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Environmental correlates for species richness among amphibians and reptiles in a climate transition area

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Abstract Correlations between environmental factors and the distribution of amphibian and reptile species richness were investigated in a climate transition area, Peneda-Gerês National Park (PNPG), in North-Western Portugal. Using presence-data at a local-scale (1 × 1 km), Ecological-Niche Factor Analysis (ENFA) identified a mixture of climatic (precipitation and number of days with fog), topographical (altitude and relief) and habitat factors (number of watercourses and water surfaces, the type of the largest water surface and tree diversity cover), as accurate predictors of species occurrence. Three factors were common for both taxonomic groups, and consistently presented a positive relation with species occurrence: precipitation, number of water surfaces, and tree diversity cover; suggesting a strong coincidence in the environmental correlates that influence amphibian and reptile species richness. Distribution patterns of observed and predicted species richness were compared using a Geographical Information System. Overall, three high species richness areas were predicted in common for both taxonomic groups and two additional areas for amphibians only. These areas matched with the observed species richness but suggested larger areas of high species richness. The location of the PNPG in a biogeographic crossroad, between Euro-Siberian and Mediterranean provinces, emphasised species richness of amphibians and reptiles and suggests a high priority conservation status for this protected area. Most of Central-Northern Portugal is located in a climatic transition area; therefore, increased species richness should be expected for other areas. Local scale studies for other protected areas should be

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planned as a framework for the development of multi-scale conservation planning by Portuguese authorities.

Keywords Amphibians · Climate transition area · Ecological-Niche Factor Analysis (ENFA) · Environmental factors · Geographical Information Systems · Habitat suitability models · Peneda-Gerês National Park · Portugal · Reptiles · Species richness

Abbreviations

a.s.l.	above sea level
EGV	Ecogeographical variables
ENFA	Ecological-Niche Factor Analysis
PNPG	Peneda-Gerês National Park

UTM Universal Transverse of Mercator

Introduction

One of the main goals of conservation nowadays is the maintenance of biological diversity (Myers et al. 2000). The socio-economic hardship and the increase of human population contribute for eroding biological diversity very rapidly in relation to historical extinction rates (Wilson 1992). For instance, one of the most important biodiversity hotspots in the world, the Mediterranean Basin, exhibits a high percentage of endemic species of several taxonomic groups, but is threatened by habitat loss and by the collapse of the traditional agro-sylvo-pastoral system (Mittermeier et al. 1998; Médail and Quézel 1999). This scenario is worrying from a conservation viewpoint. Therefore, the identification and conservation of specific important areas is urgently needed to reduce the loss of biological diversity at different levels.

Large biogeographic intersections, or biogeographic crossroads, constitute potentially attractive areas for long-term conservation of biodiversity, as they allow conserving evolutionary processes such as speciation and coevolution (Spector 2002). Most importantly, they constitute regions of rapid turnover (or high beta diversity) of species and habitats, leading to exceptionally high levels of species richness and creating the opportunity to meet goals of representativeness and complementarity in protected-areas systems (Araújo et al. 2002). In the north-west of the Iberian Peninsula there is a marked transition between the Euro-Siberian and Mediterranean biogeographic provinces (Rivas-Martínez 1987). Correspondingly, there is a clear transition between the Atlantic Mediterranean and the Continental Mediterranean climates in the series of mountains in the northern border area between Portugal and Spain (Goday 1953). The consequences of this climate transition on the geographical distribution of plants, invertebrates and vertebrates are remarkable, as they allow the co-existence of typical species from southern and northern Iberian Peninsula in a relatively small area, resulting in increased alpha, beta and gamma species richness (Serra and Carvalho 1989; Pimenta and Santarém 1996; Maravalhas 2003; Soares et al. 2005). For instance, the amphibian and reptile communities of North-Western Portugal are noticeably rich, leading to the international recognition of the area as important for the conservation of the herpetofauna (Malkmus 2004; Mateo 2006).

Biogeographical studies on species richness can be considered at various scales. However, they are usually focused on broad scales, using grid sizes of 10×10 km or larger (Araújo 1999; Kier and Barthlott 2001; Rensburg et al. 2002). These scales are usually used for species distribution atlas, to relate species distribution areas with environmental factors, or to analyse biological interactions at regional (Inger and Voris 2001; Luoto et al. 2002), continental (Cumming 2000; Franklin et al. 2000; Kier and Barthlott 2001; Rahbek and Graves 2001) and intercontinental levels (Schall and Pianka 1978). However, relatively little attention has been given to species richness patterns and the underlying environmental factors at smaller scales, namely with grid sizes ranging from 500×500 m to 2×2 km. These scales are more suitable for studying species richness in some taxonomic groups, such as beetles, passerines, or small mammals (Okland et al. 1996; Rensburg et al. 2002; Gallego et al. 2004), and plants (Heikkinen and Neuvonen 1997; Bullock et al. 2000). Additionally, local scales are far more useful for land-use planning and management decisions (Grand et al. 2004).

For conservation purposes, the study of the distribution patterns of species richness in diverse habitats or regions and their ecological determinants are vital steps for understanding the processes that affect the spatial distribution of biological diversity as well as to predict the response of ecosystems to global changes (Stoms and Estes 1993; Peterson et al. 2002). The recent advances in ecological modelling techniques and their combination with Geographical Information Systems have allowed the development of more robust and reliable models, relating biological diversity and environmental factors (Jones et al. 1997). Thus, nowadays, they are fundamental tools for the establishment of conservation strategies and evaluation of management options.

This paper aims to evaluate the effects of climate transition on the distribution of species richness at a local-scale. The Peneda-Gerês National Park, in the North-Western fringe of Portugal, is a privileged area for studying this subject since it is located in an area of transition between two biogeographic provinces. This transition influences particularly the distribution of amphibians and reptiles, since these taxonomic groups are strongly dependent on environmental parameters, and usually exhibit strong associations with climatic factors (Brito et al. 1999; Teixeira et al. 2001). Additionally, the small dispersal capability and relatively small home range size of amphibians and reptiles, in relation with birds and large mammals, emphasises their usefulness for correlating environmental factors with species richness distribution at a local scale. The main objectives of this study were to identify correlations between environmental factors and the distribution of amphibian and reptile species richness, and predict species richness within the study area for these taxonomic groups.

Methods

Study area

The Peneda-Gerês National Park (PNPG) is included in the "Natura 2000" network of European priority conservation areas. It covers an area of about 72,000 ha (latitudes 41° 36′ to 42° 07′ N and longitudes 7° 44′ to 8° 27′ W) along the border with Spain (Fig. 1). The PNPG consists of a series of complex mountains, Peneda, Soajo,

Amarela and Gerês, delimited by deep river valleys, such as Lima, Homem, Gerês, Cávado, and Beredo. The altitude ranges from 50 to 1,500 m a.s.l.. The predominantly Atlantic Mediterranean climate is characterised by high levels of precipitation and drainage, with an average annual rainfall and soil drainage above 2,800 mm/year and 2,000 mm/year, respectively (C.N.A. 1983). In the Continental Mediterranean enclaves, located mostly on the south facing slopes of the mountains and in the low altitude river valleys, average annual rainfall and soil drainage drops to 1,600 mm/ year and 1,100 mm/year, respectively (C.N.A. 1983). Additionally, the diversified orientation of the relief and altitude variations provide a wide variety of microclimates. Correspondingly, deciduous oak-forests (Quercus robur and Q. pyrenaica) and mixed deciduous and coniferous forests occupy most of the Atlantic Mediterranean areas whereas ever-green oak forests (Q. suber) occupy the Continental Mediterranean climatic-influenced areas. Pastures, with small bushes and low arboreous cover occur in the high altitude plateaus (>1000 m), located in the extreme North-Western (Castro Laboreiro) and North-Eastern (Mourela) regions of the study area (Fig. 1).



To determine the distribution of species, fieldwork was carried out from 1998 to 2002 for reptiles and from 2001 to 2003 for amphibians. The collection of data involved 360 man/days fieldwork for amphibians and 420 man/days fieldwork for reptiles, approximately. Amphibian breeding sites were surveyed using dip-netting and egg searching on water vegetation and margins, complemented with night searching for calls. Reptiles were searched using visual encounter surveys. Both taxonomic groups were also searched for in potential shelters, such as rocks and fallen logs. Published data (Malkmus 1986a, 1986b, 2004) and ad-hoc observations (road-kills and live specimens) collected by the authors and National Park staff were also recorded.

The geographic location of the amphibians and reptiles was inscribed in a georeferenced database, using the UTM 1×1 km squares as reference grid (n = 814 squares) (Fig. 2). A total of 490 UTM squares were sampled, representing 60.2% of the study area. The sampling was designed in order to cover the diversity of habitats, climates, and topographical conditions available in the study area. A total of 13 amphibian and 20 reptile species were identified in the study area (Soares et al. 2005) (Table 1). In this study, species density, i.e. the number of species per 1×1 km UTM square, was used as a measure of species richness.

Information on 18 ecogeographical variables (hereafter EGV) describing each $1 \times 1 \text{ km}$ UTM square of the study area were gathered for the analyses (Table 2). Four of the EGVs (ROCK, AGRI, WPAS, SHRU) were collected during the fieldwork, and the remaining 14 EGVs were derived from governmental data bases and military cartography.

Data analyses

Geographical Information Systems and ecological modelling techniques are increasingly being used to model wildlife distributions, to identify suitable habitats and to predict species potential distribution (e.g. Austin et al. 1996; Corsi et al. 1999; Teixeira et al. 2001; Nally and Fleishman 2003). The majority of these methods are based on presence-absence species' data sets, and they make the intuitive assumption that the presence of a species is an indicator of suitable habitat and its absence an indicator of unsuitable habitat (Hirzel et al. 2004a). In this study, reliable absence data was not available for certain species. For instance, some species were scarce (e.g. Hyla arbo*rea*), others had secretive habits (e.g. the fossorial *Blanus cinereus*), and others had relatively short activity periods (e.g. Vipera secanei) which affected their detectability. Therefore, Ecological-Niche Factor Analysis (hereafter ENFA), a modelling technique that only employs presence data, (Hirzel et al. 2004b), was used to identify the correlations between EGVs and distribution patterns of species richness and determine habitat suitability areas. ENFA has been used to determine habitat suitability areas for several taxonomic groups, such as birds (Brotons et al. 2004), mammals (Dettki et al. 2003), insects (Gallego et al. 2004) and plants (Zaniewski et al. 2002).

The ENFA principle is to compare the distributions of the EGVs between the presence data set and the whole study area. The ENFA summarises several EGVs into a few uncorrelated factors retaining most of the information. Therefore, this type of analysis quantifies the niche occupied by a species comparing its distribution in the ecological space ("the species distribution") with the distribution of all squares ("the global distribution") (Hirzel et al. 2002).



Fig. 2 Patterns of species richness distribution (number of species per 1×1 km UTM square represented by grey scale) in the Peneda-Gerês National Park: observed richness for amphibians (A) and reptiles (C) and predicted richness for amphibians (B) and reptiles (D). The value 0 corresponds to squares not surveyed. Predicted species richness was computed by Ecological-Niche Factor Analysis (ENFA). The rare and introduced amphibians (n = 4) and reptiles (n = 5) which were not analysed by ENFA are absent from the observed species richness maps to allow a direct comparison between maps (see Methods section for details)

The outputs of the ENFA include factor scores and eigenvalues. The first factor, called Marginality, is defined as the standardised difference between the species mean and the global mean on all descriptors, i.e., it describes the direction in which the species niche differs at most from the available conditions in the study area (Hirzel et al. 2002). The coefficients of the scores matrix related to the marginality factor indicate the correlation between each EGV and the factor. The marginality coefficients range from -1.0 to +1.0 and positive values mean that the species "prefers" the high values of this EGV, while negative values mean that species "prefers" the low values (Hirzel et al. 2002).

Amphibian species	NUTM	Reptile species	NUTM
Chioglossa lusitanica*	106	Emys orbicularis**	1
Salamandra salamandra	217	Mauremys leprosa**	3
Triturus boscai*	212	Blanus cinereus*	1
Triturus helveticus	10	Anguis fragilis	70
Triturus marmoratus	136	Chalcides bedriagai*	2
Alytes obstetricans	173	Chalcides striatus	75
Discoglossus galganoi*	6	Tarentola mauritanica**	3
Pelobates cultripes	4	Lacerta lepida	289
Hyla arborea	6	Lacerta schreiberi*	354
Bufo bufo	183	Podarcis bocagei*	307
Bufo calamita	71	Podarcis hispanica	162
Rana iberica*	272	Psammodromus algirus	150
Rana perezi	124	Elaphe scalaris	29
*		Coronella austriaca	54
		Coronella girondica	65
		Malpolon monspessulanus	86
		Natrix maura	121
		Natrix natrix	147
		Vipera latastei	85
		Vipera seoanei*	35

Table 1 Taxonomic list of amphibians and reptiles occurring in the Peneda-Gerês National Park. NUTM - Number of 1×1 km UTM squares with observed presence

*Endemic species to the Iberian Peninsula. **Introduced species in the study area and excluded from the analyses (Soares et al. 2005).

Category	Variable	Description (units)	Code
Topographical	Altitude	Average altitude a.s.l.(m)	ALTI
	Relief	Number of 50 m altitude isolines that intersect the square	RELI
	Orientation	0; 1–S, SW, SE; 2–E; 3–W; 4–N, NE, NW	ORIE
Climatic	Precipitation	Average annual total precipitation (mm/year)	PREC
	Insolation	Average annual insolation (h/year)	INSO
	Fog	Average annual number fog days (days/year)	FOG
Aquatic	Lotic systems	Number of watercourses	NWAT
ĥabitat	Largest watercourse	Width: 1-≤1.5 m; 2- [1.5–4 m]; 3- [4–8 m]; 4-≥8 m	LWAT
	Lentic systems	Number of water surfaces	NWSU
	Largest water surface	1- quarry; 2- spring or tank; 3- wells; 4-pond; 5- water dam	LWSU
Terrestrial	Soil type*	1- sand or clay; 2-xist; 3- granite	SOIL
habitat	Stone wall*	Available amount of stone walls (m)	STON
	Rock outcrops	Area occupied by rock outcrops (%)	ROCK
	Agriculture areas*	Area occupied by agriculture fields (%)	AGRI
	Wet pasture*	Area occupied by wet herbaceous cropland (%)	WPAS
	Shrubs	Area occupied by shrubs (%)	SHRU
	Shrubs diversity	Inverse of Simpson's Index for diversity of shrubs	DSHR
	Tree diversity	Inverse of Simpson's Index for diversity of trees	DTRE

Table 2 Ecogeographical variables (EGVs) used to characterize the $814 1 \times 1$ km UTM squares of the Peneda-Gerês National Park and to derive habitat suitability models

*EGVs excluded for the Ecological-Niche Factor Analysis because they were nearly-Boolean (see Data analyses section for details)

ENFA was developed using Biomapper 3.0 (Hirzel et al. 2004b), and followed the procedures outlined by Hirzel et al. (2002). EGVs were previously tested for linear association using the Pearson's correlation coefficient (two-tailed) with the SPSS software (LEAD Technologies 2003). The database with the observations of the species and the EGVs were converted into Idrisi-formatted maps. EGVs were checked for variability, and four variables (SOIL, STON, AGRI, WPAS) were removed as they were nearly-boolean, i.e. they presented almost no variability (Table 2). Then, EGVs were normalised using the Box-Cox algorithm, and factor scores were computed using a factor analysis.

Ecological models were not developed for three reptiles (*Emys orbicularis*, *Mauremys leprosa*, and *Tarentola mauritanica*) as they were most likely introduced in the study area (Soares et al. 2005), thus not suitable for modelling species richness.

In four amphibians (*Triturus helveticus*, *Discoglossus galganoi*, *Pelobates cultripes*, and *Hyla arborea*) and two reptiles (*Chalcides bedriagai* and *Blanus cinereus*) the models produced presented extremely large eigenvalues, precluding the use of ENFA as a modelling technique. These species were scarce in the study area and were detected in less than 10 UTM squares, each (Table 1). In these cases, small sample size can affect the model computation, since there should never be more EGVs than species records (Hirzel et al. 2004b). Despite several efforts made to produce the models for these scarce species, namely by using fewer variables, no habitat suitability models could be produced. Therefore, habitat suitability models were derived for 70 and 88% of the amphibian and reptile species, respectively.

Predicted species richness

Habitat suitability maps for each species were derived using ENFA with the distance geometric mean algorithm, following Brotons et al. (2004) and Hirzel and Arlettaz (2003). This algorithm makes no assumption on the shape of the species distribution, and takes into account the density of observation points in environmental space by computing the geometric mean to all observation points. The habitat suitability maps were presented in the form of a grid in which each square has a value ranging from 0 to 100, corresponding to no suitability and high habitat suitability, respectively. For the reasons outlined in the previous section, habitat suitability maps were not derived for the scarcer species.

The individual habitat suitability maps were then overlaid, by taxonomic group, in Idrisi for Windows (Clark Labs 2003), and the result was a habitat suitability map for species richness of amphibians and reptiles (Cumming 2000; Gioia and Piggott 2000) Subsequently, a likelihood grid was defined for each species by adopting a cut-off point at the likelihood value corresponding to the fifty percentile. This value was defined arbitrarily based on visual assessment of the models, taking into account the expectations regarding the field experience. The outcome is a map with the predicted distribution of species richness for each taxonomic group.

To evaluate the accuracy of the predicted species richness models, a cross-tabulation between observed and predicted values for amphibian and reptile species richness was performed with a confusion matrix, using Idrisi for Windows. Each column of the matrix represented the predicted species richness and each row represented the observed species richness. The number of squares within each class of observed species richness was compared against the number of squares of each class of predicted species richness. In this study, 10 and 16 classes of predicted and of observed species richness for amphibians and reptiles, respectively, were used.

Results

Environmental correlates for species richness

The ecogeographical variables (EGVs) that are mostly correlated with the occurrence of amphibian and reptile species according to the first factor (Marginality) included topographic, climatic and habitat characteristics (Tables 3 and 4).

For amphibians, precipitation, number of watercourse and surfaces, and tree diversity cover, were consistently positively correlated with species occurrence, whereas number of days with fog was negatively related (Table 3). For reptiles, precipitation, largest watercourse, number and largest water surfaces, and tree diversity cover, were consistently positively correlated with species occurrence, whereas insolation and area occupied by shrub were negatively related (Table 4).

Three EGVs related with species occurrence were common for both taxonomic groups, and consistently presented a positive relation with species occurrence: precipitation, number of water surfaces, and tree diversity cover; suggesting a strong coincidence in the environmental correlates that influence amphibian and reptile species richness (Tables 3 and 4).

Predicted species richness

The distribution of the observed amphibian species richness showed one large area, Gerês-Homem river valleys and Albergaria forest, and four smaller sites of high richness (1) transition area between Peneda mountain and Castro Laboreiro plateau (2) Ramiscal river valley (3) Lamalonga bogs, and (4) Covelães pit bogs and Beredo river valley (Fig. 2A, see Fig. 1 for toponomy). The distribution of the predicted amphibian species richness identified five large areas of high richness, which generally correspond to the areas where higher species richness was observed (Fig. 2B). However, Ecological-Niche Factor Analysis (ENFA) suggested an area of high species richness, Amarela mountain, that was not observed in the fieldwork and failed to identify an area, Covelães pit bogs, in which it was observed high species richness.

The distribution of the observed reptile species richness identified one large and continuous area, located in the Homem-Gerês river valleys and Albergaria forest (Fig. 2C). Two smaller areas of high species richness were also identified in the transition area between Peneda mountain and Castro Laboreiro plateau, and Covelães pit bogs and Beredo river valley. The distribution of the predicted reptile species richness identified five large areas of high richness, which correspond to the areas where generally higher number of species was observed (Fig. 2D). Two areas of high species richness, Ramiscal river valley and Amarela mountain, were not detected in the fieldwork but were also suggested by ENFA.

The high species richness areas predicted by ENFA were spatially common to amphibian and reptile species (Figs. 2B and 2D). The cross-tabulation of predicted against observed amphibian and reptile species richness showed a total of 12 and 6%

	ALTI	RELI	ORIE	PREC	OSNI	FOG	NWAT	LWAT	NWSU	TWSU	ROCK	SHRU	DSHR	DTRE
A. obstetricans B. bufo B. calamita C. lusitanica R. iberica R. perezi S. salamandra T. boscai T. marmoratus %	$\begin{array}{c} 0.078 \\ -0.437* \\ 0.437* \\ 0.375* \\ 0.308* \\ -0.023 \\ 0.045 \\ 0.107 \\ 0.168 \\ 0.168 \end{array}$	$\begin{array}{c} -0.190\\ 0.020\\ -0.374*\\ 0.446*\\ -0.051\\ -0.58*\\ 0.140\\ 0.140\\ -0.469*\\ 44.4\end{array}$	-0.074 0.005 0.001 -0.106 -0.1186 0.022 -0.126 -0.126 -0.126 0.022 -0.141 0	0.534* -0.092 -0.036 0.229 0.711* 0.711* 0.378 0.430* 0.295* 44.4	-0.161 -0.028 -0.207 -0.135 -0.136 *0.161 -0.161 -0.161 -0.174 -0.062	$\begin{array}{c} -0.333 \\ -0.343 \\ 0.039 \\ -0.418 \\ -0.258 \\ 0.192 \\ 0.407 \\ -0.421 \\ -0.247 \\ 44.4 \end{array}$	0.638* 0.012 -0.301 0.295 0.347* 0.347* 0.347* 0.432* 0.451* 0.279	-0.089 -0.372* -0.372* 0.239 0.032 0.103 0.103 0.055 0.068 11.1	-0.012 0.385* 0.385* 0.317 0.236 0.145 0.284* 0.284* 0.395* 0.422* 0.565* 55.5	0.070 0.385* -0.369* 0.080 -0.092 0.447* 0.447* 0.028 0.028 0.028 0.333*	0.258* -0.181 -0.149 -0.005 -0.366* 0.131 -0.078 22.2	0.149 -0.328 -0.328 -0.231 -0.131 -0.131 -0.131 -0.131 -0.131 -0.131 0.037	$\begin{array}{c} -0.073 \\ -0.076 \\ -0.093 \\ 0.030 \\ 0.078 \\ 0.09 \\ 0.044 \\ 0.044 \end{array}$	$\begin{array}{c} 0.129\\ 0.452 *\\ 0.092\\ 0.317 *\\ 0.317 *\\ 0.100\\ 0.063\\ 0.455 *\\ 0.224\\ 0.215\end{array}$
*First four most individual specie	explainin s	g EGVs fc	or each sț	secies mod	lel. % Per	centage of	occurrence	e of each]	EGV as in	iportant ex	cplaining f	actors of	the distrib	ution of

ogical-Niche Factor Analysis for individual	
obtained by the Ecole	
factor (Marginality)	
scores of the first f	
bles (EGVs) and	
Ecogeographical varia	ı species
Table 3	amphibia

Table 4 Ecogeograph species	ohical vari	iables (EG	Vs) and s	cores of th	e first fac	tor (Margi	nality) ob	tained by	the Ecolog	gical-Niche	e Factor A	malysis fo	r individu	al reptile
	ALTI	RELI	ORIE	PREC	OSNI	FOG	NWAT	LWAT	NWSU	LWSU	ROCK	SHRU	DSHR	DTRE
A. fragilis	-0.101	0.190	-0.077	0.242	-0.117	-0.115	0.079	0.591*	0.383*	0.204	-0.093	-0.416*	-0.206	0.307*
C. austriaca	0.500*	-0.078	-0.136	0.577*	-0.509*	0.262*	-0.127	-0.001	-0.110	-0.005	0.123	0.051	0.020	-0.134
C. girondica	0.002	0.174	-0.053	0.487*	0.013	-0.029	0.013	0.443*	0.461*	0.317	0.209	-0.091	-0.363*	0.190
C. striatus	0.531*	-0.534*	-0.125	0.210	-0.217	-0.038	-0.292*	0.071	0.135	0.105	-0.203	-0.145	-0.371^{*}	-0.073
E. scalaris	-0.468*	0.202	0.142	-0.172	0.107	-0.257	0.259	0.082	0.414*	0.249	-0.208	-0.310*	0.019	0.407*
L. schreiberi	0.106	-0.343*	-0.317	0.284	-0.018	-0.036	0.378*	0.222	0.420*	0.389*	-0.074	-0.250	-0.091	0.303
L. lepida	-0.313*	0.076	-0.050	0.014	0.039	-0.213	0.230	0.292	0.444*	0.340	-0.097	-0.403*	0.013	0.472*
M. monspessulanus	-0.392*	0.177	0.008	0.016	0.013	-0.460*	0.116	0.179	0.409	0.350*	-0.080	-0.219	0.056	0.459*
N. maura	-0.331^{*}	0.067	-0.048	0.082	-0.075	-0.304	0.009	0.390*	0.453*	0.467*	-0.098	-0.312	-0.036	0.308
N. natrix	0.097	0.072	-0.238	0.432*	-0.430*	-0.198	0.028	0.237	0.282*	0.259	-0.199	-0.260	-0.187	0.414*
P. algirus	-0.486*	0.196	-0.026	-0.029	0.092	-0.392*	0.341^{*}	0.216	0.315	0.228	-0.065	-0.244	0.009	0.430*
P. bocagei	0.469*	-0.358*	-0.426*	0.426^{*}	-0.288	0.260	0.075	0.147	0.236	0.165	-0.026	-0.034	-0.016	0.164
P. hispanica	-0.243	0.150	-0.103	0.205	0.185	-0.302*	0.574^{*}	0.136	0.138	0.344*	0.293	-0.187	-0.028	0.366^{*}
V. latastei	-0.028	0.375^{*}	-0.100	0.580*	-0.402*	-0.437*	0.064	0.067	0.061	0.068	0.240	-0.097	-0.251	0.111
V. seoanei	0.282	-0.448*	-0.057	-0.394^{*}	0.287	0.316^{*}	-0.142	0.033	0.303	0.131	-0.425*	-0.203	-0.120	-0.113
%	53.3	33.3	9.9	40.0	20.0	40.0	26.6	20.0	53.3	20.0	9.9	20.0	13.3	46.6
* First four most ex individual species	plaining I	EGVs for	each speci	es model.	% Percei	ntage of o	ccurrence	of each E	GV as im	iportant ex	cplaining	factors of	the distrib	oution of

correct classification rate, respectively, indicating a low correspondence between squares with equal observed and predicted richness, and suggesting that observed species richness was largely underestimated.

Discussion

This study showed that a mixture of environmental factors is the best predictor of amphibian and reptile species occurrence at a local scale, in the Peneda-Gerês National Park. These factors included (1) habitat variables, such as the number of watercourses and water surfaces, the type of the largest water surface and tree diversity cover (2) topographical variables, such as altitude and relief; and (3) climatic variables, such as precipitation and number of days with fog.

Environmental factors, such as altitude, relief or precipitation, are widely known to influence ecological processes in organisms (e.g. Brown and Lomolino 1998). Several other studies, modelling the distribution of amphibians and reptiles, and herpetofauna species richness, have identified these factors as significant for explaining the observed distribution patterns (Brito et al. 1996; Sequeira et al. 2001; Teixeira et al. 2001; Morales et al. 2002; Guisan and Hofer 2003).

The environmental factors related with water availability exhibited the highest percentages of occurrence among the ecogeographical variables (EGVs) that explained the distribution of individual species. Climatic factors, such as precipitation, presented positive coefficients for all amphibians, whereas reptiles presented positive or negative coefficients, according to the biogeographic traits of species. Reptiles typical from the Euro-Siberian biogeographic province had positive coefficients, e.g. *Coronella austriaca*, whereas characteristic species from the Mediterranean biogeographic province had negative coefficients, e.g. *Psammodromus algirus*. Habitat factors, such as the number of watercourses and water surfaces, also presented positive coefficients for most species. Interestingly, the number of water surfaces was the most frequent explanatory EGV for the distribution of both taxonomic groups.

Topographical variables, such as altitude and relief, were also identified as very important factors explaining the distribution of the species, particularly for the reptiles. For instance, altitude presented positive or negative coefficients according to the biogeographic traits of species. Typical Euro-Siberian species presented positive coefficients, e.g. *Vipera seoanei*, whereas typical Mediterranean species had negative coefficients, e.g. *Elaphe scalaris* and *Malpolon monspessulanus*. Altitude is usually correlated with climatic variables since it is known to influence, for instance precipitation or evapotranspiration (C.N.A. 1983). Relief exhibited negative scores for most of the species belonging to both taxonomic groups, which could be due to a decrease in water availability in the areas of accentuated slope and higher availability of thermoregulation spots offered by the flat areas. However, *Chioglossa lusitanica* and *Vipera latastei* stand as exceptions presenting positive scores in this EGV, the former because it inhabits clear and oxygenated running streams (Sequeira et al. 2001), and the latter because it inhabits rock outcrops with dense bush cover (Brito and Crespo 2002).

Three ecogeographical variables – precipitation, number of water surfaces, and tree diversity cover – were common for both taxonomic groups and consistently

presented a positive relation with species occurrence. Therefore, this association suggested a strong coincidence in the environmental correlates that influence amphibian and reptile species occurrence and ultimately species richness. In fact, high species richness areas for amphibians and reptiles were located in squares with at least one to six water surfaces, at least one to four species of trees, and with precipitation levels between 1,800 and 2,700 mm/year. The high number of water surfaces should be related with water availability which favours the existence of numerous amphibian breeding sites. High levels of tree cover correspond to diversified lowland habitats that account for most of the autochthonous forests and probably offer multiple microhabitats with numerous shelters (e.g. fallen logs) and ample prey availability, thus it could be considered as the ultimate factor for high levels of amphibian and reptile species richness in the study area.

The distribution patterns of observed species richness were quite similar in amphibians and reptiles, and comprised one large area, Gerês-Homem river valleys and Albergaria forest, and two smaller areas: Peneda mountain and Castro Laboreiro plateau, and Covelães pit bogs/Beredo river valley. Two additional smaller areas were identified for the amphibians: the Ramiscal river valley and the Lamalonga bogs. The distribution patterns of predicted species richness were mostly similar for both taxonomic groups and included five large and continuous areas. These areas are mostly located along steep river valleys associated with marked altitudinal changes where a climatic transition occurs. The lower river valleys present a Mediterranean climate, whereas the high river valleys usually present an Atlantic climate. Thus, river valleys act as corridors for Mediterranean and Euro-Siberian species to attain high and low altitude areas, respectively, and allow the sympatric coexistence of biogeographically distinct species. For instance, the Euro-Siberian *C. austriaca* occurs in sympatry with the Mediterranean *E. scalaris* in the Gerês river valley (Soares et al. 2005).

Local scales, such as the 1×1 km squares used in this study, proved to be suitable for studying species richness patterns of amphibians and reptiles. This scale allowed the discrimination of particular river valleys, such as the Gerês and Beredo, with high species richness. Therefore, special attention should be given to riparian habitats and ponds in mountain habitats in future conservation measures and management in the National Park. The 1×1 km scale gives insights for important areas for amphibians and reptiles that would be interesting to assess regarding other taxonomic groups for future conservation planning at local-scale. However, at least three constrains can arise when working at local scales. First, small sample size of species presence can affect model production. Indeed, the scarcer species were excluded from the analysis because the low number of observations precluded model development. This may constitute a serious problem when the target species are exactly the scarcer ones. Models for species with exceptionally low number of observations have been developed using Ecological-Niche Factor Analysis, e.g. for the Iberianrare carnivore *Martes martes* (Alvares and Brito 2006). However, this species restricts habitat selection to an extremely narrow range of habitat conditions, enabling the use of ecological modelling techniques that use presence-only data. However, for rare and/or secretive species but with wide-range and occurring in different ecological conditions, models are extremely difficult to develop (Santos et al. 2006). Second, when dealing with species richness, sub-sampling can strongly affect classification rates. In this study, a high percentage of misclassification arose mainly because the squares with low number of observed species were systematically classified by the model as having high number of species. Thus, ecological modelling suggested that observed species richness was largely underestimated and that more fieldwork would be needed to detected actual species richness in the study area. Lastly, large-scale EGVs may affect the predictive capacity of models. For instance, the amphibians are strongly dependent on the aquatic habitat type apart from the general climatic, topographic and habitat variables usually considered in these types of studies. The inadequate selection of variables can lead to failure in finding consistent correlations between environmental factors and species diversity (Busack and Jaksic 1982). Additionally, increasing the accuracy and resolution of environmental variables allows their use as predictors for studies of several ranges of geographical extents (Guisan and Hofer 2003). Thus, fine-scale EGVs, such as land-cover data from remote sensing, are advisable for species or taxonomic groups with particular biological characteristics.

Nowadays, it is broadly recognised that the identification and conservation of specific important areas is a primordial measure to reduce the loss of biological diversity at different levels. Biogeographic crossroads with increased beta diversity are among the priority areas for conservation worldwide (Spector 2002). The geographic location of Peneda-Gerês National Park in the Iberian Peninsula, and the high number of amphibians and reptiles species present in the area justify its value as an important area for conservation. But, most of Central-Northern Portugal is located in the transition area between the Atlantic Mediterranean and the Continental Mediterranean climates (Rivas-Martínez 1987). Therefore, increased species richness should be expected for other mountain areas, such as Alvão or Estrela mountains. Local scale studies for these protected areas, including also other taxonomic groups, should be planned as a framework for the development of multi-scale conservation planning by Portuguese authorities.

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References

- Alvares F, Brito JC (2006) Habitat requirements and potential areas of occurrence for the Pine Marten in North-western portugal: conservation implications. In: Santos-Reis M, Birks JD, O'Doherty EC, Proulx G (eds), *Martes* in carnivore communities. Alpha Wildlife Publications, Alberta, Canada, *in press*
- Araújo MB (1999) Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. Diversity and Distribution 5:151–163
- Araújo MB, Williams PH, Fuller RJ (2002) Dynamics of extinction and the selection of nature reserves. Proc Roy Soc, Biolog Sci 269:1971–1980
- Austin GE, Thomas CJ, Houston DC, Thompson DB (1996) Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using geographical information systems and remote sensing. J Appl Ecol 33:1541–1550
- Brito JC, Brito e Abreu F, Paulo OS, Rosa HD, Crespo EG (1996) Distribution of Schreiber's green lizard (*Lacerta schreiberi*) in Portugal: a predictive model. Herpetol J 6:43–47

- Brito JC, Crespo EG, Paulo OS (1999) Modelling wildlife distributions: logistic multiple regression vs overlap analysis. Ecography 22:251–260
- Brito JC, Crespo EG (2002) Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the north-western Iberian Peninsula. In: Schuett GW, Höggren M, Douglas ME, Greene HW (eds), Biology of the Vipers. Eagle Mountain Publishing, pp 129–138
- Brotons L, Thuiller W, Araújo MB, Hirzel AH (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27:437–448
- Brown JH, Lomolino MV (1998) Biogeography. Sinauer Associates, MA
- Bullock JM, Edwards RJ, Carey PD, Rose RJ (2000) Geographical separation of two Ulex species at three spatial scales: does competition limit species' range?. Ecography 23:257–271
- Busack SD, Jaksic FM (1982) Ecological correlates of Iberian herpetofaunal diversity: an analysis at regional and local levels. J Biogeogr 9:289–302
- Clark Labs (2003) Idrisi Kilimanjaro vs 14.01. Clark University, Worcester MA
- C.N.A. (1983) Atlas do Ambiente. Comissão Geral do Ambiente, Lisboa
- Corsi F, Duprè E, Boitani L (1999) A large-scale model of wolf distribution in Italy for conservation planning. Conserv Biol 7:150–159
- Cumming GS (2000) Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). J Biogeogr 27:425–440
- Dettki H, Lofstrand R, Edenius L (2003) Modelling habitat suitability for Moose in coastal Northern Sweden: empirical vs process-orientated approaches. Ambio 32:549–556
- Franklin DC, Woinarski JC, Noske RA (2000) Geographical patterning of species richness among granivorous birds in Australia. J Biogeogr 27:829–842
- Gallego D, Cánovas F, Esteve MA, Galián J (2004) Descriptive biogeography of *Tomicus* (Coleoptera: Scolytidae) species in Spain. J Biogeogr 31:2011–2024
- Gioia P, Pigott JP (2000) Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forests of south-western Australia. J Biogeogr 27:1065–1078
- Goday SR (1953) Apreciación sintética de los grados de vegetación de la Sierra de Gerês. In: A Flora e a Vegetação da Serra do Gerês. Simpósio da I Reunião de Botânica Peninsular. Instituto de Alta Cultura, Lisboa, pp 449–480
- Grand J, Buonaccorsi J, Cushman SA, Griffin LR, Neel MC (2004) A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. Conserv Biol 18:1063–1077
- Guisan A, Hofer U (2003) Predicting reptile distribution at the mesoscale: relation to climate and topography. J Biogeogr 30:1233–1243
- Heikkinen RK, Neuvonen S (1997) Species richness of vascular plants in the subartic landscape of northern Finland: modelling relationships to the environment. Biodivers Conserv 6:1181–1201
- Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-Niche Factor Analysis: how to compute habitat-suitability maps without absence data?. Ecology 83:2027–2036
- Hirzel AH, Arlettaz R (2003) Modelling habitat suitability for complex species distributions by environmental-distance geometric mean Environ Manage 32:614–623
- Hirzel AH, Posse B, Oggier PA, Crettenands Y, Glenz C, Arlettaz R (2004a) Ecological requirements of reintroduced species and the implications for release policy: the case of bearded vulture. J Appl Ecol 41:1103–1116
- Hirzel AH, Hausser J, Perrin N (2004b) Biomapper 3.0. Division of Conservation Biology, University of Bern. URL: http://www.unil.ch/biomapper
- Inger RF, Voris HK (2001) The biogeographical relations of the frogs and snakes of Sundaland. J Biogeogr 28:863–891
- Jones PG, Beebee SE, Tohme J, Galwey NW (1997) The use of geographical information systems in biodiversity exploration and conservation. Biodivers Conserv 6:947–958
- Kier G, Barthlott W (2001) Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. Biodivers Conserv 10:1513–1529 LEAD Technologies 2003. SPSS for Windows vs 12.0. LEAD Technologies
- Luoto M, Kuussaari M, Toivonen T (2002) Modelling butterfly distribution based on remote sensing data. J Biogeogr 29:1027–1037
- Malkmus R (1986a) Herpetologische beobachtungen im Nationalpark Peneda-Gerês/Portugal. Herpetofauna 8:18–25
- Malkmus R (1986b) Zur verbreitung der amphibien und reptilien im Parque Nacional da Peneda-Gerês. Nachrichten des Naturwissenschaftlichen Museums 94:37–87

- Malkmus R (2004) Amphibians and Reptiles of Portugal, Madeira and the Azores-Archipelago. Gantner Verlag K.G., Germany
- Maravalhas E (eds) (2003) As Borboletas de Portugal. Vento Norte, Porto
- Mateo JA (2006) Áreas importantes para la herpetofauna española In: Pleguezuelos JM, Márquez R, Lizana M (eds) Atlas e Libro Rojo de los Anfibios y Reptiles de España. Dirección General de Conservación de la Naturaleza – A.H.E., pp 485–500
- Médail F, Quézel P (1999) Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conserv Biol 13:1510–1513
- Mittermeier RA, Myers N, Thomsen JB, Da Fonseca GAB, Oliveieri S (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv Biol 12:516–520
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Morales JJ, Lizana M, Arco C (2002) Análises de la distribuición altitudinal de la herpetofauna en las sierra de Segovia Revista Española de Herpetología 16:29–42
- Nally RM, Fleishman E (2003) A successful predictive model of species richness based on indicator species. Conserv Biol 18:646–654
- Okland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers Conserv 5:75–100
- Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DR (2002) Future projections for Mexican faunas under global change scenarios. Nature 416:626–629
- Pimenta M, Santarém L (1996) Atlas das Aves Nidificantes no Parque Nacional da Peneda-Gerês. P.N. Peneda-Gerês/ICN, Lisboa
- Rahbek C, Graves GR (2001) Multiscale assessment of patterns of avian species richness. Proc Natl Acad Sci USA 98:4534–4539
- Rensburg BJ, Chown SL, Gaston KJ (2002) Species richness, environmental correlates, and spatial scale: a test using South African Birds. The American Naturalist 159:566–577
- Rivas-Martínez S (1987) Nociones sobre fitosociologia, biogeografia y bioclimatologia. In: Peinda M, Rivas-Martínez S (eds) La Vegetación de España. Universidad de Alcalán de Henares, Madrid, pp 19–45
- Santos X, Brito JC, Sillero N, Pleguezuelos JM, Llorente GA, Fahd S, Parellada X (2006) Inferring habitat-suitability areas with ecological modelling techniques and GIS: a contribution to assess the conservation status of *Vipera latastei*. Biological Conservation, *in press*
- Schall JJ, Pianka ER (1978) Geographical trends in numbers of species Science 201:679–686
- Serra MG, Carvalho ML (1989) A Flora e a Vegetação do Parque Nacional da Peneda-Gerês. Contribuição para o Plano de Ordenamento desta Área Protegida. S.N.P.R.C.N., Lisboa
- Sequeira F, Gonçalves H, Faria MM, Meneses V, Arntzen JW (2001) Habitat-structural and meteorological parameters influencing the activity and local distribution of the golden-striped salamander, *Chioglossa lusitanica*. Herpetological J 11:85–90
- Soares C, Álvares F, Loureiro A, Sillero N, Arntzen JW, Brito JC (2005) Atlas of the amphibians and reptiles of Peneda-Gerês National Park, Portugal. Herpetozoa 18 (3/4)
- Spector S (2002) Biogeographic crossroads as priority areas for biodiversity conservation. Conserv Biol 16:1480–1487
- Stoms DM, Estes JE (1993) A remote sensing research agenda for mapping and monitoring biodiversity. Int J Remote Sens 14:1839–1860
- Teixeira J, Ferrand N, Arntzen JW (2001) Biogeography of the golden-striped salamander Chioglossa lusitanica: a field survey and a spatial modelling approach. Ecography 24:618–624
- Wilson EO (1992) The Diversity of Life. W.W. Norton and Co., New York

Zaniewski AE, Lehmann A, Overton JM (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. Ecological Modell 157:261–280