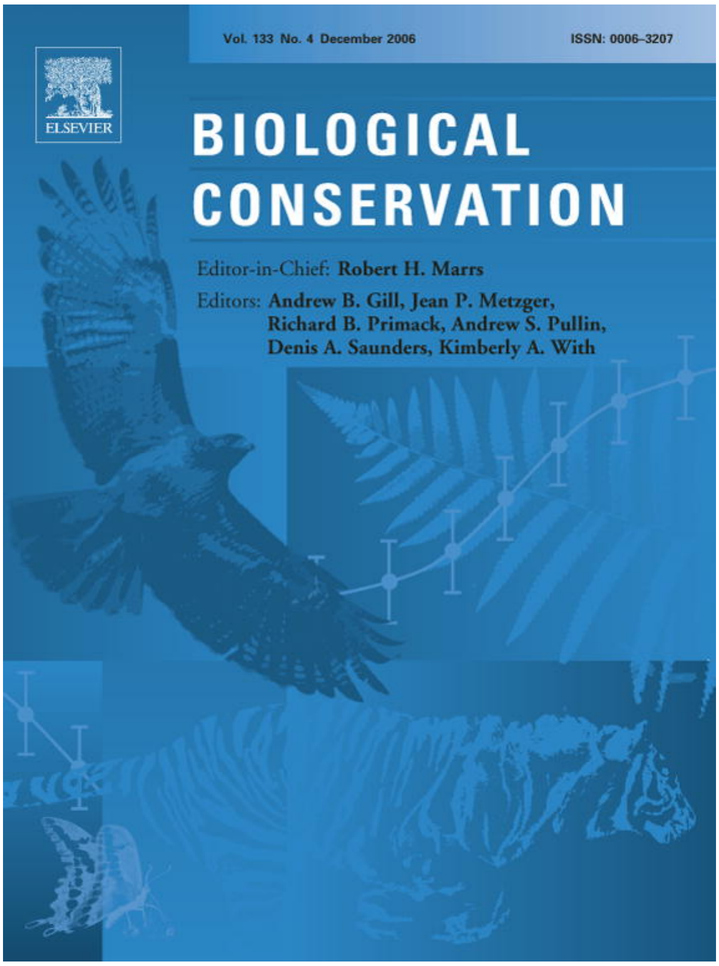

BIOLOGICAL CONSERVATION 133 (2006) 500–511

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/biocon

Are threatened lichen species well-protected in Spain? Effectiveness of a protected areas network

Isabel Martínez[a,*], Francisco Carreño[b], Adrián Escudero[a], Agustín Rubio[c]

[a]Biodiversity and Conservation Area, ESCET, University Rey Juan Carlos, c/Tulipán s/n, 28933-Móstoles, Madrid, Spain
[b]Geology Area, ESCET, University Rey Juan Carlos, c/Tulipán s/n, 28933-Móstoles, Madrid, Spain
[c]Departament of Silvopascicultura, E.T.S.I. Montes, University Politécnica of Madrid, 28040-Madrid, Spain

ARTICLE INFO

Article history:
Received 5 April 2006
Received in revised form
7 August 2006
Accepted 8 August 2006
Available online 2 October 2006

Keywords:
Lichens
Potential distribution
GIS
ENFA
Natura 2000 network

ABSTRACT

Several modelling species distribution studies have been developed, in last years, though mainly applied in higher plants, mammals or birds. However, little is known about overlooked taxa like lichens. We have evaluated the potential distribution of eleven threatened lichens in Spain and how the Natura 2000 network contributes to protect them. To overcome difficulties related to the lack of systematic surveys in those poorly known species we used only-presence data by means of ENFA (ecological-niche factor analysis). Then, we used ENFA to model the environmental niche of each species and to obtain the habitat suitability maps. In order to test the effectiveness of the Natura 2000 network, the habitat high suitability map for all species was overlapped with the network map. Our results show that all species considered present habitats requirements different from the average conditions of Spain, although clear differences exist among the species. That is, *Peltigera elisabethae* shows an extremely narrow niche, whereas *Peltigera neckeri* presents the highest ecological breadth. High temperature and long drought periods are the variables which restrict more the occurrence of these species. So, all species appear mainly confined to well-conserved forest and mountain ranges where these variables are dimmed. This mainly occurs in the oceanic northern fringe and in the higher Mediterranean mountains. In relation to the success of the Natura 2000 network, our results show that the capability of this network to protect key habitats for these species seem to be guarantied, probably because most reserves appear in mountainous areas in Spain. Evaluation of reserve network effectiveness needs the use of this type of gap analysis and especially the inclusion of 'not charismatic' organisms such as lichens.

1. Introduction

Recognition of relationships between distribution patterns and environmental factors constitutes the basis for an effective biota management and conservation. It offers possibilities for reconstruction of environmental changes in the past (Bachelet et al., 2003), and prediction for future species distributions (Skov and Svenning, 2004; Thuiller et al., 2006).

Species distribution modelling has benefited, in the last years, from the increasing availability of geographical information systems (Salem, 2003; Guisan and Thuiller, 2005). Models are currently used to detect suitable areas for the species, suggesting areas where conservation actions should be necessary (Cabeza et al., 2004; Gutiérrez, 2005), suitable regions still not colonised, or where the species has become extinct (Scott et al., 2002).

---

* *Corresponding author*: Tel.: +34 914887183; fax: +34 916647490.
E-mail address: isabel.martinez@urjc.es (I. Martínez).

0006-3207/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2006.08.003

Studies on the abundance and distribution of species conducted over areas larger than several thousands of km^2 are scarce, especially for less 'charismatic' organisms. There are almost no national-scale surveys and such a type of information has been rarely analysed in detail for conservation purposes (Vanderpoorten et al., 2005). An important research effort has been devoted on the extrapolation of species distribution from incomplete data to more efficiently obtain reliable distribution maps (Pereira and Itami, 1991; Iverson and Prasad, 1998; Peterson et al., 1999; Guisan et al., 2002; Hortal and Lobo, 2002). Similarly, you can find a plethora of statistical methods to process environmental information and reliable presence/absence data and consequently to estimate the probability of occurrence of a given species (Guisan and Zimmermann, 2000). However, for most organisms only-presence data are available at such spatial scales. So, species distribution prediction based on presence-only data has been developed (Walker and Cocks, 1991; Carpenter et al., 1993; Scott et al., 1993; Peterson et al., 1999; Hirzel et al., 2002; Robertson et al., 2001). Generally, these methods delimit the environmental niche of species within a geographical area by comparing the environmental conditions of the total geographical area with that of cells where the species has been observed. Ecological-niche factor analysis (ENFA) which was developed by Hirzel et al. (2002) is one of these modelling tools and probably the most successful (Reutter et al., 2003; Brotons et al., 2004; Engler et al., 2004; Chefaoui et al., 2005).

Lots of prediction of distribution areas of higher plants, ferns, animals have appeared in the last years (Pausas and Sáez, 2000; Hill et al., 2002; Wilson et al., 2005). However, to our knowledge it remains untouched for overlooked taxa like lichens, probably because the distributions of lichens are poorly known and simple species range mapping is still lacking for most habitats, ecosystems and countries (Hunter and Webb, 2002; Vanderpoorten et al., 2005). It is noteworthy that relatively few predictive models have been applied for rare and endangered species (Miller, 1986; Carey and Brown, 1995; Godown and Peterson, 2000; Draper et al., 2003; Engler et al., 2004), despite knowledge of distribution of these threatened species has become a priority for different conservation institutions in order to help to design conservation actions and identify those areas which need protection (Prendergast et al., 1993).

Most protected areas networks have been designed in base on target species or group of target organisms. Such strategy for establishing nature reserves usually leads to an under-representation of many important components of biodiversity (Linnell et al., 2000). Kati et al. (2004) found that in natural reserves there is a low congruence in the species richness patterns across different taxonomic groups. By other hand, Kati et al. (2003) evaluated the effectiveness of the zonification of a reserve created to protect the black vulture and other raptors for protecting the orthopteran assemblage. They concluded that the buffer zone of the reserve is more effective to orthopteran conservation than the core areas. These results suggest than the effectiveness of reserves is not always suited to protect 'not charismatic' organisms and they show the necessity to include data of this type of organisms in conservation decisions.

Our primary goals are as follows: (1) to know the potential distribution of eleven threatened lichens belonging to Peltigerales considering a complete set of environmental predictors from climate and geology to forest status; (2) to conduct a gap analysis to evaluate how the Natura 2000 network which is a continental-scale network of protected areas (Natura 2000 Network) will protect them in Spain. To our knowledge the distribution of a complete guild of endangered and close lichens at a wide scale has never been conducted. However, lichens are well-suited organisms upon which to base conservation bio-monitoring due to their sensibility to changes in microclimate (Kivistö and Kuusinen, 2000; Rheault et al., 2003). The species included in this study are cyanobacterial lichens (with *Nostoc* as main photobiont or with cephalodia). Cyanobacterial lichens are considered to be highly sensitive to alteration of the environmental conditions (Hilmo and Såstad, 2001) and most of them are included in European red lists because their populations show important declines (Randlane, 1998; Thor and Arvidsson, 1999; Nimis, 2003; Martínez et al., 2003, etc.).

2. Materials and methods

2.1. Study area

The study area is Peninsular Spain which extends on 493486 km^2. This vast territory includes a large variety of biomes, relief, climates and soil types. Altitude ranges from 0 to 3483 m in Sierra Nevada. Landscapes vary extremely, from some almost desert-like to others green and fertile. There are also long coasts, in the east along Mediterranean Sea and in the west along the Atlantic Ocean and Cantabrian Sea. Although Spain lies in the temperate zone, its rugged topography gives rise to a great diversity of climates from semiarid Mediterranean, to oceanic in the northern fringe and alpine in the high mountains. Mean annual temperature oscillate from 2.2 to 19 °C, and total annual precipitation between 203 and 2990 mm. Due to this great variety of relief and climate, Peninsular Spain presents an enormous diversity of vegetation types, from deciduous and coniferous forests, and evergreen woodland to shrubland and annual grassland (Rey-Benayas and Scheiner, 2002).

2.2. Data sets

Lichen presence and a complete set of environmental data was estimated for each of the 4928 10×10 km squared cells in which the territory was thoroughly divided. The different data sets and spatial information have been integrated into a geographic information system. In order to incorporate the available information in the system the alphanumeric data were arranged and structured into a relational database, meanwhile the spatial information was directly integrated in the GIS. Since the Iberian Spain has three different UTM zones (29, 30 and 31 N), we have generated a UTM 30 N base graticule -10 km $*$ 10 km resolution and then, this has to be done in order to transform all data coordinates into the new cartesian reference system. All parameters and the binomial presence of each lichen species are referenced to a cell of base graticule.

2.3. Lichen variables

We have included in our research eleven threatened species belonging to five genera of the Peltigerales order (Table 1). Almost all biological data came from the compilation of all collections made mainly by the authors during the last ten years (Martínez, 1999; Burgaz and Martínez, 2003). The presence of each lichen species within each square cell was considered (Fig. 1). A total of 739 presences were obtained ranging from 25 in *Sticta fuliginosa* to a maximum of 114 cells in *Peltigera collina*.

2.4. Environmental variables

Nineteen ecogeographical variables (EGV) were derived from different sources (Table 2). However, only 11 variables were selected to build models to predict the distribution of the species, being excluded environmental predictors showing correlations >0.7 in order to avoid multicollinearity problems (Table 2).

Climatic variables were derived with the simulation model for Spain CLIMOEST (Sánchez Palomares et al., 1999).The topographic parameters are derived from the Shuttle Radar Topography Mission (SRTM) data recorded in February 2000. This terrain height data sets or SRTM-DEM are mosaiked for Spain and resampled at 100 m resolution. The global accuracy for Spain is approximately ±12.96 m (Carreño, 2005). The type of rock variable has been obtained from geological cartography (Rodríguez-Fernández, 2004). The materials with high percentage of carbonate minerals are classified as calcareous, the rest as non-calcareous. The forest map of the Spanish Environmental Ministry was used in order to digitize the spatial distribution of forest class as well. Natura 2000 network sites were obtained from the 'Banco de Datos de la Naturaleza' of the Spanish Environment Ministry (see http://www.mma.es/bd_nat/menu.htm). Since ENFA only works with quantitative data, we used a semi-quantitative scale for forest-cover (Table 2). In the case of type of substrate, we smooth the boolean map with Idrisi's Filter module (Hirzel et al., 2004).

2.5. Data analysis

Ecological-niche factor analysis (ENFA) was done using Biomapper 3.1 software (Hirzel et al., 2004; see http://www.unil.ch/biomapper). ENFA uses diverse environmental variables and generates a number of uncorrelated factors with ecological meaning. The first factor represents the marginality that is the degree to which the mean of the species distribution differs from that of the available conditions of the study area. For each ecogeographical variable, marginality coefficients were calculated. Positive values show that the species are found in conditions that are higher than the average available (Hirzel et al., 2002). The rest of the factors represent decreasing amounts of information about the specialization of the species. That means how restricted is the species niche as compared with the available habitat. Specialization coefficients for each ecogeographical variable were calculated for each of the specialization factors. ENFA computes a global marginality coefficient for each species, expressing how, on all the EGVs, the species average differs from the global average, and a global specialization coefficient, expressing the ratio of global variance to species variance. The global marginality value is generally between zero and one, although occasionally can exceed one (Hirzel et al., 2002). Large values indicate that the species has habitat requirements that differ from the average conditions available. The global specialization coefficient varies from one to infinite. Tolerance value is the inverse to specialization and varies from 0 to 1. A species showing a tolerance close to one inhabits a wider niche, wider ecological requirements, than a species with a tolerance close to zero. Following Hirzel and Arlettaz (2003) we decided to use the geometric mean algorithm to build habitat suitability maps. Habitat suitability maps were built using the selected factors. The number of factors selected were those that at least explained 70% of the variance. The habitat suitability values of these maps vary from 0 (minimum habitat quality) to 100 (maximum habitat suitability).

Model validation was achieved through a jack-knife cross-validation process (Fielding and Bell, 1997). Habitat suitability maps obtained were reclassified as follows: very

Table 1 – List of species included in the study

Species	Number of squares	Area of high suitability	High suitability/Natura 2000	%
Lobaria amplissima (Scop.) Forss.	61	20 500	9909	48.3
Lobaria pulmonaria (L.) Hoffm.	88	41 000	17 216	42
Lobaria scrobiculata (Scop.) DC.	85	80 900	26 111	32.3
Nephroma laevigatum Ach.	83	52 900	18 657	35.3
Nephroma resupinatum (L.) Ach.	42	11 200	6465	57.7
Peltigera collina (Ach.) Schrad.	114	38 100	16 863	44.3
Peltigera elisabethae Gyeln.	35	3900	1536	39.4
Peltigera horizontalis (Huds.) Baumg.	69	31 100	15 484	49.8
Peltigera neckeri Hepp ex Müll. Arg.	93	76 300	26 766	35.1
Solorina saccata (L.) Ach.	44	66 900	28 131	42
Sticta fuliginosa (Hoffm.) Ach.	25	32 500	8373	25.8

Number of squares indicates total number of squares of 10 × 10 km where each species was found. Total number of squares was 4928. Area of high suitability (km^2) indicates the area of high suitability of each species in whole Spain. High suitability/Natura 2000 means the area of high suitability included in the Natura 2000 network. % indicates the percentage of the area of high suitability included in the Natura 2000 network.

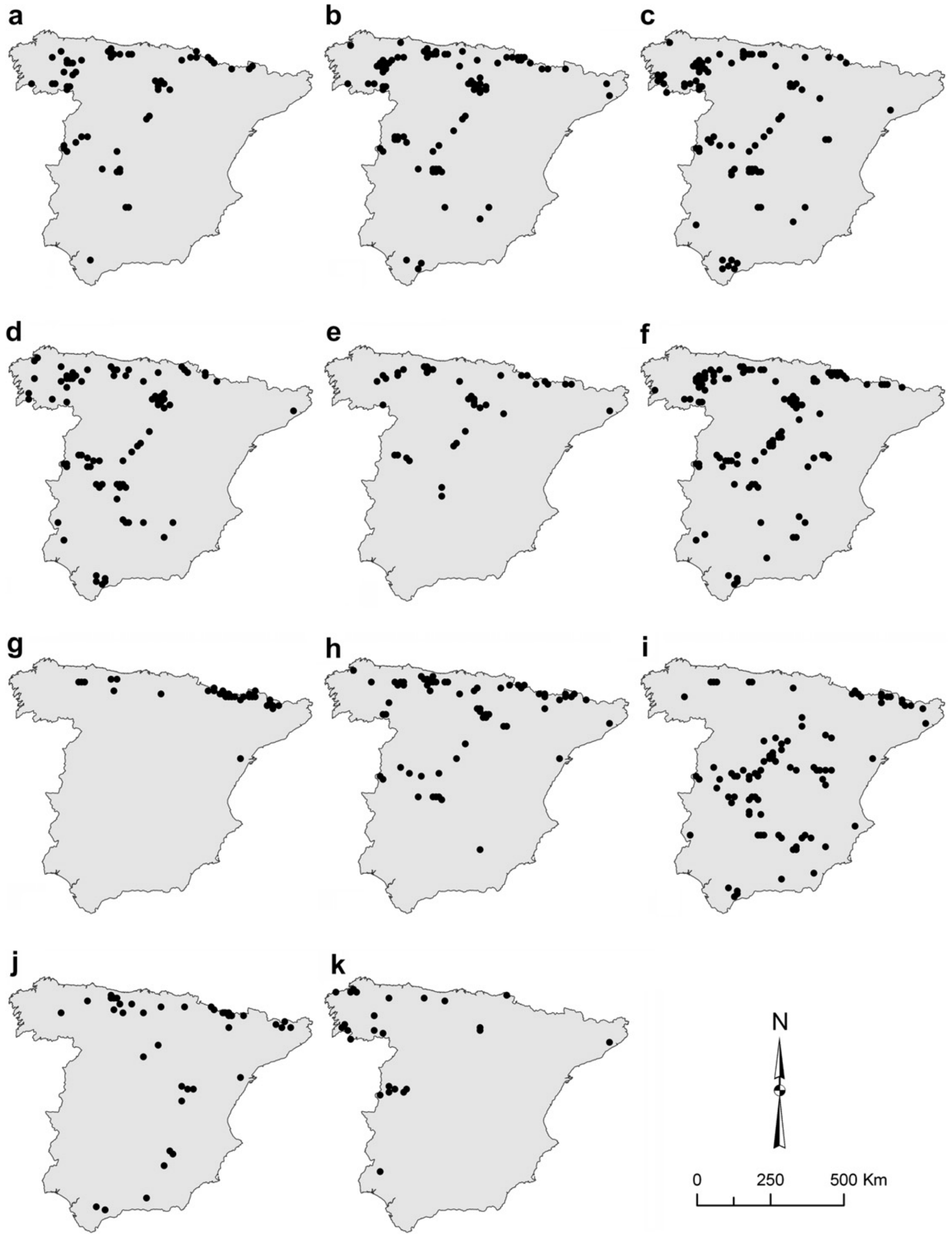

Fig. 1 – Presence of each species in Spain. (a) *Lobaria amplissima*; (b) *Lobaria pulmonaria*; (c) *Lobaria scrobiculata*; (d) *Nephroma laevigatum*; (e) *Nephroma resupinatum*; (f) *Peltigera collina*; (g) *Peltigera elisabethae*; (h) *Peltigera horizontalis*; (i) *Peltigera neckeri*; (j) *Solorina saccata*; (k) *Sticta fuliginosa*.

low habitat suitability (0–33); medium habitat suitability (34–66) and high habitat suitability (67–100). Maps of all species only showing areas with high habitat suitability were overlapped to detect which areas have a higher number of species in order to detect local 'hotspots' of threatened lichen species. Mean values of the different variables were calculated in order to characterize environmentally these high suitability areas.

Degree of protection of these species achieved by Natura 2000 network in Spain was evaluated for each species and also by overlapping the map with high habitat suitability for all species with the Natura 2000 network map. The number of cells with high suitability values included in the network was calculated (Chefaoui et al., 2005). These cells were classified in two classes: cells with at least six species and a second type for the rest.

Table 2 – List and codes of the ecogeographical variables (EGV) considered in the study

Type of variable	Variables	Code
Topography	*Maximum altitude	MAX-ALT
	Minimum altitude	MIN-ALT
	*Mean altitude	MEA-ALT
	*Altitudinal range	RAN-ALT
Geology	*Type of rock (Calcareous/non-calcareous)	R-SURF
Climate	*Annual mean temperature	TM
	Mean temperature of the warmest month	T-WAR
	*Mean temperature of the coolest month	T-COO
	*Annual precipitation	PT
	*Winter precipitation	P-WIN
	Spring precipitation	P-SPR
	*Summer precipitation	P-SUM
	Autumn precipitation	P-AUT
	Annual potential evapotranspiration	APE
	Potential water loss	PWL
	*Drought period	DP
	Water index	WI
	Temperature fluctuations	T-FLUC
Land-cover	*Type of cover (2-forests/1-shrublands/0-pastures and agricultural lands)	COVER-F

The eleven variables included in the ecological-niche factor analysis (ENFA) are signed with *.

3. Results

Global marginality values were higher than 1 for all species, evidencing a high separation of all species from the central part of the strong environmental gradient present in Spain (Table 3). The values range between 1.306 for *Peltigera neckeri* and 3.654 for *Peltigera elisabethae* (Table 3). On the other hand, the global tolerance values (the opposite of specialization ones) ranged from 0.199 to *P. elisabethae* and 0.855 to *P. neckeri* (Table 3). The score of 0.199 near to 0 indicates a very narrow niche, with a value near to 1, unlike *P. neckeri* which inhabits a wider niche.

Reduced factors for each species explained a significant fraction of the variance (Table 3). The total variance explained ranged between 70% for *Lobaria scrobiculata* and 93.5% for *P. elisabethae* (Table 3). The first selected axis or marginality, which maximizes the absolute difference between global environmental mean and the species mean varied between 13.8% of the specialization for *P. neckeri* and 26.7% for *Solorina saccata* (Table 4). This first value is very high in the case of *P. elisabethae* (88.5%) (Table 4). The second factor (specialization factor) explains also an important fraction which varied from 4.9% for *P. elisabethae* to 43.1% for *Nephroma resupinatum* (Table 4).

Total and winter precipitation together with the elevation range are the variables with higher marginality coefficients for *Lobaria amplissima*, *Lobaria pulmonaria*, *L. scrobiculata*, *Nephroma laevigatum* and *S. fuliginosa*. This suggests that their

Table 3 – Global marginality, specialization and tolerance values for the eleven species

	Lobaria amplissima	*Lobaria scrobiculata*	*Lobaria pulmonaria*	*Nephroma laevigatum*	*Nephroma resupinatum*	*Peltigera collina*	*Peltigera elisabethae*	*Peltigera horizontalis*	*Peltigera neckeri*	*Solorina saccata*	*Sticta fuliginosa*
Marginality	1.958	1.475	1.793	1.481	2.464	1.813	3.654	2.037	1.306	2.286	1.542
Specialization	1.436	1.355	1.237	1.293	1.712	1.263	5.02	1.371	1.169	1.345	1.826
Tolerance	0.696	0.738	0.809	0.773	0.584	0.792	0.199	0.729	0.855	0.744	0.548
Number of factors	4	4	4	4	4	4	2	4	5	5	3
Variance explained	78.8	70	71.4	71.2	82	72.1	93.5	73.3	76	80.2	72.9
PD	50.66	50	51.11	52.08	52.5	51.36	55	48.57	52.67	51.7	56.67
SD	0.25	0.21	0.14	0.21	0.18	0.17	0.23	0.28	0.23	0.22	0.44

Number of factors used to generate habitat suitability maps and the variance explained are also included. Values of the predicted suitability (PD) and standard deviation (SD) are also indicated for each species.

Table 4 – Variance explained by the first two ecological factors and coefficient values for the different variables in each species

L. amplissima	Factor 1 (22%)		Factor 2 (29%)	N. resup.	Factor 1 (14.6%)		Factor 2 (43.1%)
PT	0.437	T-COO	0.718	RAN-ALT	0.370	T-COO	−0.633
P-WIN	0.387	TM	0.566	PT	0.364	TM	0.462
RAN-ALT	0.375	DP	0.362	TM	−0.352	MAX-ALT	−0.458
MAX-ALT	0.341	MAX-ALT	0.102	MEA-ALT	0.345	MEA-ALT	0.272
TM	−0.299	MEA-ALT	0.098	P-SUM	0.306	RAN-ALT	0.167
P-SUM	0.297	R-SURF	0.068	P-WIN	0.284	P-WIN	−0.153
DP	−0.275	P-WIN	0.066	T-COO	−0.265	PT	0.146
MEA-ALT	0.272	PT	−0.043	DP	−0.259	DP	−0.144
T-COO	−0.203	COVER-F	0.042	COVER-F	0.111	COVER-F	−0.062
COVER-F	0.173	P-SUM	−0.01	R-SURF	0.06	R-SURF	−0.042
R-SURF	0.060	RAN-ALT	−0.002	MAX-ALT	0.4	P-SUM	−0.05
L. pulmonaria	Factor 1 (20.8%)		Factor 2 (26.1%)	*P. collina*	Factor 1 (17.5%)		Factor 2 (27.8%)
PT	0.428	T-COO	0.544	MAX-ALT	0.407	PT	0.570
RAN-ALT	0.391	PT	0.472	RAN-ALT	0.383	P-WIN	−0.555
P-WIN	0.385	P-WIN	−0.452	PT	0.373	T-COO	0.423
MAX-ALT	0.352	TM	−0.421	MEA-ALT	0.351	TM	−0.244
TM	−0.309	MAX-ALT	0.190	TM	−0.330	MAX-ALT	0.226
P-SUM	0.276	DP	0.152	P-WIN	0.328	P-SUM	−0.191
MEA-ALT	0.273	P-SUM	−0.131	P-SUM	0.248	MEA-ALT	−0.135
DP	−0.272	COVER-F	0.104	T-COO	−0.244	RAN-ALT	−0.098
T-COO	−0.203	RAN-ALT	−0.084	DP	−0.241	COVER-F	0.087
COVER-F	0.161	MEA-ALT	−0.076	COVER-F	0.168	DP	−0.071
R-SURF	0.068	R-SURF	0.008	R-SURF	0.029	R-SURF	0.021
L. scrobiculata	Factor 1 (20.3%)		Factor 2 (23.5%)	*P. elisabethae*	Factor 1 (88.5%)		Factor 2 (4.9%)
P-WIN	0.470	T-COO	0.496	P-SUM	0.471	PT	0.685
PT	0.448	TM	−0.429	RAN-ALT	0.399	P-WIN	−0.577
RAN-ALT	0.413	P-WIN	−0.397	MAX-ALT	0.393	P-SUM	−0.354
TM	−0.254	PT	0.383	MEA-ALT	0.349	T-COO	−0.216
DP	−0.230	MAX-ALT	0.359	TM	−0.344	MEA-ALT	0.098
COVER-F	0.226	DP	0.227	PT	0.280	DP	0.096
P-SUM	0.170	MEA-ALT	−0.221	T-COO	−0.276	COVER-F	−0.062
T-COO	−0.143	RAN-ALT	−0.149	DP	−0.216	R-SURF	0.043
MAX-ALT	0.35	COVER-F	0.118	P-WIN	0.113	RAN-ALT	−0.042
MEA-ALT	0.26	P-SUM	−0.025	COVER-F	0.086	MAX-ALT	−0.023
R-SURF	−0.007	R-SURF	0.008	R-SURF	0.054	TM	0.011
N. laevigatum	Factor 1 (20.9%)		Factor 2 (30.1%)	*P. horizontalis*	Factor 1 (22.4%)		Factor 2 (23.4%)
P-WIN	0.447	MAX-ALT	−0.445	RAN-ALT	0.428	PT	−0.496
PT	0.445	P-WIN	0.418	MAX-ALT	0.393	T-COO	0.442
RAN-ALT	0.431	PT	−0.402	PT	0.341	P-WIN	0.433
MAX-ALT	0.364	TM	0.356	P-SUM	0.332	TM	−0.421
MEA-ALT	0.269	MEA-ALT	0.249	TM	−0.326	DP	0.344
DP	−0.243	DP	−0.178	MEA-ALT	0.313	P-SUM	0.223
TM	−0.235	COVER-F	−0.121	DP	−0.277	COVER-F	0.104
COVER-F	0.213	P-SUM	0.065	P-WIN	0.251	RAN-ALT	0.092
P-SUM	0.187	T-COO	−0.43	T-COO	−0.248	R-SURF	0.065
T-COO	−0.127	R-SURF	−0.041	COVER-F	0.168	MEA-ALT	−0.041
R-SURF	−0.008	RAN-ALT	0.2	R-SURF	0.044	MAX-ALT	0.019
P. neckeri	Factor 1 (13.8%)		Factor 2 (29%)	*S. saccata*	Factor 1 (26.7%)		Factor 2 (17.7%)
RAN-ALT	0.511	DP	0.710	RAN-ALT	0.425	PT	0.517
MAX-ALT	0.506	T-COO	−0.443	MAX-ALT	0.419	MAX-ALT	0.517
MEA-ALT	0.422	PT	0.344	MEA-ALT	0.364	P-WIN	−0.449
TM	−0.260	P-WIN	−0.259	P-SUM	0.356	MEA-ALT	−0.386
T-COO	−0.243	MAX-ALT	−0.214	TM	−0.332	RAN-ALT	−0.202
COVER-F	0.225	RAN-ALT	0.173	PT	0.294	P-SUM	−0.189
PT	0.218	COVER-F	−0.152	T-COO	−0.258	DP	−0.137
P-SUM	0.188	R-SURF	0.075	DP	−0.243	T-COO	0.090
P-WIN	0.160	P-SUM	−0.055	P-WIN	0.182	R-SURF	0.041

(continued on next page)

Table 4 – *continued*

P. neckeri	Factor 1 (13.8%)		Factor 2 (29%)	*S. saccata*	Factor 1 (26.7%)		Factor 2 (17.7%)
DP	−0.135	TM	0.033	R-SURF	0.141	COVER-F	−0.1
R-SURF	−0.029	MEA-ALT	0.07	COVER-F	0.094	TM	−0.001

S. fuliginosa	Factor 1 (23.2%)		Factor 2 (34.8%)
P-WIN	0.568	TM	−0.557
PT	0.545	T-COO	0.454
RAN-ALT	0.362	P-WIN	−0.406
DP	−0.304	PT	0.392
P-SUM	0.218	DP	0.304
COVER-F	0.191	MAX-ALT	0.195
R-SURF	−0.175	MEA-ALT	−0.158
MAX-ALT	0.139	P-SUM	−0.098
TM	−0.131	COVER-F	−0.016
T-COO	0.077	RAN-ALT	−0.007
MEA-ALT	−0.006	R-SURF	−0.004

The amount of specialization is given between parentheses.

mean values in the presence cells differ from the mean values in Spain (Table 4). Positive coefficients indicate that these species are found in wet and mountainous places. These lichens also tend to avoid hot and dry areas, such as *L. amplissima* (TM = −0.299, DP = −0.275), *P. collina* (TM = −0.330), *N. laevigatum* (TM = −0.235, DP = −0.243), *L. pulmonaria* (TM = −0.309), *L. scrobiculata* (TM = −0.254, DP = −0.230). Moreover, *S. fuliginosa* requires high values of summer precipitation and very short drought periods. Summer precipitation is also relevant for *L. pulmonaria* and *L. amplissima* (Table 4). Similarly *Peltigera horizontalis* also occurs in mountains with high values of summer precipitation but not necessarily high winter precipitation. In the case of *P. elisabethae,* summer precipitation is the ecogeographical variable with the highest marginality coefficient. *N. resupinatum* shows a similar pattern to *Lobaria* species, but this species appears in areas with lower mean temperature. Finally, *P. neckeri* is linked to mountainous places, but in this case its moisture requirements are weaker. *P. neckeri* is found in forested areas and it has a greater capacity to support higher drought periods than the rest of species. It is noteworthy that for the majority of the species, forest cover appears at the end of the list of variables.

Habitat suitability maps (Fig. 2) show high probability of appearance in almost all these lichens in the north of Spain, following the two mountain ranges running west to east, 'Cordillera Cantábrica' and the Pyreneans, and also in minor mountain ranges in the area ('Sierra de Ancares', 'Montes de León', 'Sierra de Urbasa', 'Sierra de Aralar', etc.). Moreover, other mountain areas in the Iberian Mediterranean fraction also show high probability of occurrence, mountain ranges like 'Sistema Central' and 'Sistema Ibérico'. By other hand, *L. scrobiculata*, *N. laevigatum*, *P. collina*, *P. neckeri* and *S. saccata* present high values of appearance in some mountains located in southern Spain ('Grazalema', 'Sierra de las Nieves', 'Sierra Nevada', 'Sierra de Cazorla', etc.). Finally, two species show great differences with the rest: *P. neckeri* presents high values of probability of appearance along the Peninsular Spain; or *P. elisabethae* which shows very scarce areas with high probability of appearance, and mainly located in the Pyrenean area.

According to the Jack-knife cross-validation, predicted suitability exceeds 50 in more than 50% of the validation cells, except in the case of *P. horizontalis* (48.57%, SD = 0.28). For the other species the values range from 50% for *L. scrobiculata* to 56.67% for *S. fuliginosa* (Table 3). This suggests that our models are accurate enough.

Reclassified habitat suitability maps of each species were generated and mean ± SD were obtained for each ecogeographical variables in the three categories considered. Mean and standard deviation values for the cells with the highest suitability for each species lead for a more precise description of the niche requirements (Table 5). For instance, *P. elisabethae* grows in extreme conditions: steep and high altitude areas, with low forest cover, very low temperature and high precipitation, especially during the summer. Contrarily *P. neckeri* occurs in less steep, warmer and drier mountains supporting more than two months of drought. *S. fuliginosa* is also remarkable because it occurs in wet and warm mountains areas, avoiding hot and dry places because it only supports a drought period of less than half month. By the other hand, it is the only species which is mainly found in non-calcareous conditions. Finally, *Lobaria* species show contrasting results. Thus *L. scrobiculata* is the most tolerant species of the group in temperature and rainfall terms. Moreover, it can live in areas with less cover forest compared with the two other *Lobaria* species (Table 5).

The area of high suitability for each species was calculated and the percentage of these areas included in the Natura 2000 network was also calculated (Table 1). Six of the species present a percentage higher than 40%, being *N. resupinatum* the better represented species in the Natura 2000 network. Contrarily, *S. fuliginosa* has the lowest representation in the network (Table 1).

Maps of each species with the cells with the highest habitat suitability (67–100) were overlapped, reaching a total area of 164799 km^2. Afterwards the resulting map was compared

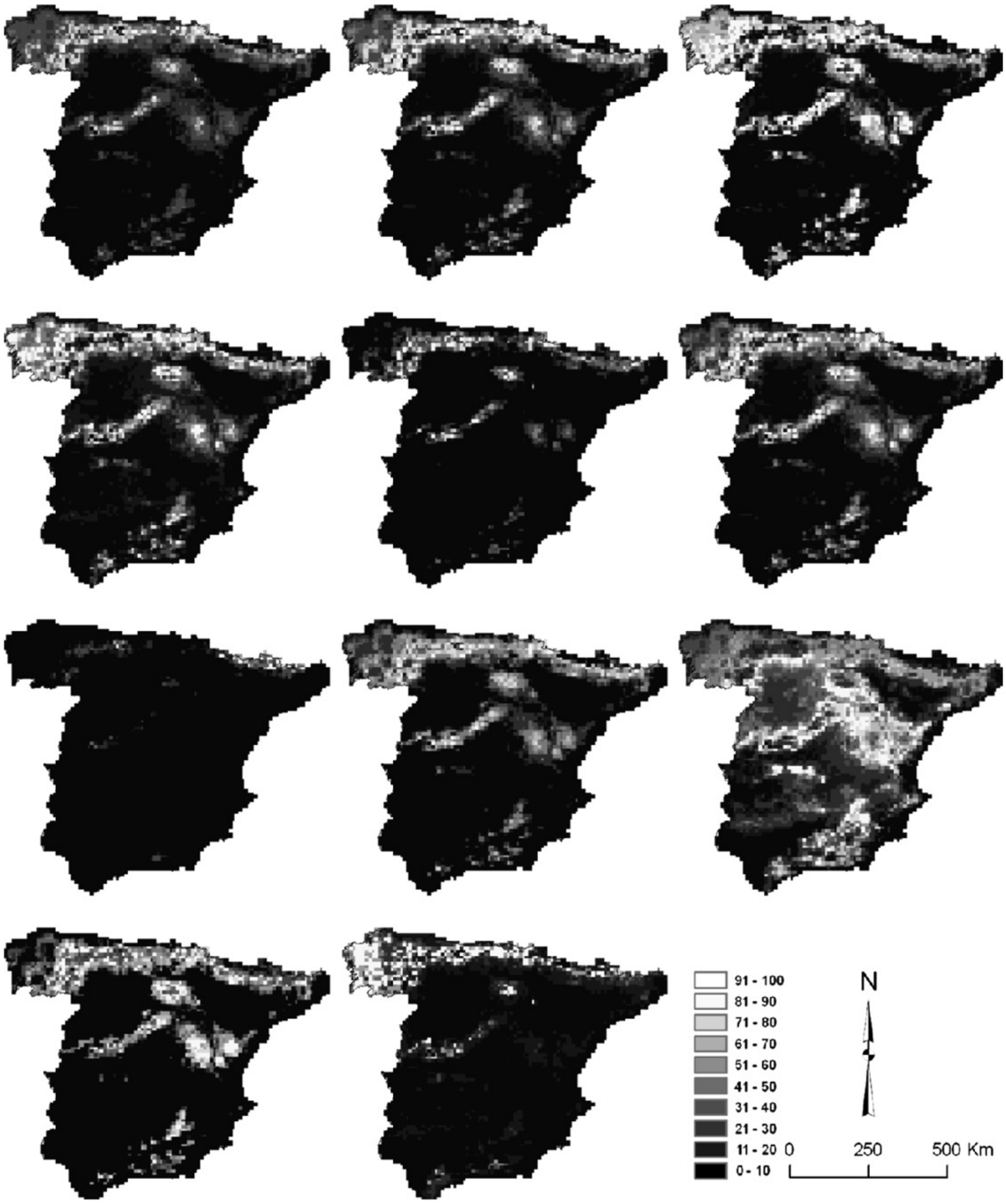

Fig. 2 – Habitat-suitability maps for each species in Spain computed by ecological-niche factor analysis. The scale indicates the habitat suitability values presented by each colour in the map (0 = low suitability; 100 = high suitability). (a) *Lobaria amplissima*; (b) *Lobaria pulmonaria*; (c) *Lobaria scrobiculata*; (d) *Nephroma laevigatum*; (e) *Nephroma resupinatum*; (f) *Peltigera collina*; (g) *Peltigera elisabethae*; (h) *Peltigera horizontalis*; (i) *Peltigera neckeri*; (j) *Solorina saccata*; (k) *Sticta fuliginosa*.

with the Natura 2000 network map (Fig. 3). The areas with high probability of appearance for a higher number of species are mainly located in the north of Spain, especially along the 'Cordillera Cantábrica' and some places in the Pyrenees, 'Sistema Central' and 'Sistema Ibérico' (Fig. 3). We calculated also the percentage of cells with high habitat suitability that will be included in the Natura 2000 network. Nature network comprises a percentage of 70.58% cells with high habitat suitability for at least six species. That represents an area of 15951 km^2. The percentage of the areas with high values of probability of appearance with less than six species that be included in the network is clearly lower (49.3%). That represents an area of 70105 km^2.

4. Discussion

The lichens considered in this study are mainly distributed along temperate and boreal areas of Europe and North America and almost all of them need long forest continuity (Rose, 1976; McCune, 1993; Kuusinen, 1996). Obviously, most of these species find their rear and southern margin of their distributions in Spain and depend on areas where they can find similar ecological conditions. It is known that Spain accommodates a great diversity of climates and habitats due to its geographical situation, between the African and European continents (Rey-Benayas and Scheiner, 2002) and may provide suitable habitats for these species.

As expected, all species included in this study show global marginality coefficients above 1, so they have habitats requirements that differ from the average conditions of Spain. These lichens inhabit regions with conditions far apart from the norm, like the Pyreneans and other mountainous areas. Nevertheless, outstanding differences on the requirements of each species arise. *P. elisabethae* shows the highest marginality value confirming an extremely narrow niche whereas *P. neckeri* presents the highest ecological breadth. The global tolerance values decrease from *P. neckeri* and *L. pulmonaria* to *N. resupinatum* and *P. elisabethae*, meaning that the first two species are not very specialized in relation to their ecological niche, and they can occur along relatively large areas, being the high temperature and length of the drought period the most limiting factors. In contrast, the other three species are quite specialized, mainly *P. elisabethae* which shows a very low value of tolerance.

Comparison of the marginality coefficients for each of the ecogeographical variables suggests the existence of specific differences between the eleven lichens. Obviously most of these species have their optimal conditions in deciduous forests of temperate Central and Northern Europe, such as *L. amplissima*, *L. pulmonaria* and *P. horizontalis*. Climate constraints and man-induced historical changes in the Iberian forest structure and cover (Thompson, 2005) are probably responsible for the confinement of these species in wet and mountainous places, mainly located in northern Spain where the environment remains similar to Central Europe. Consequently, these species avoid areas with high temperatures and extended summer drought period which are the most conspicuous features of the major part of Spain (the Mediterranean Spain) (Valladares, 2004). So, in lower latitudes, these species appear confined to mountain ranges probably because the rugged terrain together with an orographic increase in precipitation maintain relatively well-conserved forests with continuous canopy (Belinchón et al., in press).

Conservation of lichens still receives scarce attention by the Governmental organizations in most countries. One of the few initiatives is the Action Plans for the lichen species conservation developed by the United Kingdom (see www.ukbap.org.uk). Anyway, to develop conservation actions it is necessary to identify which are the areas where threatened species live and also to identify potential areas where these species can be introduced with the objective to increase the number of populations of these species (Zoller et al., 1999, 2000). For this purpose, the use of predictive models should be encouraged. Additionally, such models may be used to evaluate the effectiveness of protected areas or even to propose new reserves to protect species. The bryophytes, other overlooked taxa, have received more attention than lichens. So, Vanderpoorten et al. (2005) investigated which environmental variables maximized species diversity and the presence of species with high conservation value. They pointed out the importance of this type of studies in relation to Natura 2000 network and the possibility to detect interesting conser-

Table 5 – Mean and SD (between parentheses) for each variable in the highest suitability areas for the species considered in the study

Species	MAX-ALT	MEA-ALT	RAN-ALT	TM	T-COO	PT	P-WIN	P-SUM	DP	R-SURF	COVER-F
L. amplissima	1517 (382)	1063.1 (354.6)	817.5 (236.7)	9.1 (1.7)	−1.5 (2.0)	1409.9 (285)	470.7 (117.5)	178.7 (63.5)	0.4 (0.6)	45.4	51.7
L. scrobiculata	1188.4 (447.8)	852.8 (400.2)	586.1 (253.4)	10.9 (1.7)	0.0 (2.4)	1111.6 (326.6)	379.7 (151.7)	136.6 (51.5)	0.96 (0.9)	44.13	42.3
L. pulmonaria	1433.2 (415.4)	1001.5 (367.4)	763.5 (261.9)	9.7 (1.7)	−1.06 (2.2)	1262.4 (296.1)	418.8 (139.3)	164.8 (62.2)	0.6 (0.8)	38.8	46.3
N. laevigatum	1250.7 (454)	864.7 (396.1)	674.3 (256.1)	10.7 (1.8)	−0.08 (2.5)	1225.2 (315.7)	417.7 (148.4)	151.4 (60.5)	0.8 (0.9)	43.5	44.4
N. resupinatum	1672.3 (299.8)	1204.2 (266.6)	854.5 (221.8)	8.4 (1.3)	−2.3 (1.4)	1396.4 (274.3)	462.5 (121.3)	176.7 (60.8)	0.35 (0.6)	31.2	49.1
P. collina	1467.8 (361.5)	1054.5 (345.3)	732.5 (248.6)	9.7 (1.5)	−1.3 (2.0)	1206.5 (360.1)	400.3 (153.6)	155.8 (63.3)	0.7 (0.8)	38.32	44.9
P. elisabethae	2445 (303.9)	1792.9 (335.2)	1429.1 (175.3)	5.6 (1.35)	−5.01 (1.1)	1413.8 (366.4)	311.6 (154.9)	337.9 (42.2)	0	38.5	38.5
P. horizontales	1618.9 (368.2)	1154.4 (334.6)	840.3 (251.2)	8.9 (1.6)	−2.02 (1.9)	1286.0 (358.4)	412.3 (159.9)	178.1 (1.6)	0.45 (0.7)	35.0	45.6
P. neckeri	1260.9 (193.8)	995.7 (192.5)	465.3 (239.7)	11.4 (1.7)	−0.8 (1.8)	714.7 (237.2)	22.2 (111.5)	94.6 (34.6)	2.1 (0.8)	33.5	46.8
S. saccata	1400.9 (307.7)	1049.7 (295.7)	624.1 (267.1)	11.6 (1.9)	−1.3 (1.8)	982.7 (359)	311.0 (151.9)	137.6 (56.5)	1.05 (0.9)	23.6	39.9
S. fuliginosa	1052.5 (594.6)	699.2 (467.3)	626.1 (325.0)	11.0 (3.0)	0.9 (2.7)	1407 (156.8)	496.4 (96.6)	165.6 (48.2)	0.4 (0.6)	51.1	41.8

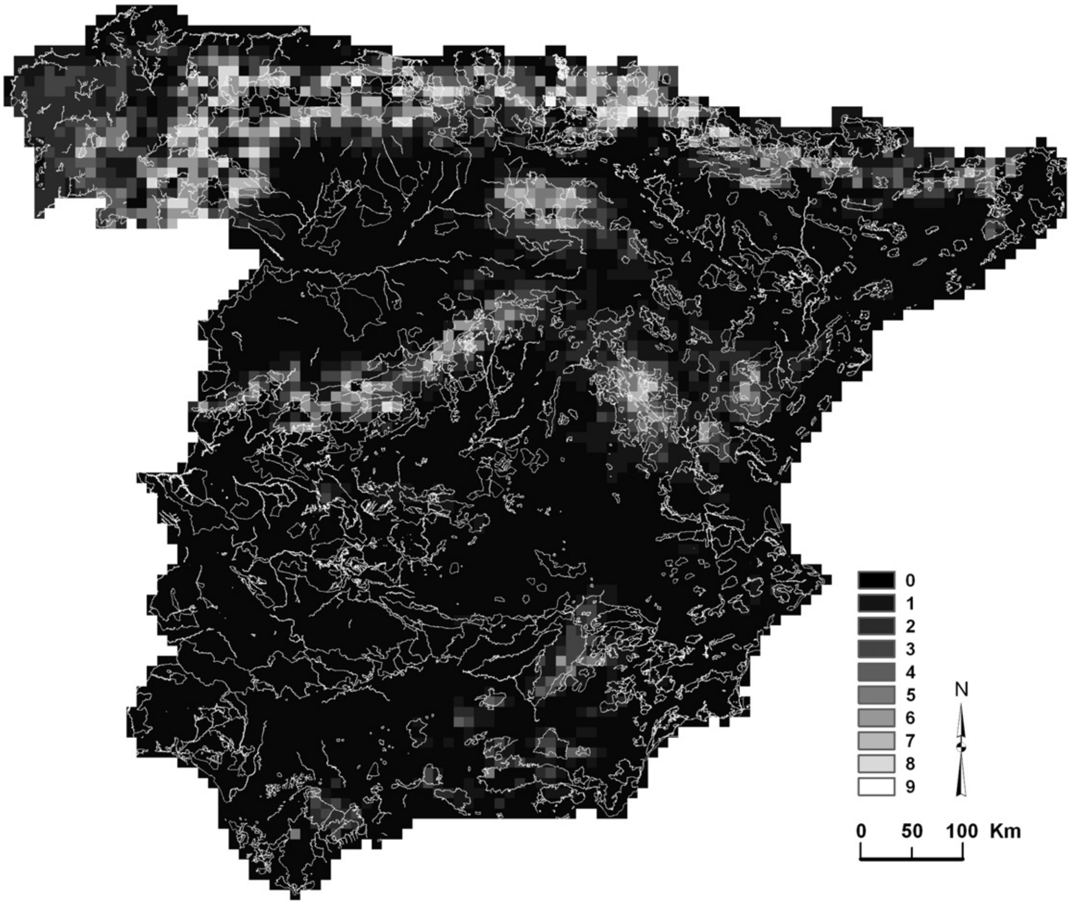

Fig. 3 – Map of Spain showing the very high suitability areas for all species overlapped with the Natura 2000 network. The scale indicates the number of species which have a very high suitability value in the area.

vation areas for bryophytes. Our results suggest that the use of only-presence data for these overlooked taxa is a valuable tool to improve the conservation of poorly known species.

Natura 2000 network has been proposed after a detailed gap analysis for critical habitats and species, mainly animals and vascular plants (Orella et al., 1998). Among the biological criteria which have been considered there are no lichens in spite of these organisms being especially sensible to environmental changes (Rheault et al., 2003). It has been predicted that this methodology will be efficient to protect less studied or inconspicuous organisms. However, to our knowledge, its effectiveness for protecting endangered lichens species at a regional scale has never been evaluated. This is one of the main problems in conservation, because the majority of the actions are related to groups of organisms such as mammals, birds or vascular plants. It has already been demonstrated that organisms such as insects, amphibious or reptiles usually fall outside of protected areas network when based on those 'important' or 'charismatic' organisms (de la Montaña and Rey-Benayas, 2003; Kati et al., 2003).

Our results showed that 70% of the areas with the highest suitability values for at least six species will be included in the network. This suggests that at least for these lichens the capability of the Natura network to protect key habitats seem to be guarantied. Areas outside the network appear concentrated in the north-western tip of the Iberian Peninsula. Probably the network should be completed with some local hotspot in this region. The percentage of cells included in the network decreases (49.3%) after considering cells with high suitability for less species. In this case, the non-protected areas are evenly distributed along Spain. Noteworthy that those areas with the highest suitability values which include nine or above of these threatened species are included 100% in the network. In this sense, some studies have proved that the Natura 2000 network improve the conservation of other group of 'not charismatic' species (Chefaoui et al., 2005). Nevertheless, percentage of high suitability areas included in the Natura 2000 network is rather low for some species with higher ecological breadths such as *L. scrobiculata*, *N. laevigatum* or *P. neckeri*.

Finally, we can conclude that the effectiveness of the Natura 2000 network to protect threatened lichen species is quite high, although some additions should be necessary mainly in some areas of north-western Spain. Our results show that the effectiveness of the network is higher in the Mediterranean area, probably because well-preserved forests in this area are scarce and almost all of them will be included in the network. However, extrapolation of these findings to other lichens with non-forests habitat optima should be conducted with caution. For instances, Mota (2001) has shown the inefficient cover of gypsum soil ecosystems in the Natura 2000 network. This type of studies including 'not charismatic' organisms may be useful to improve reserve design. Since only need presence data they can be easily conducted at different spatial scales from complete reserve networks to the establishment of a core conservation zone within a reserve. They may help to validate proposed reserves but also as a tool for selecting adequate areas.

Acknowledgement

We are very grateful to two anonymous referees for constructive comments. We are also grateful to Jose Luis Margalet for English revision of the manuscript. This work was partially funded by the Spanish Ministerio de Medio Ambiente (MMA 071/2002).

REFERENCES

Bachelet, D., Neilson, R.P., Hickler, T., Drapek, R.J., Lenihan, R.J., Sykes, J.M., Smith, B., Sitch, B., Thonicke, K., 2003. Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles 17, 1411–1421.

Belinchón, R., Martínez, I., Escudero, A., Aragón, G., Valladares, F. Edge effects on epiphytic communities in a Mediterranean Quercus pyrenaica forest. Journal of Vegetation Science, in press.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437–448.

Burgaz, A.R., Martínez, I. 2003. Peltigerales: Lobariaceae, Nephromataceae, Peltigeraceae. Sociedad Española de Liquenología, Murcia.

Cabeza, M., Araújo, M.B., Wilson, R.J., Thomas, C.D., Cowley, M.J.R., Moilanen, A., 2004. Combining probabilities of occurrence with spatial reserve design. Journal of Applied Ecology 41, 252–262.

Carey, P.D., Brown, N.J., 1995. The use of GIS to identify sites that will become suitable for a rare orchid, *Himantoglossum hircinum* L., in future changed climate. Biodiversity Letters 2, 117–123.

Carpenter, G., Gillison, A.N., Winter, J., 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation 2, 667–680.

Carreño, F., 2005. Análisis de la influencia de variables topográficas y usos del suelo en los modelos digitales de elevaciones SRTM. In: Proceedings X Conferencia de la Sociedad Iberoamericana de Sistemas de Información Geográfica (XCISIG), San Juan, Puerto Rico.

Chefaoui, R.M., Hortal, J., Lobo, J.M., 2005. Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian Copris species. Biological Conservation 122, 327–338.

Draper, D., Roselló-Graell, A., García, C., Tauleigne, C., Sergio, C., 2003. Application of GIS in plant conservation programmes in Portugal. Biological Conservation 113, 337–349.

de la Montaña, E., Rey-Benayas, J.M., 2003. ¿Coinciden los espacios naturales protegidos con las áreas relevantes de diversidad de herpetofauna en España peninsular y Baleares? Ecosistemas 2002/2. Available from : <http//www.aeet.org/ecosistemas/022/investigacion2.htm>.

Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology 41, 263–274.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38–49.

Godown, M.E., Peterson, A.T., 2000. Preliminary distributional analysis of US endangered bird species. Biodiversity and Conservation 9, 1313–1322.

Guisan, A., Edwards, T.C., Hastie, J.T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89–100.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993–1009.

Gutiérrez, D., 2005. Effectiveness of existing reserves in the long-term protection of a regionally rare butterfly. Conservation Biology 19, 1586–1597.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J., et al, 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proceedings of the Royal Society B 269, 2163–2171.

Hilmo, O., Såstad, S.M., 2001. Colonization of old-forest lichens in a young and an old boreal Picea abies forest: an experimental approach. Biological Conservation 102, 251–259.

Hirzel, A.H., Arlettaz, R., 2003. Modelling habitat suitability for complex species distributions by the environmental-distance geometric mean. Environmental Management 32, 614–623.

Hirzel, A.H., 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, A.H., Hausser, J., Perrin, N., 2004. Biomapper 3.1. Lab. of Conservation Biology, Department of Ecology and Evolution, University of Lausanne. Available from: <http://www.unil.ch/biomapper>.

Hortal, H., Lobo, J.M., 2002. Una metodología para predecir la distribución espacial de la diversidad biológica. Ecología 16, 151–178.

Hunter, M.L., Webb, S.L., 2002. Enlisting taxonomists to survey poorly known taxa for biodiversity conservation: a lichen case study. Conservation Biology 16, 660–665.

Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United Status. Ecological Monographs 68, 465–485.

Kati, V., Dufrêne, M., Legakis, A., Grill, A., Lebrun, P., 2003. Conservation management for Orthoptera in the Dadia reserve, Greece. Biological Conservation 115, 33–44.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Testing the value of six taxonomic groups as biodiversity indicators at a local scale. Conservation Biology 18, 667–675.

Kivistö, L., Kuusinen, M., 2000. Edge effects on the epiphytic lichen flora of Picea abies in middle boreal Finland. The Lichenologist 32, 387–398.

Kuusinen, M., 1996. Importance of spruce swamp-forests for epiphyte diversity and flora on Picea abies in southern and middle boreal Finland. Ecography 19, 41–51.

Linnell, J.D.C., Swenson, J.E., Andersen, R., 2000. Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? Biodiversity and Conservation 9, 857–868.

Martínez, I., 1999. Taxonomía del género Peltigera Willd. (Ascomycetes liquenizados) en la Península Ibérica y estudio de sus hongos liquenícolas. Ruizia 15, 3–200.

Martínez, I., Aragón, G., Carrión, F.J., Escudero, A., Burgaz, A.R., Coppins, B., 2003. Threatened lichens in central Spain. Cryptogamie, Mycologie 24, 73–97.

McCune, B., 1993. Gradients in epiphyte biomass in three Pseudotsuga–Tsuga forests of different ages in western Oregon and Washington. The Bryologist 96, 405–411.

Miller, R.I., 1986. Predicting rare plant distribution patterns in the southern Appalachians of the south-eastern USA. Journal of Biogeography 13, 293–311.

Mota, J.F., 2001. Análisis de agrupamientos o de "cluster" aplicado al estudio de la flora y vegetación de yesos. Aplicaciones ambientales del análisis multivariante 2001, 143–176.

Nimis, P.L., 2003. Checklist of the lichens of Italy 3.0. University of Trieste. Available from: <http://dbiodbs.univ.trieste.it>.

Orella, J.C., Simón, J.C., Vaquero, J., Cuadrado, A., Mantilla, B., Garzo, M.A., Sánchez, E., 1998. La Lista Nacional de Lugares de la Directiva Hábitats 92/43 CEE. Metodología y proceso de elaboración. Ecología 12, 3–65.

Pausas, J.G., Sáez, Ll., 2000. Pteridophyte richness in the NE Iberian Peninsula: biogeographic patterns. Plant Ecology 148, 195–205.

Pereira, J.M.C., Itami, R.M., 1991. GIS-based habitat modelling using logistic multiple regresión: a study of the Mt. Graham Red Squirrel. Photogrammetric Engineering and Remote Sensing 57, 1475–1486.

Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335–337.

Randlane, T., 1998. Red list of Estonian macrolichens. Folia Cryptogamica Estonica 32, 75–79.

Reutter, B., Helfer, V., Hirzel, A.H., Vogel, P., 2003. Modelling habitat-suitability using museum collections: an example with three sympatric Apodemus species from the Alps. Journal of Biogeography 30, 581–590.

Rey-Benayas, J.M., Scheiner, S.M., 2002. Plant diversity, biogeography and environment in Iberia: patterns and possible causal factors. Journal of Vegetation Science 13, 245–258.

Rheault, H., Drapeau, P., Bergeron, Y., Esseen, P.A., 2003. Edge effects on epiphytic lichen in managed black spruce forests of eastern North America. Canadian Journal of Forest Research 33, 23–32.

Robertson, M.P., Caithness, N., Villet, M.H., 2001. A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. Diversity and Distributions 7, 15–27.

Rodríguez-Fernández, L.R., 2004. Mapa geológico de España 1:2.000.000. In: Vera, J.A. (Ed.), Geología de España. SGE-IGME, Madrid.

Rose, F., 1976. Lichenological indicators of age and environmental continuity in woodlands. In: Brown, H., Hawksworth, D.L., Bailey, R.H. (Eds.), Lichenology: Progress and Problems. Academic Press, London, pp. 279–307.

Salem, B.B., 2003. Application of GIS to biodiversity monitoring. Journal of Arid Environments 54, 91–114.

Sánchez Palomares, O., Sánchez Serrano, F., Carretero, M.P., 1999. Modelos y cartografía de estimaciones climáticas termopluviométricas para la España peninsular. INIA, Madrid.

Scott, J.M., Davis, F.W., Csuti, B., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards, T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123, 1–41.

Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.D., 2002. Predicting Species Occurrences. Island Press, Washington.

Skov, F., Svenning, J.-Ch., 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27, 366–380.

Thompson, J.D., 2005. Plant evolution in the Mediterranean. Oxford University Press, New York.

Thor, G., Arvidsson, L., 1999. Rödlistade lavar I Sverige-Artfakta [Swedish Red Data Book of Lichens]. Artdatabanken, SLU, Uppsala.

Thuiller, W., Lavorel, S., Sykes, M.T., Araújo, M.B., 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12, 49–60.

Valladares, F. (Ed.), 2004. Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, Madrid.

Vanderpoorten, A., Sotiaux, A., Engels, P., 2005. A GIS-based survey for the conservation of bryophytes at the landscape scale. Biological Conservation 121, 189–194.

Walker, P.A., Cocks, P.A., 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography Letters 1, 108–118.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., Montserrat, V.J., 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8, 1138–1146.

Zoller, S., Lutzoni, F., Scheidegger, C., 1999. Genetic variation within and among populations of the threatened lichen *Lobaria pulmonaria* in Switzerland and implications for its conservation. Molecular Ecology 8, 2049–2059.

Zoller, S., Frey, B., Scheidegger, C., 2000. Juvenile development and diaspore survival in the threatened epiphytic lichen species *Sticta fuliginosa*, *Leptogium saturninum* and *Menegazzia terebrata*: conclusions for in-situ conservation. Plant Biology 2, 496–504.