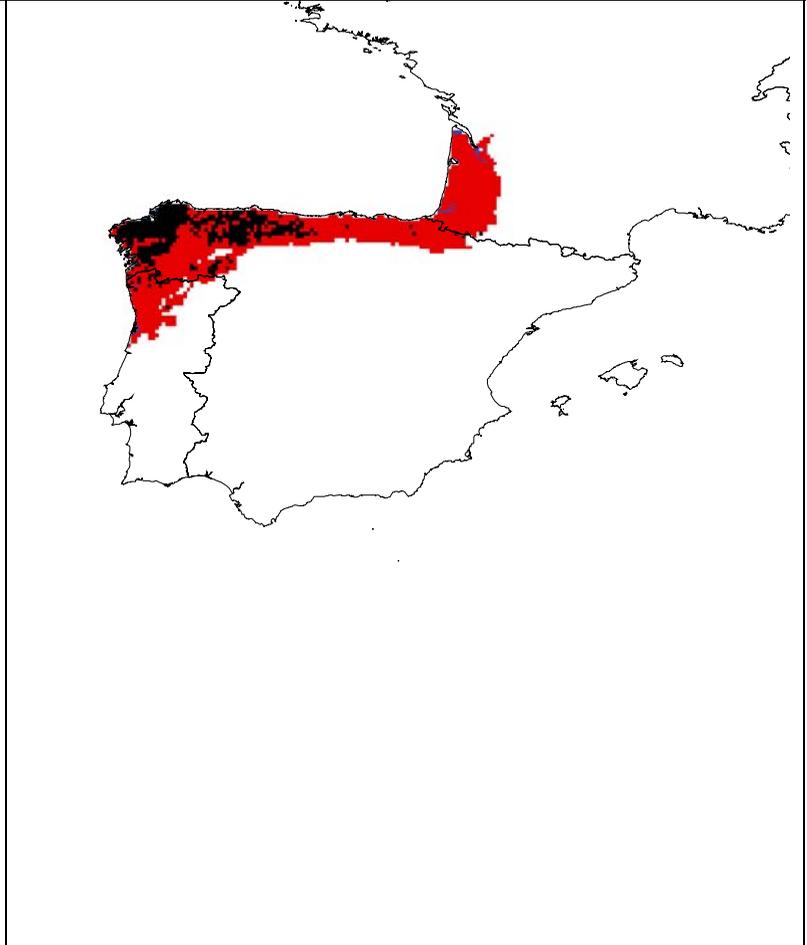
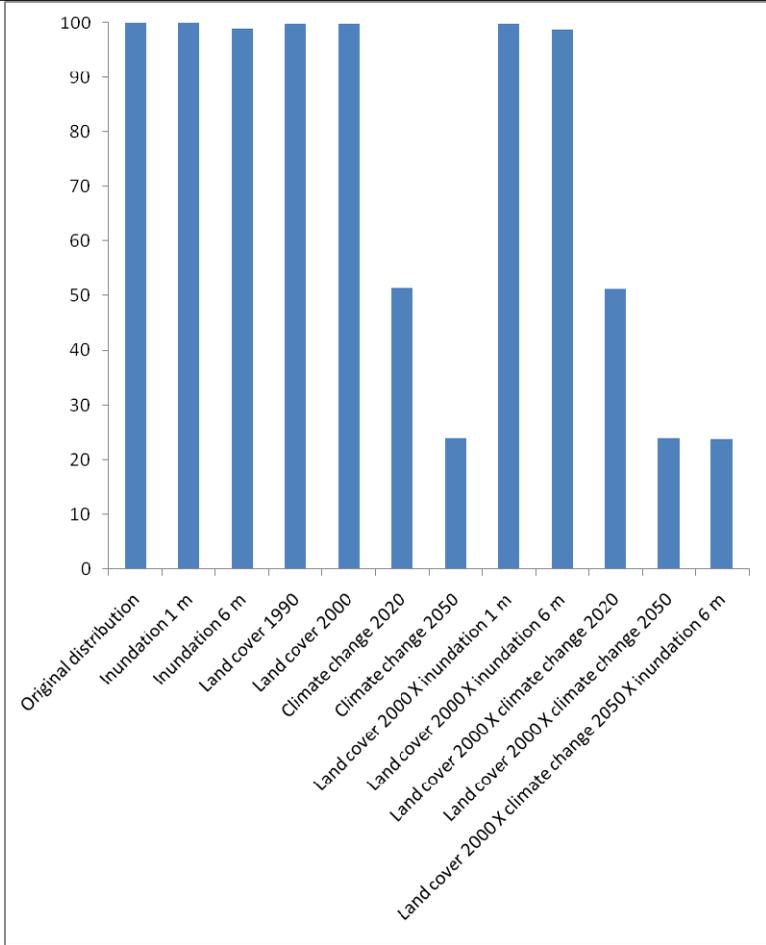


Herpetofauna

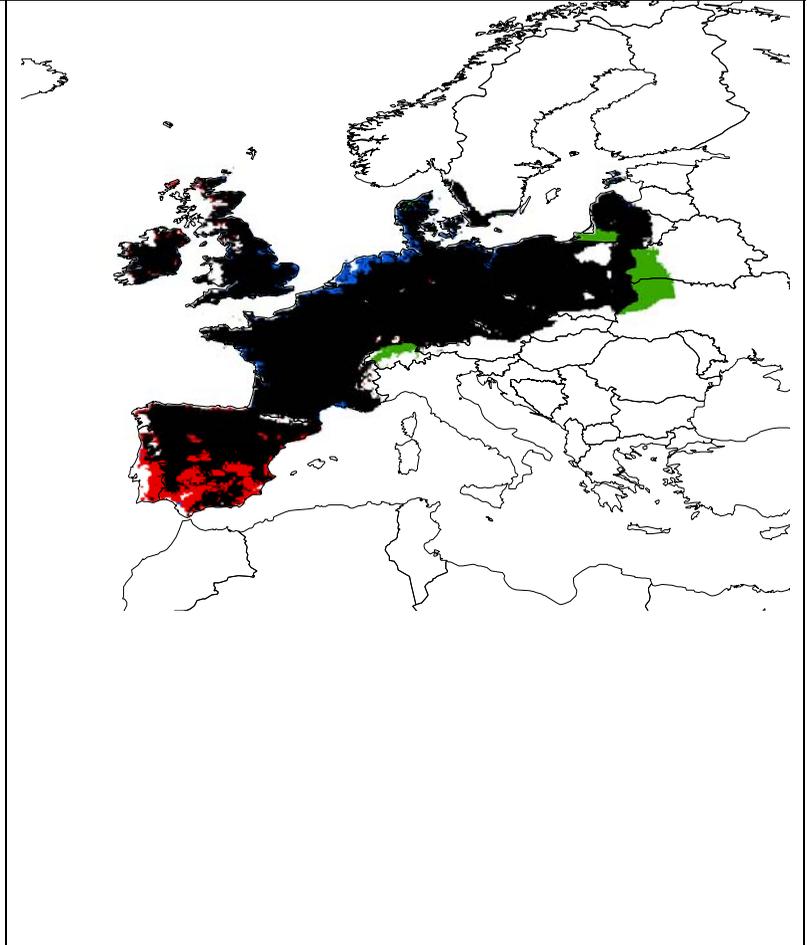
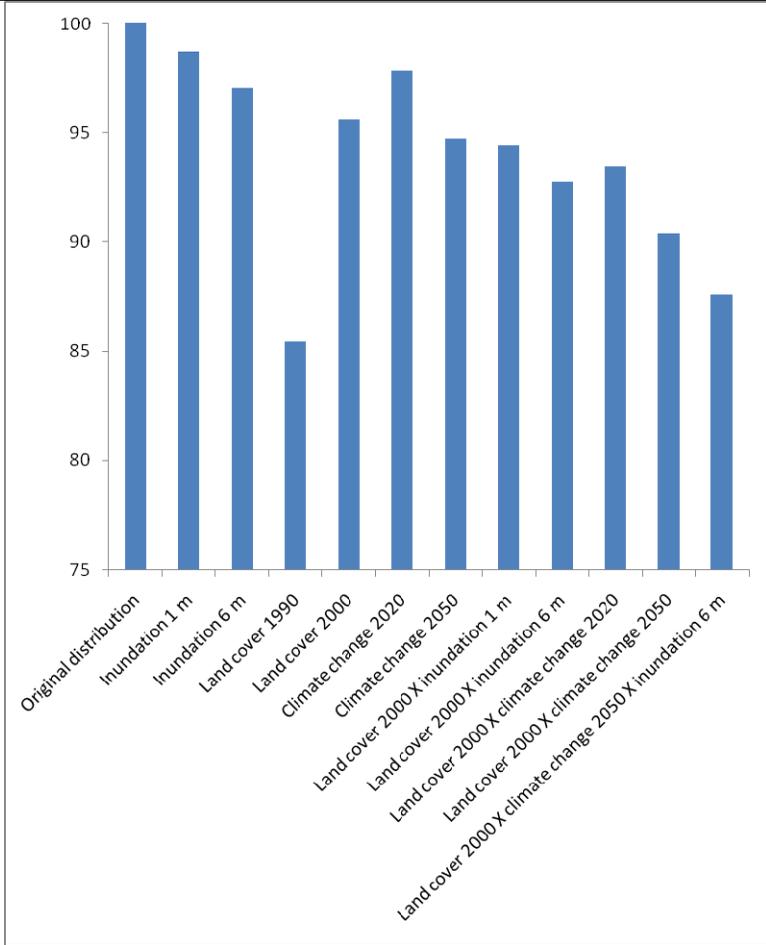
Bombina bombina Distributed across Central and Eastern Europe. Affected by land-use change and habitat modification, but not by marine intrusion. Potential for broad climate-related loss of southern portion of distributional area; some potential for northward expansion, at least in climatic terms.



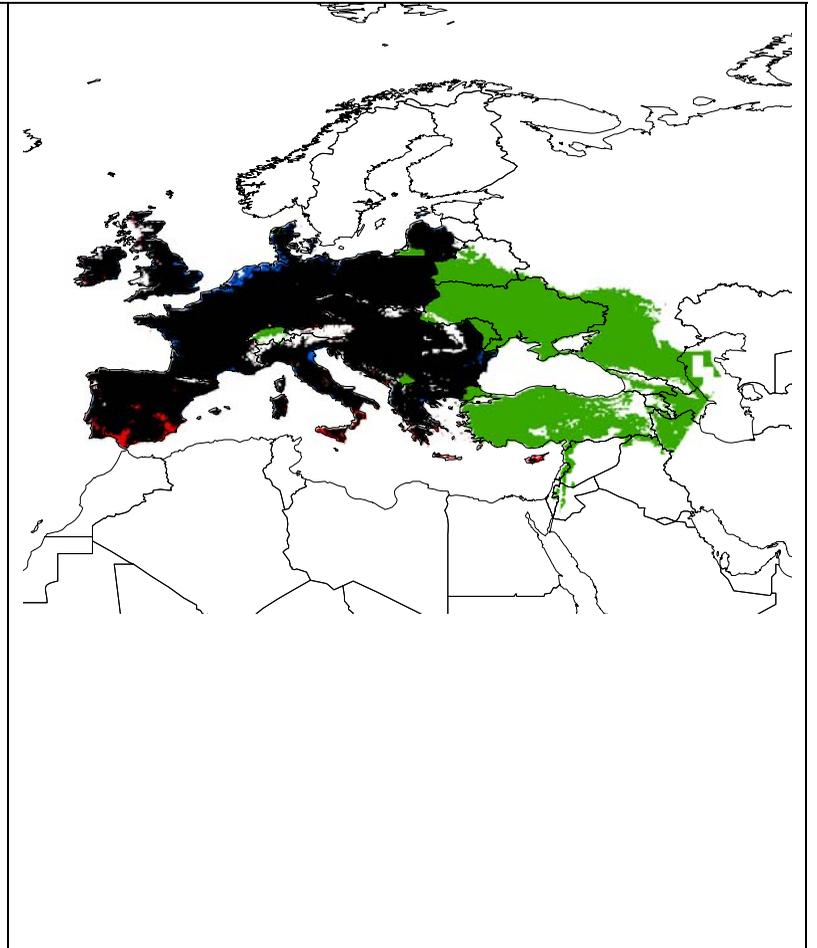
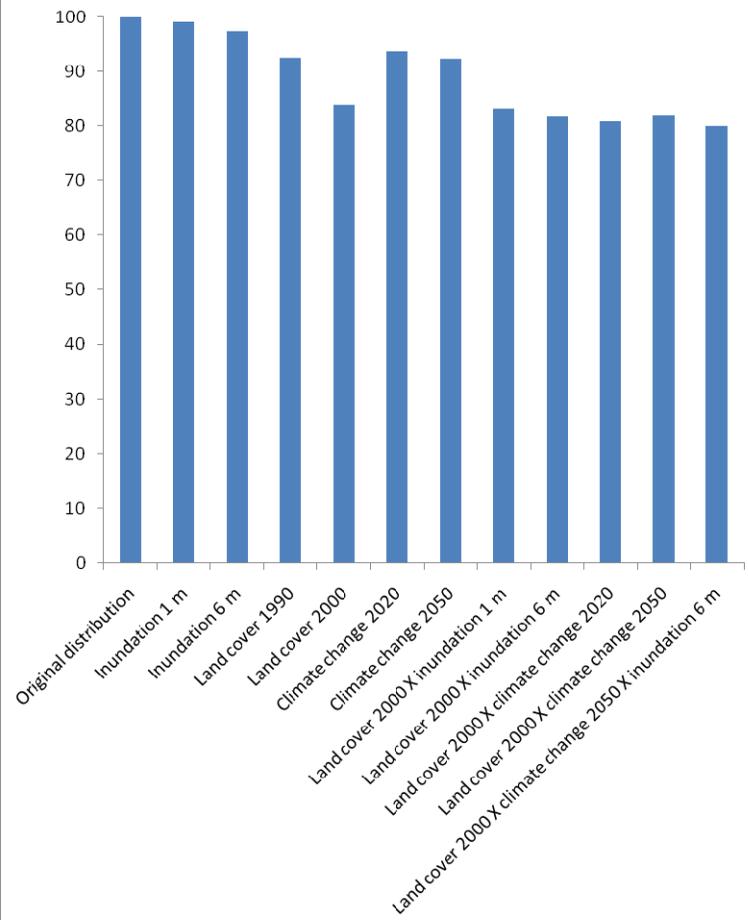
Vipera seoanei Restricted to extreme northern Portugal, northern Spain, and extreme southwestern France. Unclear how much it is affected by land use change, and not affected by marine intrusion. Potentially very strong effects of climate change.



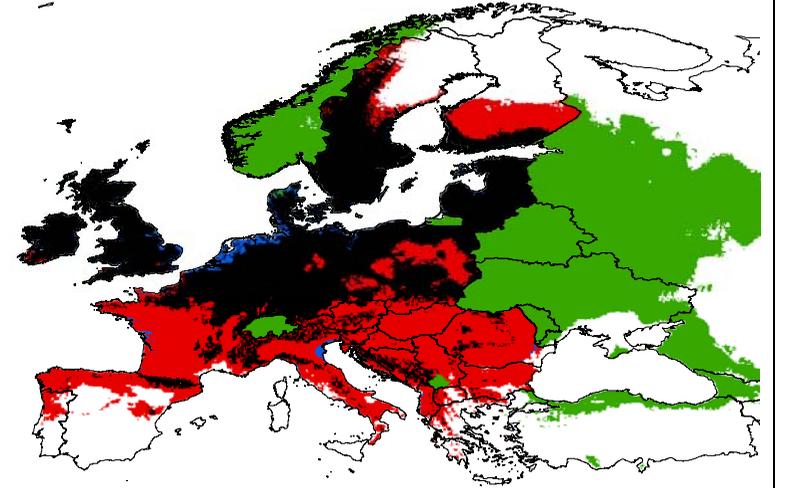
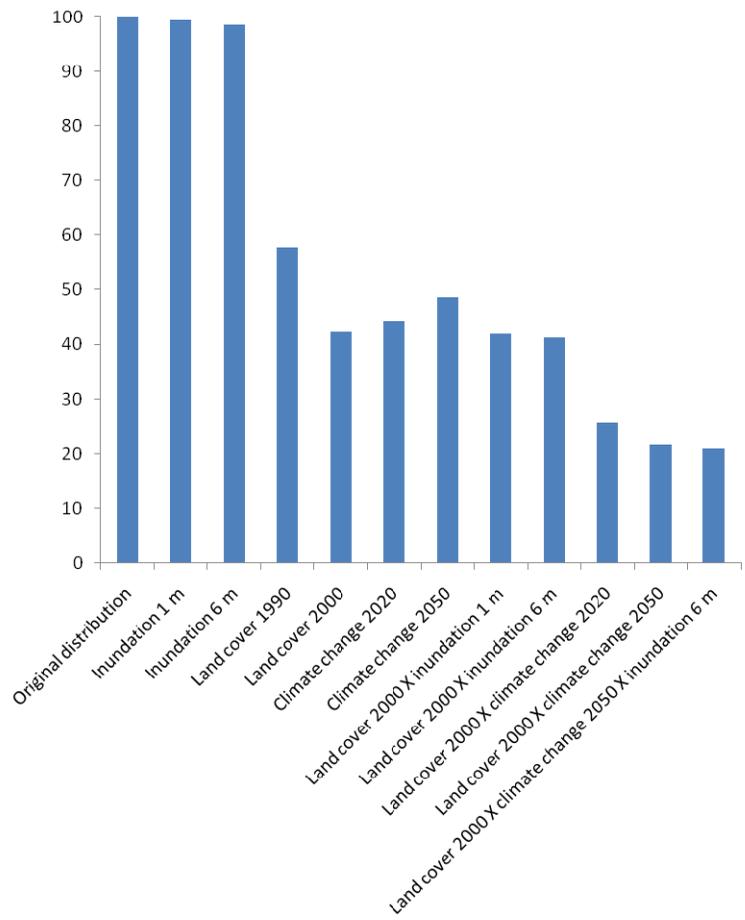
Bufo calamita Broadly distributed across Europe. Some effects of land-use change; some reduction from marine intrusion. Negligible effects of climate change.



Emys orbicularis Broadly distributed across Europe.
Affected by land-use change, but only limited effects
of climate change and marine intrusion.

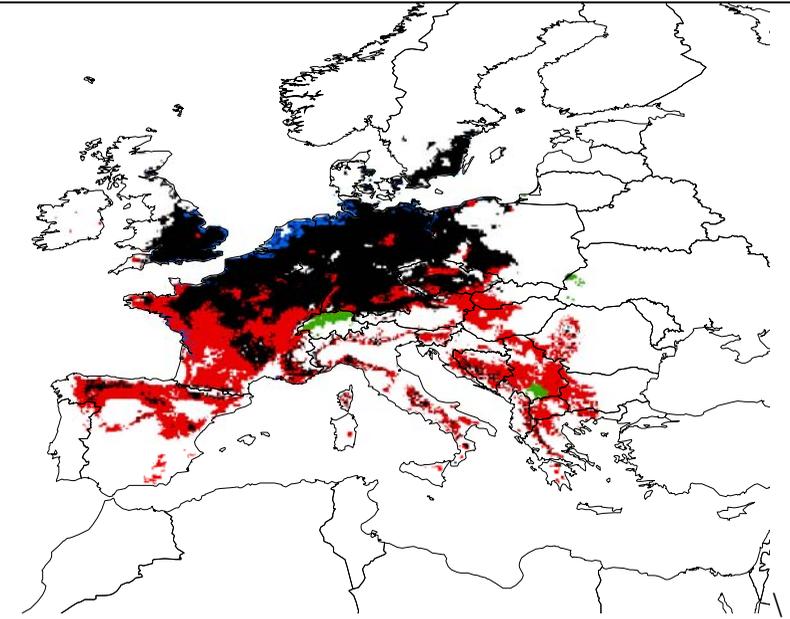
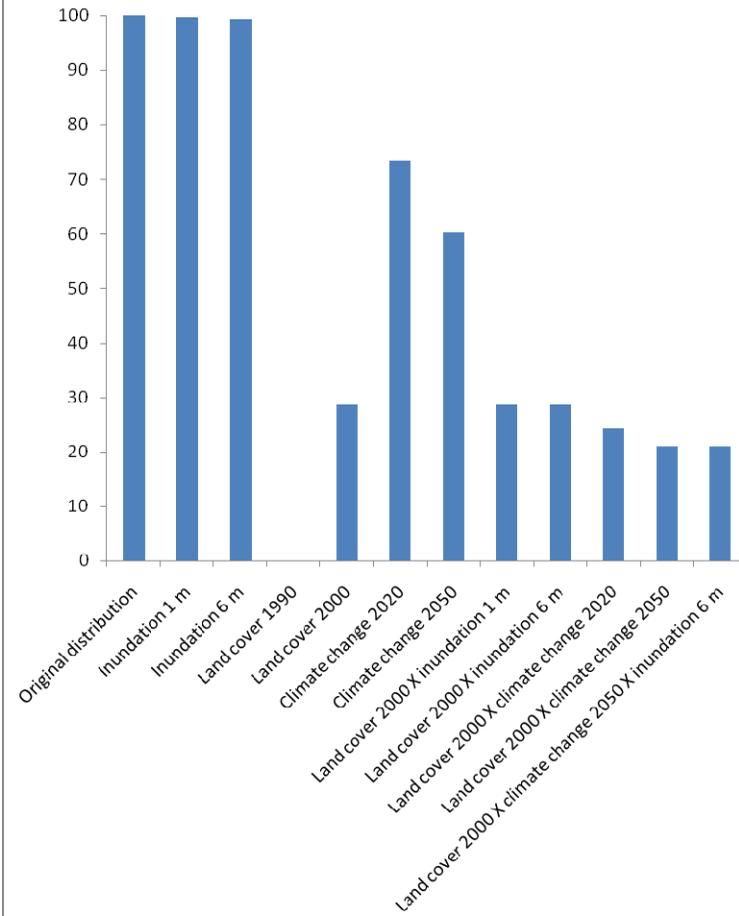


Triturus cristatus Widely distributed across Europe, where vulnerable to land-use change (note some areas outside extent of CORINE). Effects of marine intrusion projected to be minimal; climate change should be pronounced, particularly across southern parts of range.

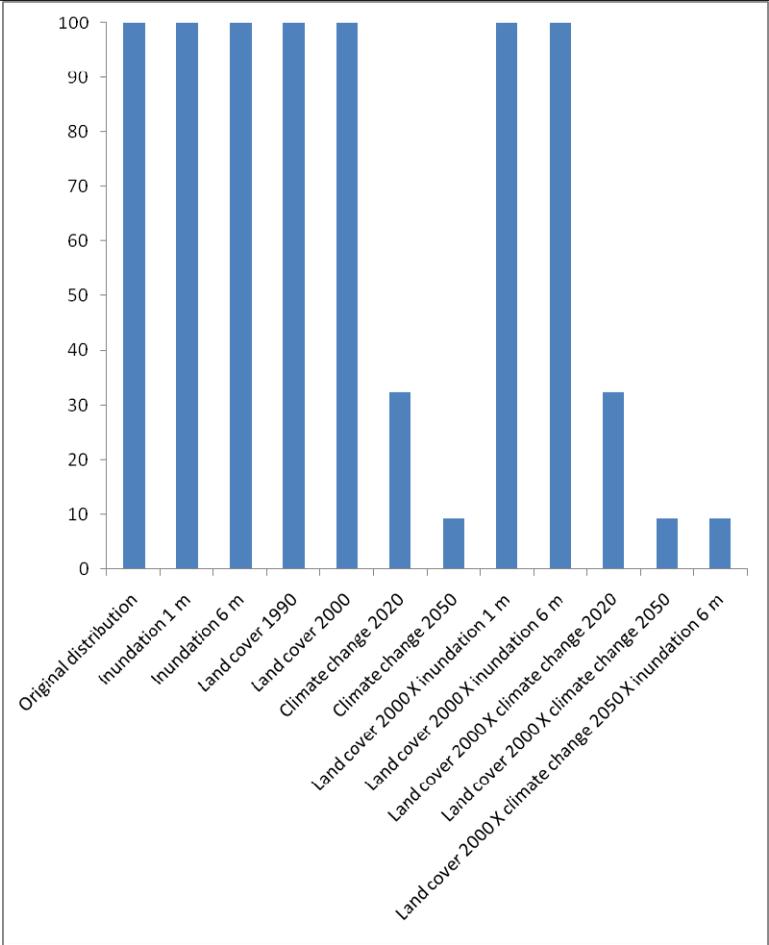


Plants

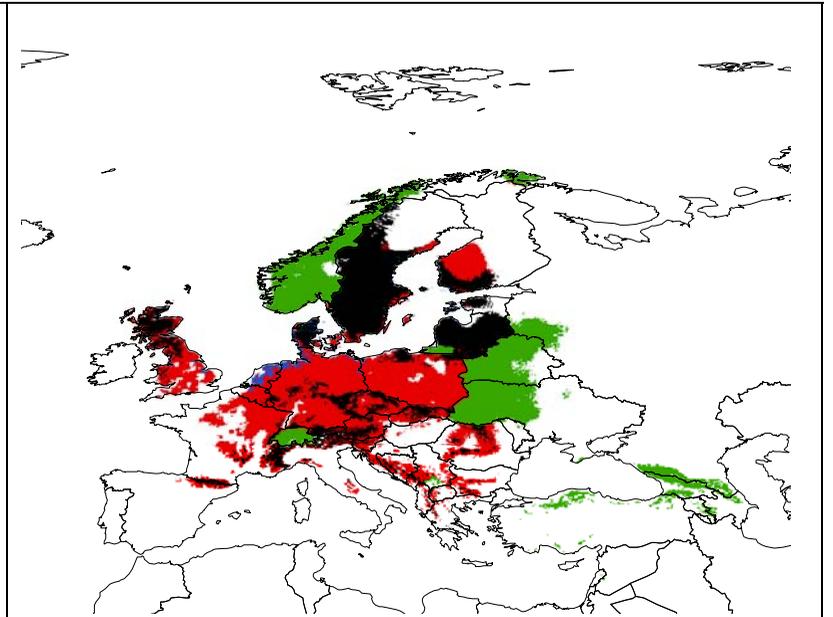
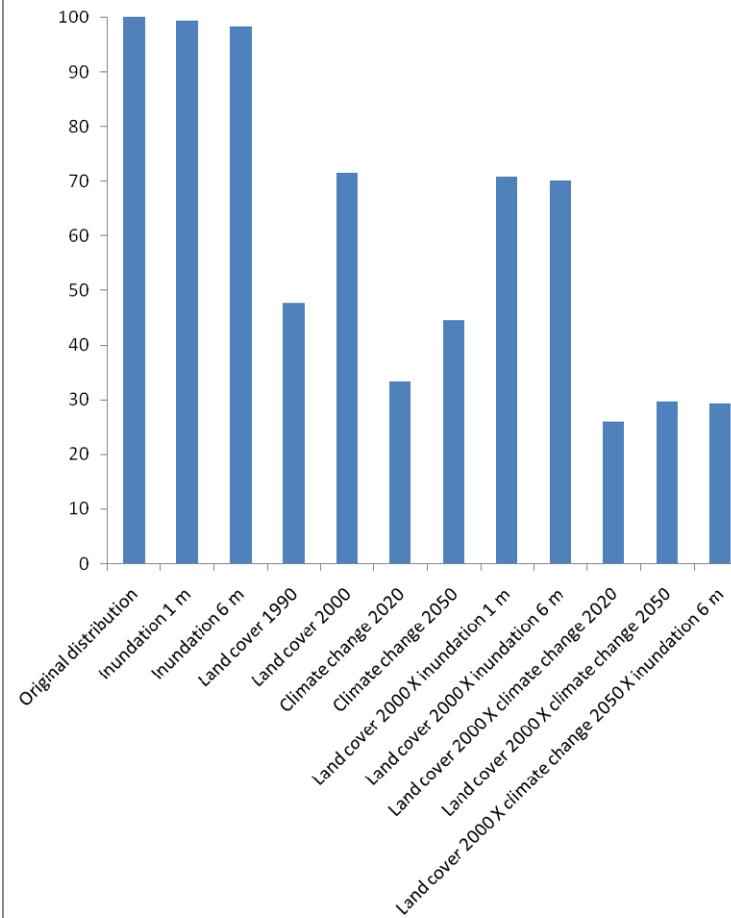
Apium repens Broadly distributed across much of Europe. Very specific in habitat use, so vulnerable to land-use change. Climate change has the potential to remove areas of potential distribution from the southern part of the species' distribution; effects of marine inundation minor in comparison.



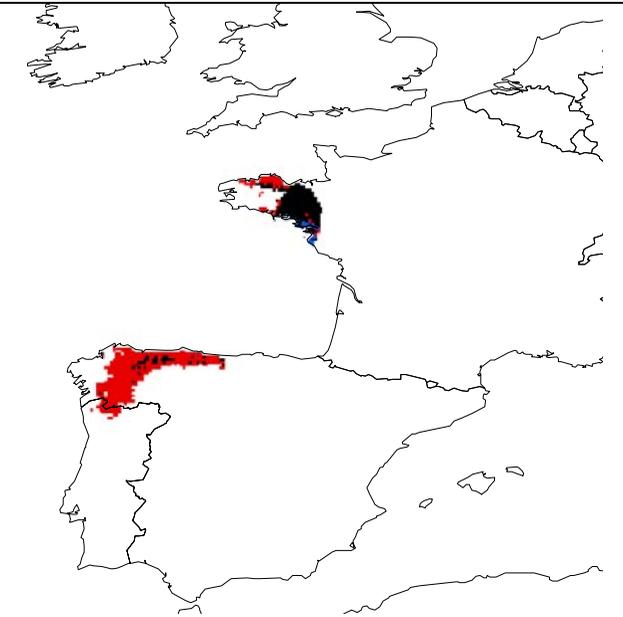
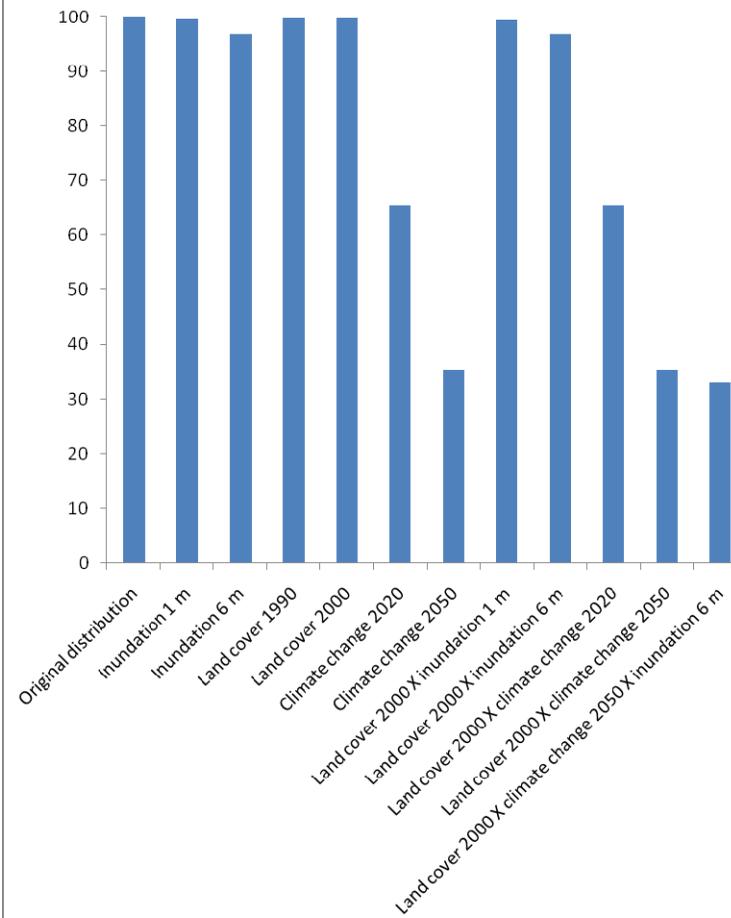
Narcissus nevadensis Microendemic in the Sierra Nevada of southern Spain. Effects of land-use change and marine intrusion minimal; climate change effects potentially disastrous.



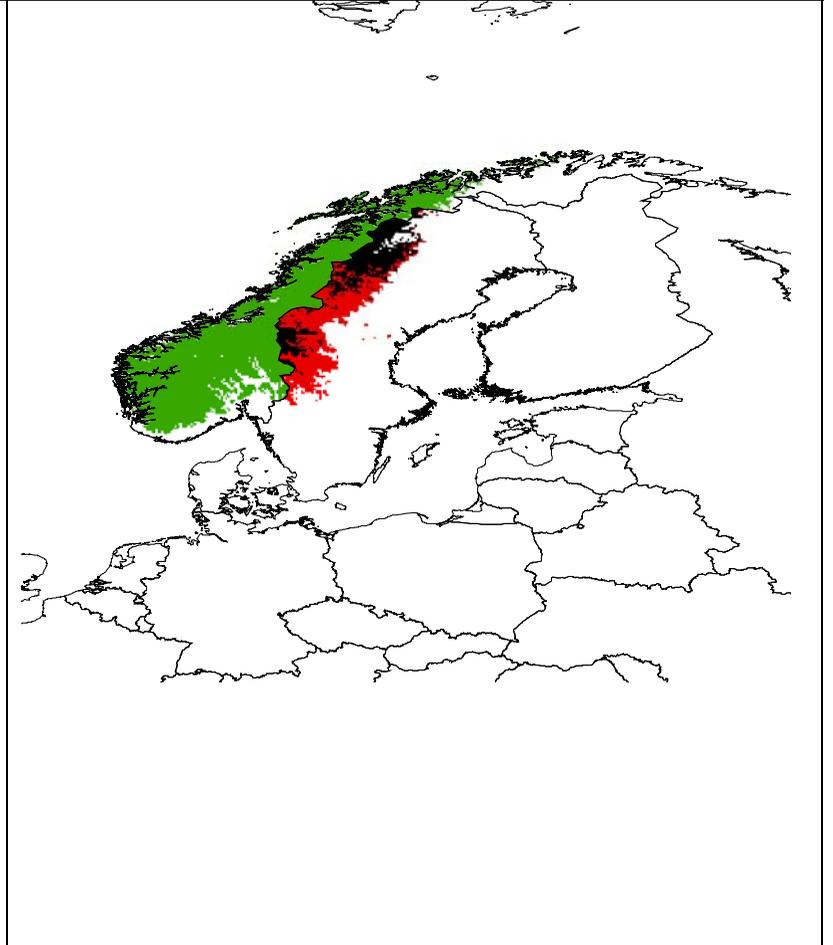
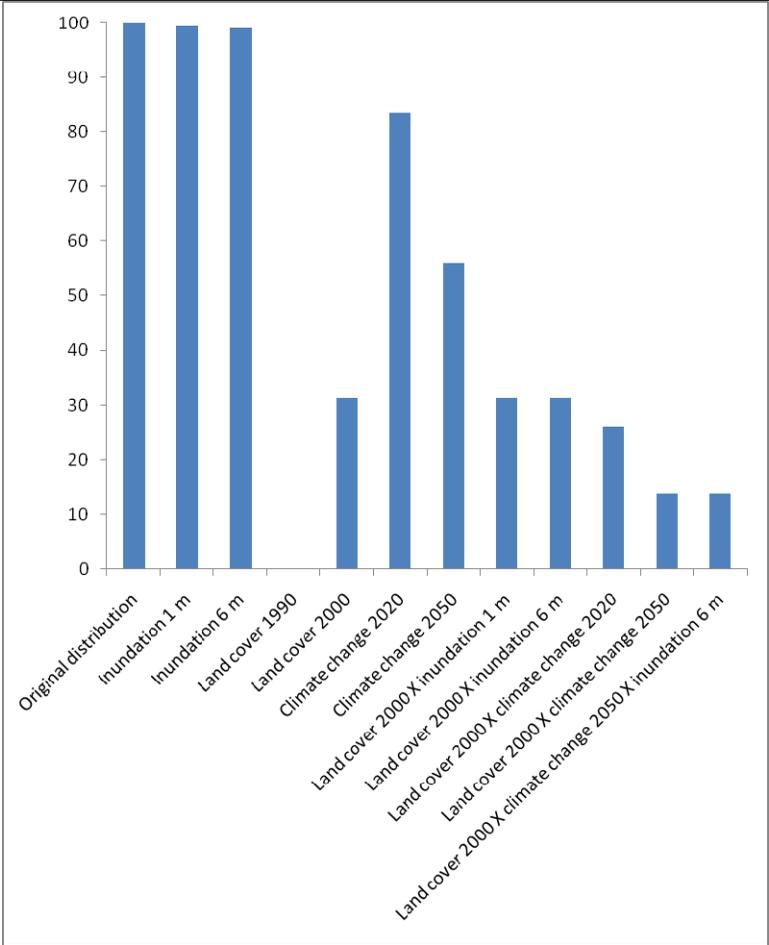
Cypripedium calceolus Widespread, and somewhat vulnerable to land-use change (some areas outside extent of CORINE); effects of marine intrusion minimal, but climate change may remove half or more of the southern part of the European distribution.



Eryngium viviparum Narrowly endemic to two disjunct areas of Atlantic France, Portugal, and Spain. Marine intrusion effects nil. Climate change effects have the potential to remove the entire southern portion of the species' distributional area.

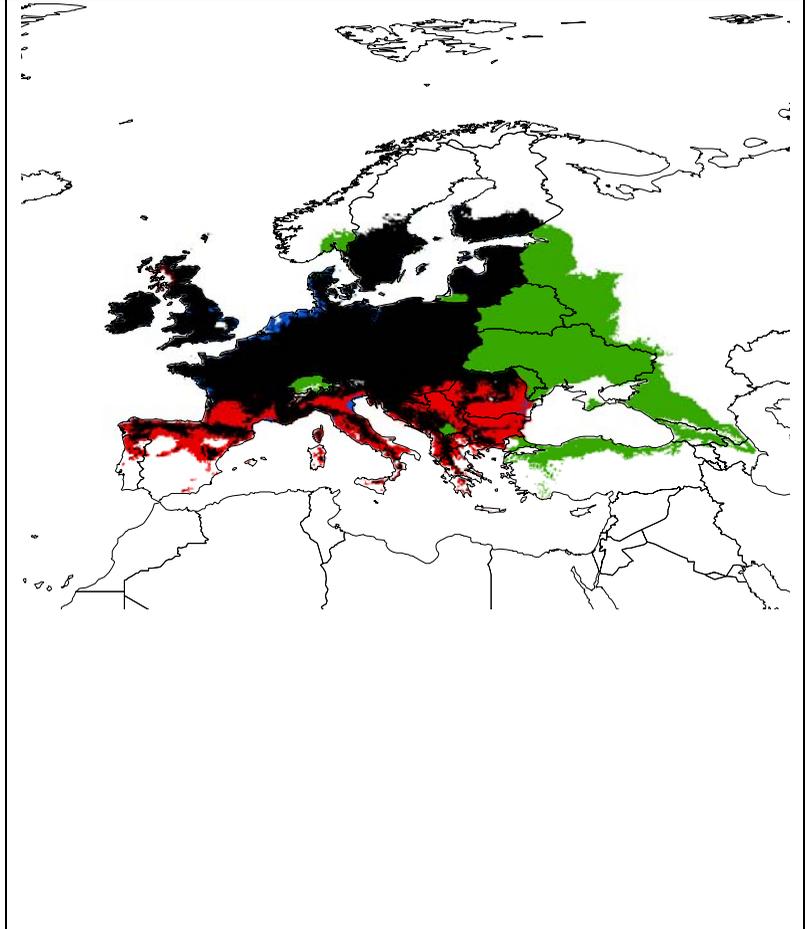
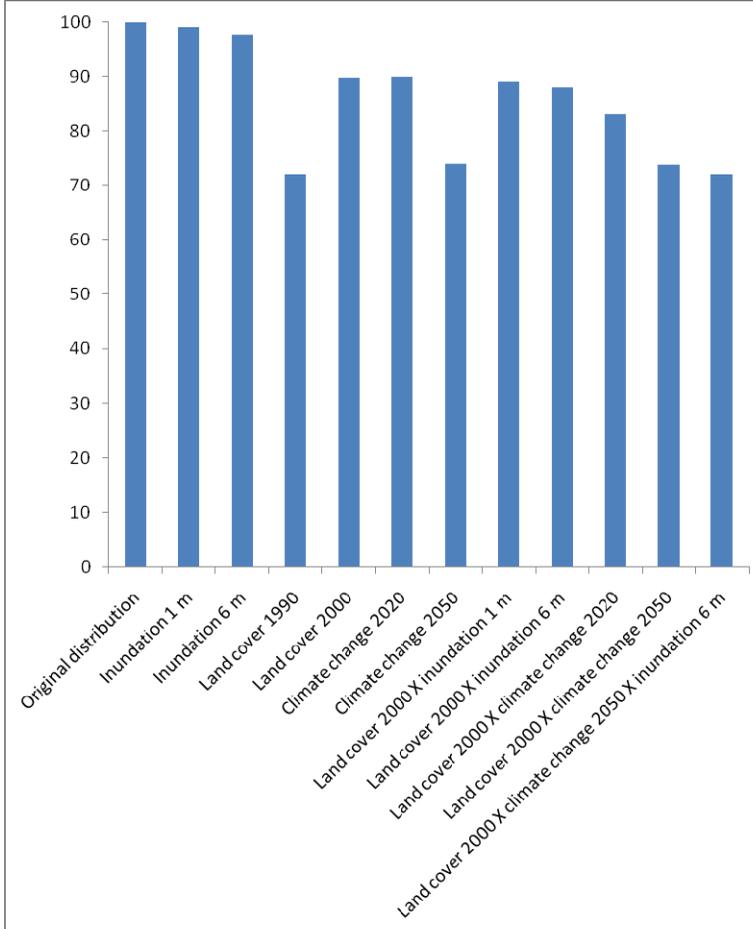


Primula scandinavica Arctic/Alpine distribution. Restricted to bogs and marshes, so vulnerable to land use change. Marine intrusion effects nil. Climate change effects may remove a substantial part of the species' distributional potential.

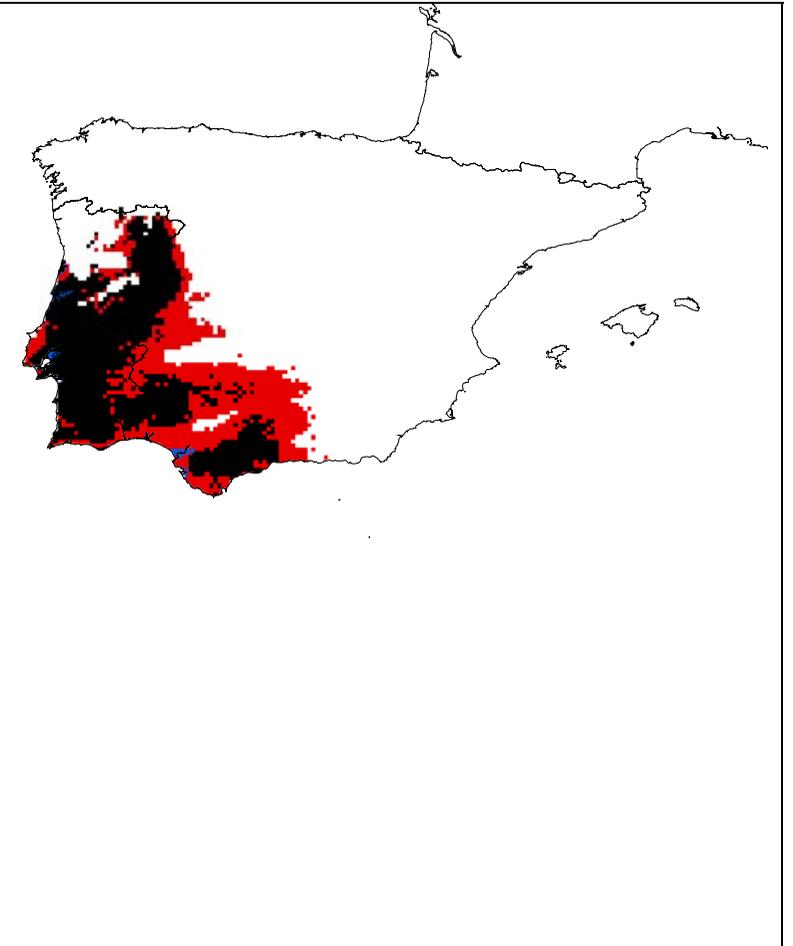
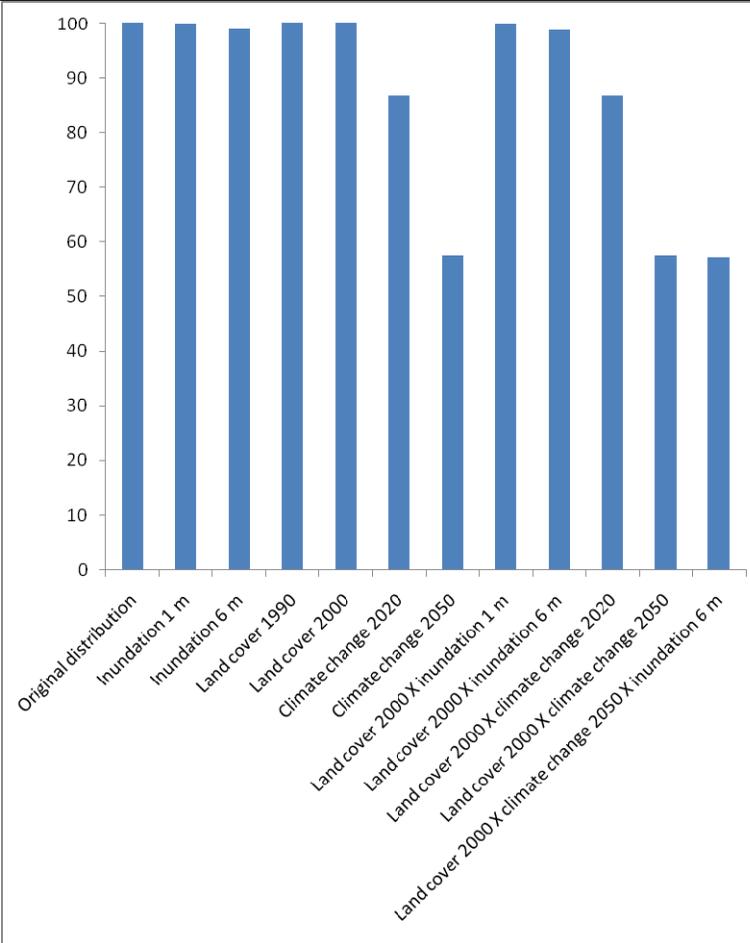


Invertebrates

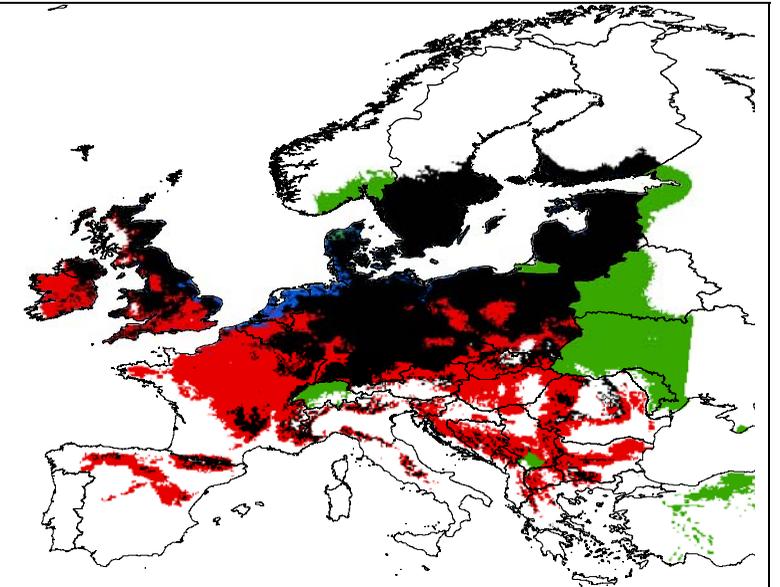
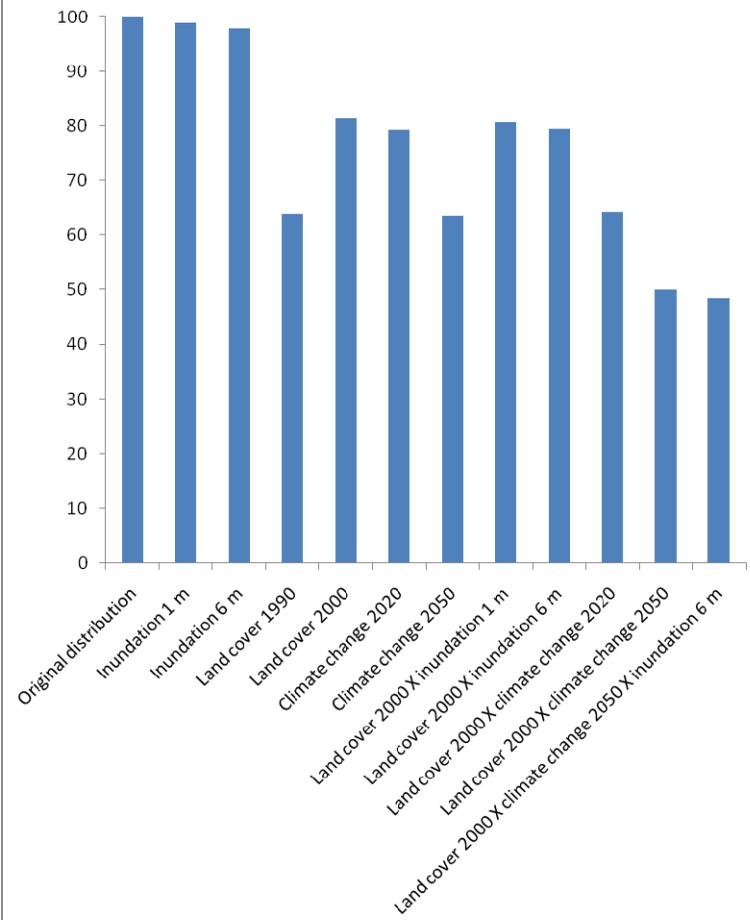
Euphydryas aurinia Broadly distributed across Europe, and found in a diversity of habitat types. Land use change effects visible in the map are mainly owing to limitations to the extent of CORINE. Effects of marine intrusion minor. Climate change may remove some of the southern portion of the species' distributional potential.



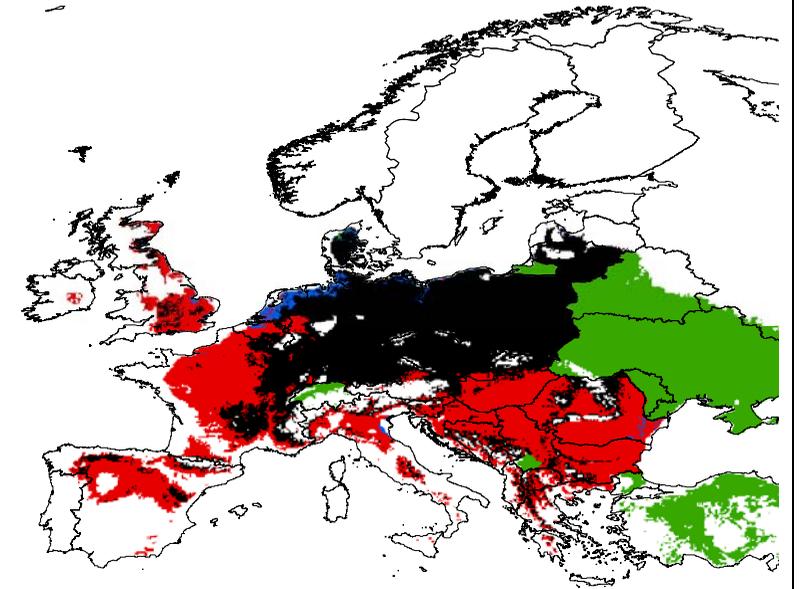
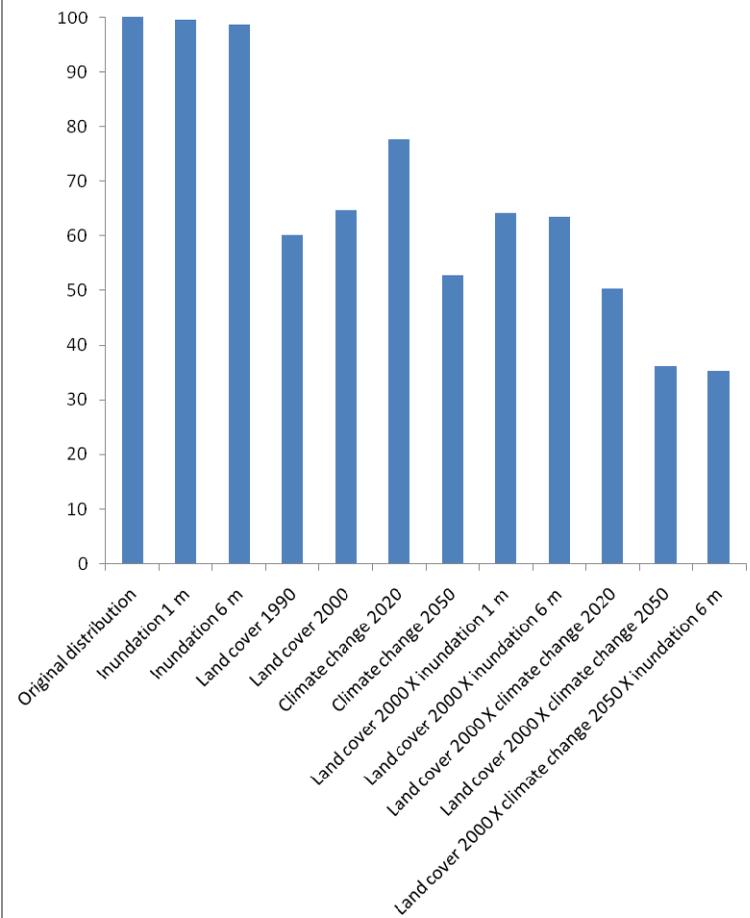
Macrothele calpeiana Endemic to the southwestern part of the Iberian Peninsula. A habitat specialist, so may be vulnerable to land-use change, although not visible in our results. Marine intrusion effects negligible. Climate change effects may remove the eastern portion of the species' distributional potential.



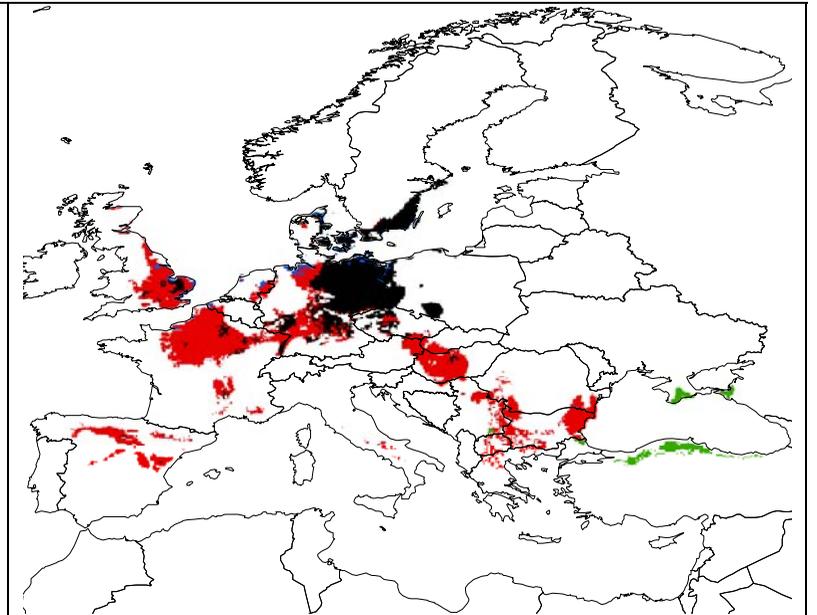
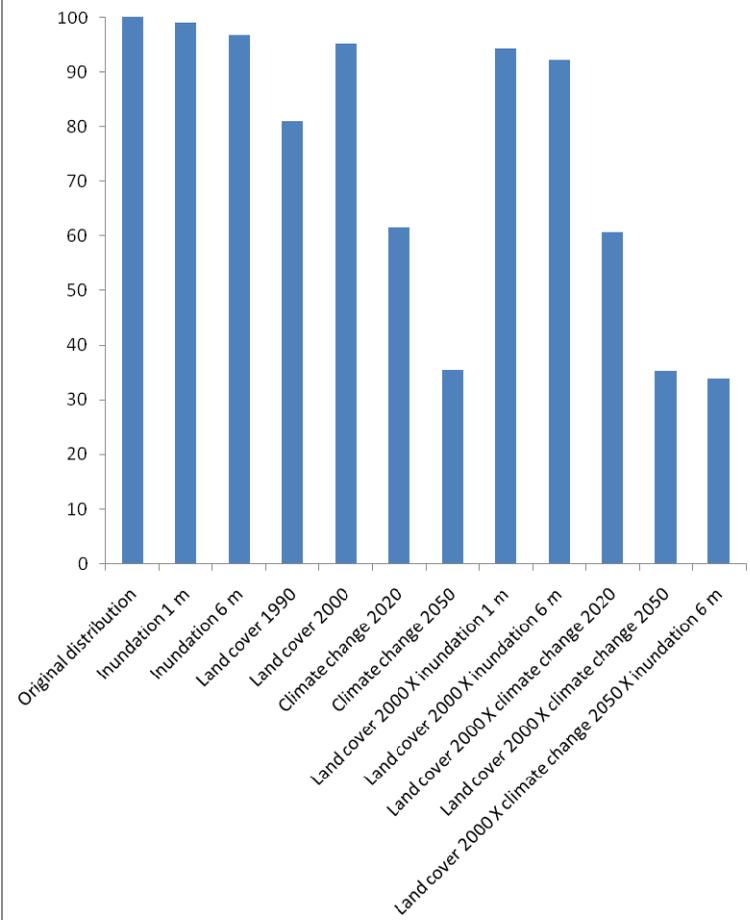
Maculinea arion Broadly distributed across central and eastern Europe. Potential for effects of land-use change (though part of range is outside CORINE extent), and climate change may remove a significant portion of the species' potential distribution. Not affected significantly by marine intrusion.



Lycaena dispar Broadly distributed across Europe, and potentially affected by land-use change in some areas (note eastern parts are outside of CORINE extent). Climate change effects potentially serious in southern and southwestern parts of present range. Negligible effects of marine intrusion.



Helicopsis striata Broadly distributed, but locally, across central and northern Europe, so some vulnerability to land-use change. Marine intrusion effects negligible. Climate change effects have potential to remove western half of species' distributional potential.



VI. Bibliography

- Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecological Modelling* 162:211-232.
- Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species-climate impact models under climate change. *Global Change Biology* 11:1504-1513.
- Brown, J. S., and N. B. Pavlovic. 1992. Evolution in heterogeneous environments: Effects of migration on habitat specialization. *Evolutionary Ecology* 6:360-382.
- Butchart, S., A. Stattersfield, J. Baillie, L. Bennun, S. Stuart, H. Akçakaya, C. Hilton-Taylor, and G. Mace. 2005. Using Red List Indices to measure progress towards the 2010 target and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360:255-268.
- Butchart, S. H. M., A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. Akçakaya, J. E. M. Baillie, S. N. Stuart, C. Hilton-Taylor, and G. M. Mace. 2004. Measuring global trends in the status of biodiversity: Red List indices for birds. *PLoS Biology* 2:e383.
- Chapman, A. D. 2005. Principles of Data Quality. Global Biodiversity Information Facility, Copenhagen.
- Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294:151-153.
- Fitzpatrick, M. C., J. F. Weltzin, N. J. Sanders, and R. R. Dunn. 2007. The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography* 16:24-33.
- Foden, W., G. F. Midgley, G. Hughes, W. J. Bond, W. Thuiller, M. T. Hoffman, P. Kaleme, L. G. Underhill, A. Rebelo, and L. Hannah. 2007. A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions* 13:645-653.
- Holt, R. D. 1996. Adaptive evolution in source-sink environments: Direct and indirect effects of density-dependence on niche evolution. *Oikos* 75:182-192.
- Holt, R. D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5:159-178.
- Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. *Evolutionary Ecology* 6:433-447.
- Kawecki, T. J. 1995. Demography of source-sink populations and the evolution of ecological niches. *Evolutionary Ecology* 9:38-44.
- Kawecki, T. J., and S. C. Stearns. 1993. The evolution of life histories in spatially heterogeneous environments: Optimal reaction norms revisited. *Evolutionary Ecology* 7:155-174.
- Li, X., R. J. Rowley, J. C. Kostelnick, D. Braaten, and J. Meisel. In press. GIS analysis of global inundation impacts from sea level rise. *Photogrammetric Engineering and Remote Sensing*.
- Loh, J., R. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. The Living Planet Index: Using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society B* 360:289-295.
- Martínez-Meyer, E., and A. T. Peterson. 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography* 33:1779-1789.
- Martínez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004a. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography* 13:305-314.
- Martínez-Meyer, E., A. T. Peterson, and A. G. Navarro-Sigüenza. 2004b. Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). *Proceedings of the Royal Society B* 271:1151-1157.

- Pearson, R. G., C. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102-117.
- Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* 78:419-433.
- Peterson, A. T., and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modeling: An example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography* 17:135-144.
- Peterson, A. T., M. Papeş, and J. Soberón. 2008a. Rethinking receiver operating characteristic analysis applications in ecological niche modelling. *Ecological Modelling* 213:63-72.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265-1267.
- Peterson, A. T., A. Stewart, K. I. Mohamed, and M. B. Araújo. 2008b. Shifting global invasive potential of European plants with climate change. *PLoS ONE* 3:e2441.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Power, C., A. Simms, and R. White. 2001. Hierarchical fuzzy pattern matching for the regional comparison of land use maps. *International Journal of Geographical Information Science* 15:77-100.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.
- Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2:1-10.
- Soberón, J., and A. T. Peterson. 2009. Monitoring biodiversity loss with primary species-occurrence data: Toward national-level indicators for the 2010 Target of the Convention on Biological Diversity. *AMBIO* 38:29-34.
- Stockwell, D. R. B., and D. P. Peters. 1999. The GARP modelling system: Problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* 13:143-158.
- Svenning, J.-C., and F. Skov. 2004. Limited filling of the potential range in European tree species. *Ecology Letters* 7:565-573.
- Thuiller, W., G. F. Midgely, G. O. Hughes, B. Bomhard, G. Drew, M. C. Rutherford, and F. I. Woodward. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology* 12:759-776.