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ORIGINAL PAPER

Potential loss of genetic variability despite well established network of reserves: the case of the Iberian endemic lizard *Lacerta schreiberi*

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Abstract Although future anthropogenic climate change is recognized as one of the major threats to European species, its implementation during reserve planning has only been started recently. We here describe climate change impacts on the Iberian endemic lizard *Lacerta schreiberi* expecting serious declines and range reductions due to a loss of suitable climate space in the next future. We apply species distribution models to assess possible future changes in the lizard's range, identify areas with high extinction risk meriting conservation efforts and analyze whether the Natura 2000 network in its current stage will offer a sufficient protection for the genetically most valuable lineages. Despite a very good coverage and connectivity of the most valuable populations of *L. schreiberi* with the existing protected sites network, our results predict a strong loss of genetic variability by 2080. Also, two main patterns become evident: While the genetically less diverse north-western populations may be less affected by climate change, the climate change effects on the southern isolates and the genetically most diverse populations within the Central System may be devastating. To improve a successful prospective conservation of *L. schreiberi* the management of protected sites needs to consider the processes that threaten this species. Furthermore, our study highlights the urgent need to consider climate change effects on evolutionary significant units within the Natura 2000 framework.

Keywords *Lacerta schreiberi* · BIOMOD · Climate change · Extinction risk · Iberian Peninsula · Species distribution models

Abbreviations

IPCC	Interngovernmental Panel on Climate Change
SDM	Species distribution model
BIO5	Maximum temperature of the warmest month
BIO6	Minimum temperature of the coldest month

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BIO13	Precipitation of the wettest month
BIO14	Precipitation of the driest month
BIO15	Precipitation seasonality
AUC	Area under the receiver operating characteristic curve
TSS	True skills statistics
ANN	Artificial neural networks
CTA	Classification tree analysis
GAM	Generalized additive models
GBM	Generalized boosting models
GLM	Generalized linear models
MARS	Multivariate adaptive regression splines
MDA	Mixture discriminant analysis
RF	Random forests
SRE	Surface range envelopes

Introduction

Along habitat loss, fragmentation and degradation, anthropogenic climate change will pose a significant threat to global biodiversity (e.g. Stuart et al. 2004; Thomas et al. 2004; Thuiller et al. 2005). A number of recent studies have documented direct and indirect effects of anthropogenic climate change on species. These may range from changes in the phenology of individuals to alterations in entire population demographies (Parmesan and Yohe 2003; Chamaillé-Jammes et al. 2006; Parmesan 2006) affecting species' geographic distributions (Tingley and Beissinger 2009) leading even to extinctions (Thomas et al. 2004). However, species are not equally threatened by anthropogenic climate change as endemic species with a narrow ecological niche breadth and a restricted distribution are particularly at high risk (Malcom et al. 2006; Schwartz et al. 2006; Ohlemüller et al. 2008). It has been shown that climate change affects also the effectivity of global reserve networks (Heller and Zavaleta 2009).

Within Europe, the Natura 2000 network is the heart piece of EU nature and biodiversity policy and comprises a network of Special Areas of Conservation established under the 1992 Habitat Directive 92/43/EEC and Special Protection Areas as defined by the 1979 Birds Directive 79/409/EEC. One central goal of Natura 2000 is the fulfilment of a political commitment to halt biodiversity loss within all EU member states by 2010, with biodiversity comprising species diversity, genetic variations within species, and ecosystems as whole. Several decrees of species and habitat prioritization were defined to meet these goals. For example, for species listed in Annex II of the Habitat Directive, the establishment of protected areas is required, whereas species listed in Annex IV need a strict protection within the whole territory of the member states. Traditionally, reserve networks where planned for species and ecosystem conservation, while species' genetic structure has only recently been suggested as prioritization measure (Crandall et al. 2000; Newbold and Siikamäki 2009).

Climate change scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) indicate that within the next century summer temperatures may rise and annual rainfall may decrease markedly within Europe (IPCC 2007). Lower precipitation in spring and summer in association with higher evapotranspiration could lead to reduced soil moisture during summer months in Central Europe and the Mediterranean area (Wang 2005; Araújo et al. 2006). Today, many parts of the Iberian Peninsula are already affected by hydrological stress (Araújo et al. 2006), which may be amplified in the next future reducing the mean annual runoffs of streams (Arnell 1999). Unfortunately, although recognized as being one of the major threats to European species (Thuiller et al. 2005; Araújo et al. 2006; Habel et al. 2010), future anthropogenic climate change has only recently been implemented during reserve planning (Araújo et al. 2004; Hannah et al. 2007; Vos et al. 2008) but was not considered in the initial stages of Natura 2000 (Araújo et al. 2007; Hannah et al. 2007). Recent efforts have identified the most critically affected regions (i.e. arctic and mountain habitats, coastal wetlands and Mediterranean regions) and focus on an improvement of the coherency of Natura 2000 sites to allow unhampered species migrations. These shall facilitate possible range shifts of species as a response to climate change as predicted by several authors (e.g. Araújo et al. 2006; Thuiller et al. 2006; Levinsky et al. 2007). However, these efforts are still at the very beginning, since detailed predictions how species may respond to climate change based on a mechanistic understanding of the underlying factors and processes are difficult to develop for the vast majority of species due to limited data availability (Kearney and Porter 2004; Kearney et al. 2008; Rödder et al. 2009). On the other hand, statistical species distribution models (SDMs) are easier to compute but may show contradictory predictions (Pearson et al. 2006; Araújo and New 2007; Rödder and Lötters 2009; Rödder et al. 2009; Thuiller et al. 2009).

Within Europe, the Iberian Peninsula has been recognized as one of the regions most affected by climate change (Araújo et al. 2006; Levinsky et al. 2007) being at the same time the major western refuge for species during Pleistocene glaciations from which large areas have been recolonized (Hewitt 2000), but also as a place of speciation and endemism (Bilton et al. 1998). With a significant number of 65 reptile species native to Spain and 30 species native to Portugal the Iberian Peninsula represents the most important centre of reptile diversity in Europe and is characterized by the highest endemic reptile species richness in Europe (Cox and Temple 2009). Unfortunately, in comparison to endotherms (birds and mammals) as well as insects, reptiles have been rather neglected in studies about climate change effects on distribution patterns (but see Araújo et al. 2006). Nevertheless, reptile species do have a high conservation priority (Gibbon et al. 2000; Araújo et al. 2006; Beebee et al. 2009) and it has been shown that climate change is an increasingly serious threat (Araújo et al. 2006). An effective protection of its unique biodiversity is therefore most warranted (Araújo et al. 2007).

We here focus on Schreiber's green lizard (*Lacerta schreiberi* Bedriaga, 1878), a lacertid lizard endemic to the Iberian Peninsula (Fig. 1; Brito et al. 1996). The species shows a well pronounced genetic differentiation within its range and several evolutionary significant units have been identified (Paulo et al. 2001, 2002, Godinho et al. 2008). In the wake of climate warming, we hypothesize that this endemic will experience serious declines and range reductions especially in its southern isolated populations due to a loss of suitable climate space. Schreiber's green lizard is listed in the annexes II and IV of the Habitats Directive of the European Community (94/43/EEC) with special emphasis on vulnerable southern isolated populations. Therefore, we see an urgent need to identify areas with high risk of extinction and to select priority areas for a prospective protection and management of habitats. To evaluate regions which are supposed to be the most vulnerable we computed SDMs with an ensemble forecasting approach as suggested by Araújo and New (2007). Such SDMs are good tools to assess the distribution of endangered and endemic species under current, past, and future climatic conditions on a regional scale by inferring a species' environmental requirements from localities where it is currently

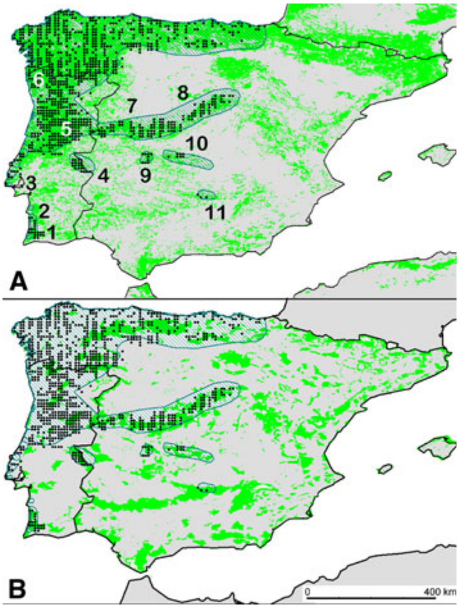

Fig. 1 Coverage of the current distribution of *L. schreiberi* with suitable habitats (**a**, *green areas* representing tree cover) and the Natura 2000 reserve network (**b**, *green areas*) in Portugal and Spain according to the EU habitat directive. Note that the genetically highly diverse populations within the Central System and the southern isolated populations are well covered with suitable habitats integrated in the Natura 2000 network. Species records are indicated as *black dots* and the species' spatial distribution according to www.redlist.org in *red*. Consecutive numbers in a according to mountains: *1* Monchique, *2* Cercal, *3* Sintra, *4* S. Mamede, *5* Estrela (the city Malcata is about 70 km eastward situated), *6* Arga, *7* Gredos, *8* Guadarrama, *9* Guadalupe, *10* Toledo, *11* San Andrés. (Color figure online)

distributed (Guisan and Zimmermann 2000; Jeschke and Strayer 2008; Contreras et al. 2009; Rödder and Dambach 2010). Furthermore, these models can help to prioritize conservation planning by identifying potential range losses and gains (Wang 2005). The aims of this study are (1) to identify possible future changes in the lizard's range in order to identify areas with high extinction risk meriting conservation efforts and (2) to analyze whether the Natura 2000 network in its current stage will offer a sufficient protection.

Materials and methods

Study species

Schreiber's green lizard (*Lacerta schreiberi* Bedriaga, 1878) is a medium sized lacertid lizard (adult snout–vent length: 117–120 mm) endemic to the Iberian Peninsula. Its present-day distribution centre is located in the north-western part of the peninsula (Galicia, northern and central Portugal) and radiates along a series of mountain ranges that cross the peninsula from west to east, the Iberian Central System (Estrela–Gredos–Guadarrama) of Spain. The species also occurs in isolated, scattered, mainly montane populations in the south of Portugal (Monchique, Cercal and Sintra mountains) and Spain (Guadalupe, Toledo and further southeast in the San Andrés mountains) (Brito et al. 1998).

In its continuous north-western distribution range within the Atlantic climatic corridor, the species inhabits coastal zones and deciduous forests or humid mountain habitats. However, it shows a narrow ecological range within the Mediterranean climate with a strong preference for riparian habitats in the southern and central parts of its range. These patterns indicate that *L. schreiberi* has a narrow ecological range, resulting in small and fragmented populations in its southern distributional range (Brito et al. 1999a, b), which suggests that the species had a wider distribution, when the climate was colder and wetter (Paulo et al. 2001).

Detailed genetic analyses of Schreiber's green lizard indicate that populations of the Iberian Central System exhibit the highest genetic variability, whereas a decreased variability could be observed in its north-western distribution centre and in population isolates in the south (Paulo et al. 2001, 2002; Godinho et al. 2008). The steep topography of this region, which has apparently served as glacial refuge in the Portuguese and Spanish parts of the mountain system, allowed these separated populations to persist climatic fluctuations in warm interior river valleys or migration to higher altitudes (Paulo et al. 2001, 2002; Godinho et al. 2008). Therefore, the Iberian Central System has been considered as the core area of the species distribution. An analysis based on a combination of mtDNA and nuclear DNA data revealed multiple admixtures of these two population groups and extensive gene flow along a west–east gradient of the mountain system. Furthermore, the data indicated that an old population expansion southwards was followed by episodes of contraction and more recently by a postglacial expansion to the north-western of the Peninsula, which shaped the present-day distribution of Schreiber‘s green lizard (Godinho et al. 2008). Accurate distributional data and information about habitat requirements as well as detailed genetic data of this species identify *L. schreiberi* as a convenient candidate for modelling reliable regional future distribution patterns under consideration of conservation management for this species (Brito et al. 1999a; Godinho et al. 2003; Godinho et al. 2008; Stuart-Fox et al. 2009).

Study area and species records

As *Lacerta schreiberi* is endemic to the Iberian Peninsula, our study area covered 8977 grid cells with a resolution of 5 arc min between −9.4583° to 0.6250°E and 36.1250°–44.4583°N. Within this area, a total number of 943 species records covering the whole currently known range of *L. schreiberi* were compiled from various sources. These included scientific publications (Brito et al. 1996; Brito et al. 1998; Godinho et al. 1999) and online databases [Global Biodiversity Information Facility (GBIF; www.gbif.org); HerpNET (www.herpnet.org)].

Climate, Natura 2000 and landcover data

For current conditions, we obtained monthly temperature and precipitation data with spatial resolutions of 2.5 and 5 arc min from the WorldClim database (www.worldclim.org; Hijmans et al. 2005a). These monthly values were interpolated from observed climate data between 1950 and 2000 at weather stations using a thin-plate smoothing spline with altitude, longitude and latitude as independent variables (Hijmans et al. 2005a). Based on these monthly values, 19 so called bioclim variables (Busby 1991; Beaumont et al. 2005) were computed with DIVA-GIS 7.1.6 (www.diva-gis.org; Hijmans et al. 2005b). Multicolinearity of predictor variables may hamper the transferability of SDMs through space and time (Heikkinen et al. 2006). To reduce multicolinearity, we extracted all 19 bioclimate variables at each species record and computed pair-wise Pearson correlation coefficients. Subsequently, we selected a final set of predictor variables comprising the ‘minimum temperature of the coldest month’ (BIO6), the ‘maximum temperature of the warmest month’ (BIO5), the ‘precipitation of the wettest month’ (BIO13), the ‘precipitation in the driest month’ (BIO14) and ‘precipitation seasonality’ (BIO15) with $r^2 < 0.75$. These variables describe environmental conditions being physiologically important for *L. schreiberi*, what may significantly enhance the reliability of SDM predictions (Rödder et al. 2009).

For future climate scenarios, we downloaded interpolations of eight different climate change predictions of the third and fourth assessment of the IPCC (2007) for the year 2080 with a spatial resolution of 2.5 arc min (available through http://gisweb.ciat.cgiar.org/GCMPage; Ramirez and Jarvis 2008). These climate change scenarios are derived from simulations of four climate models (CCCma-CGCM2 (Flato et al. 2000; Flato and Boer 2001), CSIRO-MK2 (Gordon and O′Farrell 1997), NIES99 (Emori et al. 1999), and UKMO-HadCM3 (Gordon et al. 2000; Pope et al. 2000)) for the two IPCC story lines A2a and B2a. The A2a story line describes a highly heterogeneous future with regionally oriented economics, wherein a high population growth rate accompanied with an increased energy use, land use changes and slow technological improvements is assumed. The B2a story line also assumes regionally oriented economics, but with a stronger focus on environmental protection and social equity. In contrast to the A2a story line, the B2a story line assumes a lower population growth rate but more diverse technological inventions and slower land use changes.

Information on current land cover with a spatial resolution of 30 arc sec (approximately 900 × 900 m in the study area) was gathered from the Global Land Cover 2000 database (GLC 2000; available from http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php). In order to meet the habitat requirements of *L. schreiberi*, we reclassified the original land cover categories into ‘Tree cover’ (original categories 1–8) and ‘Other’ (original categories 9–22). The latter includes all categories which exhibit strong human impacts and which are deemed to be unsuitable for these pristine habitat species. Areas labelled as ‘Tree cover’ are covered with undisturbed either broadleaved deciduous or evergreen woodland, with crown cover between 15 and 100% and tree height ranges from 3 to >30 m.

Spatial information on the Portuguese and Spanish Natura 2000 sites managed under the EU Habitat Directive was obtained via the homepage of the European Environmental Agency (http://ec.europa.eu/environment/nature/natura2000/db_gis/). In Spain, sites for the Natura 2000 network were selected after a detailed gap analysis for critical habitats and species. However, possible impacts of climate change were not considered (Orella et al. 1998; Araújo et al. 2007).

Species distribution models

SDMs for *L. schreiberi* were computed using bioclim variables with a spatial resolution of 5 arc min and nine different model algorithms implemented in the BIOMOD package (Thuiller 2003; Thuiller et al. 2009) for R (R Develpment Core Team 2008). The model algorithms comprised generalised linear models (GLM, McCullagh and Nelder 1989), generalised additive models (GAM, Hastie and Tibishirani 1990), generalized boosted models (GBM, Ridgeway 1999), multivariate adaptive regression splines (MARS, Friedman 1991), classification tree analysis (CTA, Breiman et al. 1984), mixture discriminant analysis (MDA, Hastie et al. 1994), artificial neural networks (ANN, Ripley 1996), random forests (Breiman 2001) and rectilinear environmental envelopes similar to the BIOCLIM algorithm (SRE, Busby 1991). The general settings for each algorithm were the following:

in GLM analyses, we allowed quadratic terms stepwise ranked by the Akaike Information Criterion (Akaike 1973); in GBM analyses, we use a five-fold cross-validation approach and allowed a maximum number of 3000 trees; in GAMs a smoothing factor of four was used for the spline function (similar to a polynomial of degree three); in CAT, a 50-fold cross-validation was applied to estimate the optimal tree length; in ANN, a three-fold cross-validation was used to determine the best amount of weight decay and the number of hidden layers; finally, in SRE the multirectangular environmental envelope was fitted on 95% of the environmental space occupied.

Model performance was internally tested in BIOMOD via a two-fold data splitting approach (80% training/20% test) and the three different indices "area under the receiver operating characteristic curve" (AUC, Hanley and McNeil 1982), Cohen's Kappa (Monserud and Leemans 1992) and the true skill statistic (TSS, Allouche et al. 2006). Additionally, each model′s sensitivity and specificity was measured. Sensitivity is defined as the ratio of positive sites correctly predicted over the total number of positive sites in the sample, while specificity is the ratio of negative sites correctly predicted over the total number of negative sites. Results obtained from all nine methods were compared to derive consensus predictions based on the different results weighted by their predictive performance on test data measured in terms of AUC scores. This approach has recently been suggested to be superior to predictions derived from single models (Marmion et al. 2009). The final ensemble was projected onto environmental layers representing current and possible future conditions with a spatial resolution of 2.5 arc min (see above). Subsequently, future projections assuming the IPCC story lines A2a and B2a were summarized by computing averages per grid cells. SDMs and corresponding ensemble forecasts were performed with BIOMOD package (Thuiller 2003; Thuiller et al. 2009) for R (R Develpment Core Team 2008), whereby the consensus prediction was tested with the AUC and Kappa statistics in DIVA-GIS.

The predictive performance per variable was assessed using a randomisation procedure as implemented in BIOMOD, which is independent of the model technique. It uses a Pearson correlation between the model′s predictions at the fitted values and predictions at sites where the variable under investigation has been randomly permutated. In cases showing a high correlation, the variable permutated is classified as being not important for the model. This procedure is repeated multiple times and the variables in each model are ranked by the average correlation coefficients (Thuiller et al. 2009).

Next to climate affecting a species distribution on a macro scale (Thuiller et al. 2004), land cover information may be important for the spatial distribution of a species on a local scale, i.e. within reserves (Weinsheimer et al. 2010). Therefore, we addressed the availability of suitable microhabitats within the potential distribution of *L. schreiberi* derived from climate data through a subsequent overlay with land cover information (see above).

Results

Model characterization and performance

The predictive ability varied among the nine algorithms applied being best in random forests, artificial neural networks, generalized boosting models and classification tree analyses yielding highest levels in terms of AUC, Kappa and TSS as well as model sensitivity and specificity (Table 1). The variables most frequently considered as being

Table 1 Predictive performance across model techniques and evaluation indices using either 80% of the species records as training data and the remaining records as test data or the full set of records for model training

Index	Algorithm	20% test	Full set	Cutoff	Sensitivity	Specificity
AUC	ANN	0.90	0.91	206.0	85.4	85.4
	CTA	0.86	0.91	90.0	86.9	87.7
	GAM	0.89	0.90	103.7	84.3	84.3
	GBM	0.90	0.91	91.6	85.9	85.9
	GLM	0.88	0.89	107.3	84.2	84.4
	MARS	0.90	0.90	233.0	83.6	83.5
	MDA	0.87	0.87	86.0	80.2	80.2
	RF	0.93	1.00	587.0	100.0	100.0
	SRE	NA	NA	NA	NA	NA
Kappa	ANN	0.51	0.51	520.0	65.4	92.5
	CTA	0.52	0.57	310.0	74.3	92.4
	GAM	0.51	0.51	281.2	65.9	92.3
	GBM	0.52	0.54	183.8	78.5	90.1
	GLM	0.51	0.51	300.0	64.4	92.6
	MARS	0.52	0.51	390.0	65.5	92.5
	MDA	0.48	0.46	480.0	61.6	91.2
	RF	0.56	1.00	520.0	100.0	100.0
	SRE	0.21	0.21	10.0	82.5	64.6
TSS	ANN	0.69	0.71	170.0	88.6	82.9
	CTA	0.69	0.75	100.0	85.9	88.8
	GAM	0.69	0.69	85.1	87.1	81.7
	GBM	0.69	0.72	102.4	85.2	87.2
	GLM	0.68	0.69	90.9	86.7	82.3
	MARS	0.68	0.67	200.0	87.8	79.7
	MDA	0.61	0.62	40.0	87.4	74.2
	RF	0.78	1.00	520.0	100.0	100.0
	SRE	0.45	0.47	10.0	82.5	64.6

20% test values represent AUC, Kappa and TSS averages of models trained with 80% of the species records, where all other metrics were computed using the full data set. Abbreviations for the test statistics are *AUC* area under the receiver operating characteristic curve and *TSS* true skills statistics. Algorithms are abbreviated as *ANN* artificial neural networks, *CTA* classification tree analysis, *GAM* generalized additive models, *GBM* generalized boosting models, *GLM* generalized linear models, *MARS* multivariate adaptive regression splines, *MDA* mixture discriminate analysis, RF random forests, SRE surface range envelopes. Note that SRE does not allow computing AUC values since this model only generates presences and absences but no probabilities of occurrence (Thuiller 2003; Thuiller et al. 2009)

important were ‘precipitation of the wettest month’ followed by ‘precipitation of the driest month’ and ‘maximum temperature of the warmest month’ (Table 2).

According to the classification of Swets (1988) and Monserud and Leemans (1992) for AUC and Kappa statistics, the discrimination ability of our ensemble prediction of *L. schreiberi* on a grid with a resolution of 2.5 arc min was ‘good’ to ‘excellent’ (AUC = 0.907; Kappa = 0.719). Optimizing Kappa, the cut-off value for presence-absence maps based on the ensemble forecast was a prediction of 12.5. Figure 2 shows the

Table 2 Variations in variable importance among modelling techniques

Algorithm	BIO5	BIO6	BIO13	BIO14	BIO15
ANN	0.55	0.05	1.07	0.59	0.47
CTA	0.41	0.15	0.60	0.21	0.29
GAM	0.33	0.02	1.01	0.48	0.28
GBM	0.08	0.04	0.77	0.08	0.12
GLM	0.38	0.03	1.07	0.56	0.47
MARS	0.26	0.00	0.87	0.33	0.28
MDA	0.13	0.00	0.94	0.28	0.21
RF	0.34	0.19	0.45	0.20	0.32
SRE	0.19	0.01	0.27	0.05	0.11

High values reflect a high importance

BIO5 maximum temperature of the warmest month, *BIO6* minimum temperature of the coldest month, *BIO13* precipitation of the wettest month, *BIO14* precipitation of the driest month, *BIO15* precipitation seasonality. For further abbreviations see Table 1

predicted potential distribution of *L. schreiberi* under current and future conditions assuming the IPCC A2a and B2a story lines. Under current conditions, our model describes the lizard′s known distribution, even the southern isolates, very well. Highest predicted suitability is centred in the north-western part of its known range. Combination of the potential distribution with land cover information revealed that all currently known populations occur in areas with high degrees of forest cover (Fig. 1).

Future projections

Our SDM suggest predominately a stable range size of *L. schreiberi* in terms of the number of suitable 2.5 arc min grid cells the future climate change scenario B2a but losses of up to 20% assuming A2a conditions (Table 3). Future predictions for the distribution of *L. schreiberi* within in the western and central parts of the Iberian Central System mountain system (eastwards until Malcata) indicate a nearly complete loss of suitable habitats by 2080. The central and western *L. schreiberi* populations of the Central System, which are the genetically most variable, are at high risk of extinction (Fig. 2). In the next future, the environmental conditions might only be suitable for the populations that are situated west of Malcata (see Fig. 1a). For the populations in southern Iberia (i.e. in San Andrés, Toledo, Guadalupe as well as of Cercal and Monchique) our models indicate nearly a complete loss of environmentally suitable habitats in the future. Furthermore, our results forecast degraded climate suitability in the Sintra and S. Mamede mountains. Beneath the influence of the Atlantic climate within the continuous north-western distribution range of *L. schreiberi* it is likely that it will find suitable climate space in future times.

Coverage with the Natura 2000 network

At present the Natura 2000 network almost completely covers the range of the species in the Central System as well as the southern populations in the Monchique, Cercal and S. Mamede mountains and the isolates in the Guadalupe, Toledo and San Andrés mountains (Fig. 1). In its north-western distribution large parts of the species’ range in the Cantabrian

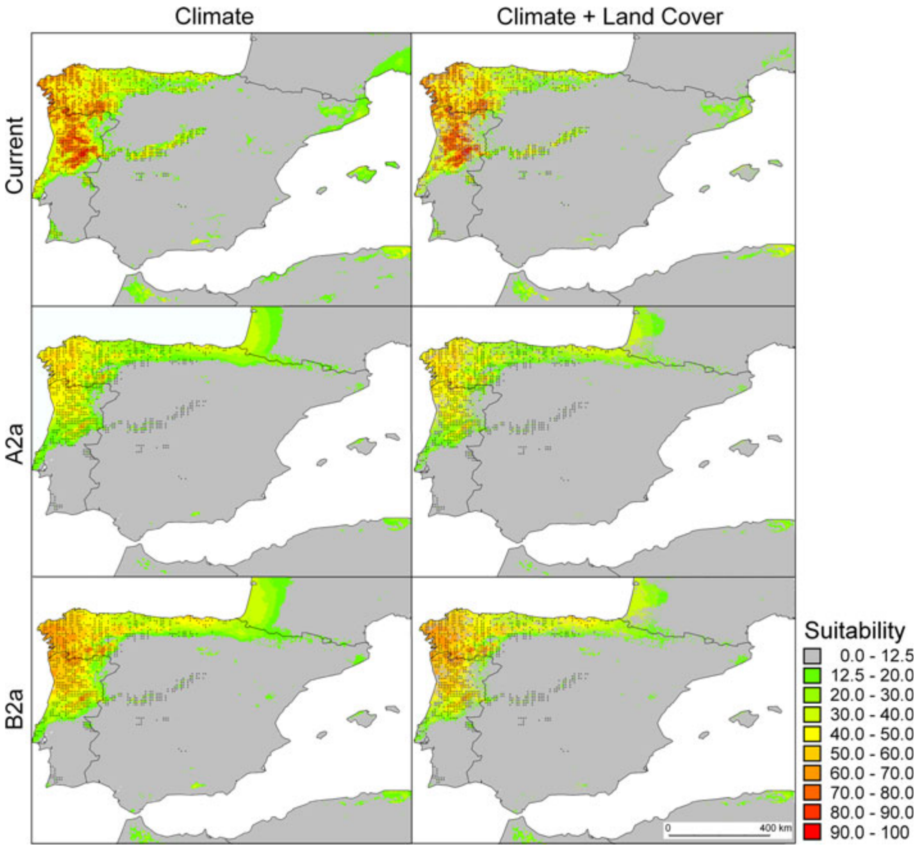

Fig. 2 Potential distribution of *Lacerta schreiberi* under current environmental conditions and projections for 2080 according to two IPCC scenarios (A2a, B2a) derived from either climate only or climate and land use data. Species records used for model building are indicated as *black dots*. (Color figure online)

Table 3 Predicted range gains and losses of *Lacerta schreiberi* in terms of the number of suitable 2.5 arc min grid cells under current and future climate change scenarios A2a and B2a

Potential distribution	Total				Natura 2000 sites only			
Scenario	A2a	A2a (%)	B2a	B2a (%)	A2a	A2a (%)	B2a	B2a (%)
CCCma	7,937	−25.5	10,462	−1.7	1,408	−33.0	2,238	+6.5
CSIRO	10,970	+3.0	10,223	−4.0	2,239	+6.5	1,859	−11.6
HadCM3	9,169	−13.9	13,413	+26.0	1,531	−27.2	2,388	+13.6
NIES99	5,487	−48.5	8,095	−24.0	788	−62.5	1,319	−37.3
Average	8,390.8	−21.2	10,548.3	−0.9	1,491.5	−29.0	1,951.0	−7.2
Current	10,647				2,102			

Values refer to *L. schreiberi*'s total potential distribution and the number of grid cells situated within the Natura 2000 network of protected areas according to the Habitat directive applying climate variables only. Percentages relative to current conditions are given mountains are protected, but the majority of *L. schreiberi*'s range in Galicia is not embedded within the Natura 2000 network, particularly those north of the Arga mountains. In its southern distribution range the populations of the Sintra mountains are also currently not protected. Currently, 19.7% of *L. schreiberi*'s potential distribution is on average situated within the Natura 2000 network of protected areas. Assuming the A2a and B2a climate change scenarios, projected losses comprise on average 7.2–29.0% (Table 3). However, those areas currently harbouring the genetically most diverse populations will be climatically unsuitable in each scenario.

Discussion

Efficacy of existing Nature 2000 network

Our results predict a strong loss of genetic variability by 2080 despite a very good coverage and connectivity of most valuable populations of *L. schreiberi* with the Natura 2000 Network. Additionally two main patterns become evident: While the genetically less diverse north-western populations may be less affected by climate change, the climate change effects on the southern isolates and the genetically most diverse populations within the central range may be devastating. Within the former, a high degree of concordance between the occurrence of *L. schreiberi* and Natura 2000 sites (Portugal: Monchique, Cercal and S. Mamede mountains; Spain: Guadalupe, Toledo and San Andrés mountains) is warranted under current conditions. Among them, as suggested by Brito et al. (1999b), the Cercal, Monchique and S. Mamede mountain populations are those with the highest conservation priority in Portugal. However, despite the well established network of protected sites, effects of climate warming are supposed to be more devastating in the southern and central parts compared to the more humid parts of the peninsula. It appears to be unlikely that the species will find any suitable habitat in the next future. Field studies have shown that suitable habitats for *L. schreiberi* comprise river or stream margins covered with dense vegetation, which are exclusively situated in mountainous cool and humid regions within this area (Brito et al. 1998). Historically, these small and fragmented populations represent relicts of a wider distribution, when the climate was colder and wetter (Paulo et al. 2001). These sites are characterized by lower annual sunlight hours and high precipitation and are considered as "Atlantic islands" in a Mediterranean area (Brito et al. 1998), indicating that the species reaches its ecological potency even under current climate conditions.

Within the Iberian Central System, there is also a high degree of present-day concordance between the current distribution of *L. schreiberi* and Natura 2000 sites. Since populations along this mountain system show high values of heterozygosity and mean number of alleles for proteins, microsatellites and single copy nuclear polymorphisms as well as extensive gene flow across a west–east gradient (Godinho et al. 2008), these populations have to be considered as the genetically most valuable ones. Particularly the central and eastern part of this mountain system is well protected through the Natura 2000 reserve network (Fig. 1). Nevertheless, our future predictions are devastating for the species' range in the eastern and central parts of this mountain system (westwards until Malcata) and indicate a nearly complete loss of suitable habitats by 2080. This outlines that, despite a well established Natura 2000 network, the genetically most variable central and eastern *L. schreiberi* populations of the Central system are at high risk of extinction (Fig. 2). Only for the populations situated west of Malcata environmental conditions may be suitable in the next future. With regard to the genetic structure and the evolutionary history of this species, the preservation of such core populations should have high conservation priority, e.g. as proposed by Crandall et al. (2000) and Latta (2008).

In contrast to the southern and central populations, the potential distribution of *L. schreiberi* is continuous further northwest and characterized by high suitability scores suggesting limited environmental restrictions. Indeed, it has been shown that the species has a wider ecological potency in this region as it also inhabits marshes in coastal and low altitude zones as well as deciduous forest or humid mountain habitats in a typical Atlantic climate (Brito et al. 1996; Brito et al. 1999b; Paulo et al. 2001). In Portugal, for example, the species is present only in regions with levels of precipitation above 800 mm year^{-1} and is mainly found at the margins of watercourses and humid forests of the English and Pyrenean oak (Brito et al. 1999b). Contrary to the southern populations, the coastal northern and inland northern populations have recently expanded their range with an increasing population size estimated to exceed 1 million individuals (Brito et al. 1999b), which meets the high prediction values of our model very well. Our future predictions for the continuous north-western distribution range of the species are not as devastating as for the populations of the Central System or the southern parts of the peninsula. Beneath the influence of the Atlantic climate it is likely that the species will find suitable climate space in future times.

Management recommendations

Considering the low dispersal capacity of reptiles and the rapid warming in Europe it is difficult to propose some reliable recommendations for the adaptive management of *L. schreiberi* in future times. In general, particularly river banks and their agricultural utilized surroundings should be restored to increase the space of available and suitable habitats for the species. Furthermore, extensive forestation is needed to mitigate the effects of hydrological stress and global warming, especially in central and southern parts of *L. schreiberi*'s range. Afforested corridors can facilitate migrations of individuals between populations and towards higher altitudes and should therefore be established, although different corridor sizes may be required depending on the surrounding landscape (Ficetola et al. 2009). As suggested by previous authors (Brito et al. 1999b), vegetation clear-cutting and enlargement of monoculture plantations (*Eucalyptus* and cork oak) up to the fringe of protected sites should be inhibited. Habitats of *L. schreiberi* within the central and southern distribution range are characterized by a steep topography, which have most likely served as refuges during past climatic fluctuations (Paulo et al. 2001, 2002; Godinho et al. 2008), should have the highest conservation priority. As this lizard has a low dispersal capacity it is crucial to preserve suitable habitats at different altitudes in close proximity and to establish corridors between fragmented populations.

Apart from global warming populations occurring in areas with high human density are threatened by a loss in habitat availability and habitat quality (Brito et al. 1999b; Malkmus 2004). Therefore, we suggest focusing management strategies on populations that occur in areas with reduced human pressure such as in the Cercal and Monchique or the S. Mamede mountains. Furthermore, we follow Brito et al. (1999b) in their claim to include the Monchique and Cercal habitats in the PPA system (Portuguese protected areas) and suggest to strongly enlarge the Natura 2000 sites in Galicia to guarantee a better representation of the species possible future distribution.

To reduce the loss of genetic variability suggested by our model a captive breeding program such as proposed by Brito et al. (1999b) for isolated Portuguese populations should also include populations of the Portuguese and most important of the Spanish parts of the Central system (Gredos and Guadarrama mountains), as they are exposed to a high extinction risk. Additionally, a translocation or reintroduction of individuals of the eastern Central System to depleted populations or unoccupied areas which lay further north-west and show high climate suitability in the future may be considered. However, the latter deserves a thorough assessment of the genetic structure of the most proximate populations in order to avoid possible negative effects.

Our results illustrate that a successful prospective conservation of *L. schreiberi* cannot be achieved by isolating the management of protected sites within the Natura 2000 network from the processes that threaten them. Fortunately, recent advances in spatial modelling techniques allow detailed spatial predictions of critical habitats under current conditions (Mücher et al. 2009), which may also be projected onto climate change scenarios in order to assess potentially suitable areas arising in the next future. Such simulations may provide a suitable basis for preventive habitat conservation. Facing the dynamics of climate change, protected-area networks and, as suggested by several authors (Heller and Zavaleta 2009), European conventions and legislation need to be more flexible in regard to their classification, reclassification and declassification.

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