CrossMark

ORIGINAL PAPER

Case study of the implications of climate change for lichen diversity and distributions

Marta Rubio-Salcedo[1] · Achilleas Psomas[2] · María Prieto[1] ·
Niklaus E. Zimmermann[2] · Isabel Martínez[1]

Abstract There is ample evidence for species distributional changes in response to recent climate change, but most studies are biased toward better known taxa. Thus, an integrated approach is needed that includes the "cryptic diversity" represented partly by lichens, which are among the most sensitive organisms to environmental change due to their physiological characteristics. The use of functional traits and ecological attributes may improve the interpretation of how species respond to climate change. Thus, we quantified the future climate change impacts on 41 lichen species distributed in the Iberian Peninsula using ensemble climatic suitability maps (derived from generalized linear and generalized additive models, and classification and regression tree analysis) and different metrics. We also determined the lichen traits/attributes that might be related to a shared response to climate change. The results indicated a loss of bioclimatic space for 75% of the species studied and an increase for 10 species, especially in Mediterranean ones. Most of the species that will lose more than 70% of their current modeled distribution area comprised big macrolichens with cyanobacteria as the photobiont, thereby indicating a great biomass loss in forests, which might affect nutrient cycles. We also found that the predicted distributions were trait-related. Smaller species, green-algae lichens, and saxicolous and epiphyte species will respond better to future climate change. The results of this type of study may help to identify the species that are most vulnerable to climate change and facilitate the development of conservation measures to avoid their decline.

✉ Isabel Martínez
isabel.martinez@urjc.es

1   Área de Biodiversidad y Conservación, ESCET, Universidad Rey Juan Carlos, c/ Tulipán s/n, 28933 Móstoles, Madrid, Spain

2   Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland

Introduction

The negative effects of climate change on biodiversity can range from loss of genetic diversity to reductions in the distribution area of habitats and ecosystems (e.g., Chen et al. 2011; Thuiller et al. 2011; Summers et al. 2012). Species are shifting their latitudinal distributions, elevation ranges, and phenologies in response to recent climate changes (Lavorel and Garnier 2002; Root et al. 2003; Parmesan and Yohe 2003; Wilson et al. 2005). By contrast, other species are expanding their distributions due to the broadening of their bioclimatic area (Ellis et al. 2007a; Seoane and Carrascal 2008). Despite the lack of agreement on biodiversity loss patterns, most models indicate alarming consequences due to the speed and magnitude of climate change (Pereira et al. 2010; Chen et al. 2011; Thuiller et al. 2011).

Predictive models are powerful tools and they are used widely to obtain an initial understanding of climate impacts (Thuiller et al. 2006; Pereira et al. 2010) on species distributions. The bioclimatic envelope approach reflects both the direct and indirect influences of climate on species distribution areas (Pearson and Dawson 2003; Carter et al. 2006; Zimmermann et al. 2010; Araújo and Peterson 2012). These models are very useful as a first approximation to forecast the potential effects of climate change on large-scale species distributions (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Pearson and Dawson 2003; Pereira et al. 2010).

To improve the interpretation of predictive models, recent studies have evaluated the roles of specific traits and attributes in the responses of species to climate change. Identifying the main characteristics that determine the susceptibility of species to environmental change is crucial for ecological forecasting and conservation planning (Diamond et al. 2011; Kharouba et al. 2013; Summers et al. 2012). In plant ecology, an area where the number of studies of this subject has increased remarkably in recent years, certain ecological attributes and traits, such as habitat tolerance, rarity, leaf area, and dispersal ability affect the accuracy of distribution models. Thus, these traits should be considered because they might also affect the response of individual species to climate change (McPherson and Jetz 2007; Pöyry et al. 2008; Chen et al. 2011). However, it is unclear whether the attributes and traits that affect susceptibility will lead to predictable differences in the rate and extent of range shifts in response to climate change (Angert et al. 2011).

Lichens are among the most sensitive organisms to environmental change (Pinho et al. 2011; Branquinho et al. 2015), where this sensitivity is related mainly to their physiological characteristics. Lichens comprise a symbiotic association between a fungus and a photobiont partner, and they grow in a variety of land ecosystems, ranging from Antarctica to deserts and the highest mountains (Nash III 2008). These organisms are poikilohydric and they cannot regulate their water content, and thus they are dependent upon their surrounding environment (Green et al. 2011). Temperature is also an important factor that regulates mechanisms related to lichen growth, physiology, and performance (Hamada 1983; Pisani et al. 2007; Alam 2014). These ecophysiological and biological constraints make them ideal candidates for investigating the impact of climate changes.

Previous studies have shown that lichens are constrained by climate at different scales and some used predictive models to test the influence of climate change on the future distribution area, growth, and diversity of lichen species (e.g., Aptroot and van Herk 2002, 2007; Herk et al. 2002; Søchting 2004; Ellis 2015; Ellis et al. 2007a, b, 2014;

Giordani and Incerti 2008; Lisewski and Ellis 2010; Colesie et al. 2014; Allen and Lendemer 2016). Most of these studies were conducted in the center and north of Europe and North America where the predictions of climate change are weaker than those in more southern areas such as the Iberian Peninsula. The Iberian Peninsula is a suitable territory for evaluating the effects of climate change on biodiversity because although climate change impacts may be heterogeneous, a large proportion of the country could be at risk due to warming. This is due to the dominance of the Mediterranean climate with a severe summer drought, as well as the presence of mountainous areas with species at the southernmost limit of their range, and its geographical isolation (Benito et al. 2008). In addition, very little is known about the roles and importance of the ecological attributes and functional traits of non-vascular cryptogams, particularly bryophytes and lichens. Few studies have considered how lichen traits are related to ecological processes (but see Lakatos et al. 2006; Asplund and Wardle 2013; Giordani et al. 2013; Matos et al. 2015) despite their significant contribution to biodiversity and their functional importance in many ecosystems (Cornelissen et al. 2007; Ellis 2012). Based on previous research, we identified three key traits in lichens, i.e., species thallus size, growth form, and primary photobiont type, which could potentially determine their susceptibility to environmental factors because they are related mainly to water uptake and loss, as well as two ecological attributes, i.e., the modeled current distribution range (as a proxy for the distribution area size) and the main substrate type (Lange et al. 1986; Eldridge and Rosentreter 1999; Gauslaa and Solhaug 1999; Ellis and Coppins 2006; Shiver et al. 2011; Aragón et al. 2012; Ellis 2012; Merinero et al. 2014; Matos et al. 2015).

The main objective of this study was to determine the vulnerability and susceptibility of lichen species to possible distribution variations (shifts/contractions/enlargements) caused by climate change in a subset of lichen species in the Iberian Peninsula. According to the Intergovernmental Panel on Climate Change (IPCC 2001), vulnerability is "the degree to which a system is susceptible to injury, damage, or harm," and susceptibility is "the degree to which a system is open, liable, or sensitive to climate stimuli." The vulnerability of a given system is a function of its exposure to climate change effects, its susceptibility, and its ability to adapt to these conditions. We also aimed to determine the lichen traits and attributes that might be related to shared responses to climate change. Our main hypotheses are that lichen species will exhibit different future responses depending of their current distribution, and that some traits and attributes will determine the susceptibility of species, such as the type of photobiont or species size.

Methods

Study area

The study area corresponded to the Iberian Peninsula at latitudes ranging from 36°S to 44°N and longitudes from 19°W to 5°E. This territory covers 581.442 km^2 and it is well known for its heterogeneous landscape. This area of Southwest Europe comprises three biogeographical regions: Atlantic, Mediterranean, and Alpine (Costa et al. 2005; European Environment Agency 2009). The altitude ranges from sea level to more than 3000 m. The mean annual temperature varies between 10 °C on the northern plateau to over 18 °C in many different areas along the coast. Due to the heterogeneous landscape of this area, the maximum temperature can exceed 40 °C, mainly in southern Spain, or −20 °C in many

inland territories and the higher levels of the main mountain ranges. Rainfall is the most important climatic element in this territory, where the annual precipitation varies between >2000 and <200 mm in the most arid southeastern areas. Another important climatic characteristic of the Iberian Peninsula is the high percentage of the area (around 80%) that is subject to dry or very dry summers with a strong summer drought (Pérez and Boscolo 2010).

According to IPCC models, the Iberian Peninsula is one of the areas of European that is most likely to experience a great increase in temperature as well as important changes in its precipitation regime. For instance, in the last 100 years, the average temperature has increased slightly more in the Iberian Peninsula than the rest of Europe (1 °C compared with 0.9 °C). This increase has been as high as 2 °C in the southeastern areas (Comisión de Coordinación de Políticas de Cambio Climático 2007; IPCC 2007). In addition, the European Environmental Agency currently predicts a rise in the average temperature in the Iberian Peninsula of around 4 °C by 2080 (Met Office UK 2011). Extreme summers are likely to become four times as common in the Iberian Peninsula and southern Europe. In general, precipitation is projected to decrease all over Spain, where this decrease is expected to accelerate at the end of the twenty first century. The annual precipitation is projected to decrease by 20% in the central, northern, and eastern regions, and by around 30% in the southwest (Met Office UK 2011). In addition to an increase in the duration of droughts, increases in the occurrence of heavy precipitation events are predicted (Barrera-Escoda et al. 2014).

Species selection

The lichen species included in this study correspond exclusively to recently revised taxa with well-known ecological requirements and distribution areas (Burgaz and Martínez 2003; Martínez et al. 2003; Aragón and Otálora 2004; Aragón et al. 2004, 2005; Otálora et al. 2008, 2010; Burgaz and Ahti 2009; Carballal et al. 2010; Prieto et al. 2010, 2012; Muñiz and Hladún 2011), thereby avoiding the problems caused by insufficient or inaccurate records to ensure that the presence points captured the entire suitable environmental range for each species. This approach also avoided false presence points associated with taxonomically difficult species.

Our objective was to identify the general responses to climate change in functional and ecological traits and attributes, so we selected a group of species belonging to 23 genera, which encompassed a wide range of biological and functional characteristics. We selected species to cover all geographical distribution ranges (from strictly Mediterranean to temperate or Arctic alpine distributions, according to Nimis and Martellos (2008); except we followed Vitikainen (1994) and Burgaz and Martínez (2003) for *Peltigera* and *Sticta* genera), as well as covering the studied range of traits and attributes, ranging from rare to common species with different sizes, growth forms, and photobionts (Table 1).

Presence data points

We obtained point-based presence-only records for each species from bibliographic sources and herbaria. First, we selected 70 species, but we finally chose 41 lichen species as those with the minimal number of presence points (>20 independent presence points) required to obtain sufficiently robust predictions and accurate calculations (Chefaoui and Lobo 2008) (see Appendix S1 in Supporting Information).

Table 1 Traits and attributes of the studied species

Species	Size	GF	Photo	Subs	World distribution	Modeled distributions			Loss	Relative exposure	Shift
						Current	Future	Gain			
Buellia. cedricola	S	Cr	G	E	M	14,159	41,472	229.18	36.28	192.9	67.64
Calicium glaucellum	S	Cr	G	E	Temp, BM	8300	28,100	327.71	89.16	238.55	95.05
Catapyrenium cinereum	S	S	G	T	BM, AA	11,111	1484	0.85	87.49	−86.64	78.87
C. daedaleum	S	S	G	T	BM, AA	22,396	4863	2.52	80.80	−78.29	68.81
Cetraria crespoae	S	Fr	G	E	M	22,684	6475	14.07	85.53	−71.46	77.75
Chaenotheca chrysocephala	S	Cr	G	E	BM	49,127	26,479	12.22	58.32	−46.1	45.90
Cladonia mediterranea	S	Fr	G	T	M	18,336	30,660	111.99	44.78	67.21	60.20
Dirina ceratoniae	S	Cr	G	E	M	8610	8215	49.78	54.37	−4.59	53.42
Fuscopannaria ignobilis	S	S	C	E	MA	22,297	27,403	84.45	61.55	22.9	65.66
Koerberia biformis	S	S	C	E	mT	15,184	15,024	90.5	91.56	−1.05	97.88
Leptogium aragonii	S	Fo	C	Sx	H	24,105	10,435	27.72	84.43	−56.71	78.41
L. furfuraceum	S	Fo	C	E	mT, hS	45,735	74,121	159.26	97.19	62.07	97.85
L. lichenoides	L	Fo	C	Sx	H	25,196	9761	12.05	73.31	−61.26	61.74
L. pulvinatum	S	Fo	C	T	H	22,100	21,700	67.42	69.23	−1.81	68.94
Lobaria amplissima	L	Fo	C	E	mT	16,700	2000	6.59	94.61	−88.02	90.37
L. pulmonaria	L	Fo	G	E	Tem, H	17,500	6200	28	92.57	−64.57	89.76
Lobarina scrobiculata	L	Fo	C	E	mT	19,800	25,100	58.08	31.31	26.77	39.42
Nephroma laevigatum	L	Fo	C	E	mT, hS	24,800	20,500	47.98	65.32	−17.34	62.03
N. parile	L	Fo	C	E	CT, BM	17,000	3200	9.41	90.59	−81.18	84.15
N. resupinatum	L	Fo	C	E	Tem, H	30,800	10,800	19.16	84.09	−64.94	76.81
Peltigera canina	L	Fo	C	T	H	20,600	7900	14.56	76.21	−61.65	65.84
P. collina	L	Fo	C	E	H	30,800	10,500	9.09	75.00	−65.91	62.71
P. elisabethae	L	Fo	C	T	H	24,300	4900	0	79.84	−79.84	66.89
P. horizontalis	L	Fo	C	E	H	22,900	3100	3.93	90.39	−86.46	83.91

Table 1 continued

Species	Size	GF	Photo	Subs	World distribution	Modeled distributions		Gain	Loss	Relative exposure	Shift
						Current	Future				
P. hymenina	L	Fo	C	T	mT	21,300	2900	0	86.38	−86.38	76.66
P. leucophlebia	L	Fo	G	T	H	19,400	4000	0	79.38	−79.38	66.37
P. membranacea	L	Fo	C	T	H	30,300	7000	0	76.90	−76.9	62.80
P. monticola	L	Fo	C	T	H	22,329	5916	6.56	80.07	−73.51	68.88
P. neckeri	L	Fo	C	T	H	14,100	17,400	80.85	57.45	23.4	61.90
P. polydactylon	L	Fo	C	T	H	12,800	2200	0	82.81	−82.81	71.62
P. praetextata	L	Fo	C	T	H	21,400	5400	7.48	82.24	−74.77	71.91
P. venosa	L	Fo	G	T	H	17,400	4800	0	72.41	−72.41	57.27
Pertusaria paramerae	S	Cr	G	E	M	42,820	7055	12.5	96.02	−83.52	93.17
Placidium imbecillum	S	S	G	T	BM	7716	542	0.29	93.26	−92.98	87.66
Pyrrhospora lusitanica	S	Cr	G	E	MA	14,159	22,469	82.73	24.04	58.69	41.34
Solenopsora holophaea	S	S	G	Sx	MA	9900	26,900	174.75	3.03	171.72	47.82
Solorina saccata	L	Fo	C	T	CT, AA	28,200	8800	0	68.79	−68.79	52.71
Staurolemma omphalarioides	S	Fo	C	E	mT, MA	5440	2438	44.67	99.85	−55.18	99.73
Sticta fuliginosa	L	Fo	C	E	mT	16,600	11,200	57.83	90.36	−32.53	88.48
Teloschistes chrysophthalmus	S	Fr	G	E	mT, hS	9604	5193	24.31	70.24	−45.93	62.81
Waynea adscendens	S	S	G	E	MA	14,159	39,311	225.64	48	177.64	72.54
Mean ± SD						20,541	−6542.70	51.32	73.30	−21.97	0.70
						9657.04	14,976.41	74.45	21.6	85.41	0.15

Size (thallus size): S, small; L, large. GF (growth form): Cr, crustose; S, squamulose; Fr, fruticose; Fo, foliose. Photo (photobiont type): G, green-algae; C, cyanobacteria. Current distribution: km² of modeled current distribution (likelihood > 70%). Subs (substratum type): E, epiphyte; T, terricolous; Sx, saxicolous. World distribution: M, Mediterranean; MA, Mediterranean Atlantic; Tem, temperate; CT, cool temperate; mT, mild temperate; BM, boreal montane; AA, Arctic alpine; hS, humid subtropical; H, Holarctic. Specific impact values for climate change. Modeled distribution: extension (km²) of climatic suitability areas (likelihood threshold > 70%) under current and future climatic conditions

We homogenized and stored the data in two databases at different resolutions, with presence points at 1 and 10 km². We used coarse levels for modeling and projecting, depending on the input data resolution. The models referred to a 584,675-cell grid when working at the 1 km² scale, whereas the models referred to a 6089-cell grid when the resolution was 10 km² (Appendix S2).

Independent climatic variables

We obtained raw climatic variables for the Iberian Peninsula from Ninyerola et al. (2005; available at http://opengis.uab.es/wms/iberia/espanol/es_cartografia.htm) and transformed the monthly data into 19 "bioclimatic variables" (Worldclim, http://www.worldclim.org/bioclim; see Busby (1991) and Hijmans et al. (2005) for details of the variables and methods used to generate the climate layers) with R version 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria). To avoid problems of multicollinearity, only uncorrelated variables (Pearson's correlation coefficient < 0.7 and $P > 0.05$) were included in the models. For two correlated variables, we selected the most meaningful based on their importance for lichen biology and previous evaluations of the influence of climate on the presence and abundance of lichen species in the Iberian Peninsula (Aragón et al. 2010, 2012; Martínez et al. 2014; Concostrina-Zubiri et al. 2014a, b; Merinero et al. 2014; Matos et al. 2015; Otálora et al. 2015; Matos et al. in prep.). Thus, from the original 19 climate variables, we considered only five variables that described the baseline climate data: BIO1 (mean annual temperature, °C), BIO8 (mean temperature in the wettest quarter, °C), BIO9 (mean temperature in the driest quarter, °C), BIO12 (annual precipitation, mm), and BIO17 (precipitation in the driest quarter, mm) (descriptions of the variables and values are provided in Appendix S3).

Future climate scenarios

The future climate in 2080 (2051–2080) was represented by the A1B scenario (characterized by the balanced development of energy technology between fossil fuel and non-fossil fuel; Nakicenovic and Swart 2000) with three regional climate model (RCM) runs, which originated from the ENSEMBLES EU project, where global circulation model (GCM) data were physically downscaled from the 4th IPCC assessment report (IPCC 2007). The A1scenario family, which includes the A1B scenario, describes a future world with rapid economic growth, a mid-century global population peak with a subsequent decline, and the rapid introduction of new and more efficient technology. The A1 scenario family develops into three groups that describe alternative directions for technological change in the energy system, one of which is the A1B scenario (https://www.ipcc.ch/pdf/special-reports/spm/sres-sp.pdf).

The projected global average surface warming in the Iberian Peninsula for the end of the twentyfirst century has a best estimate of 2.8°C in the A1B scenario. According to the same scenario, the estimated precipitation in the Iberian Peninsula is around -0.2 mm day^{-1} (https://www.ipcc.ch/publications_and_data/ar4/syr/es/mains3.html).

RCMs downscale the very coarse resolution climate model output of GCMs (usually 1–2° Lat/Long per grid cell) to a much finer spatial resolution (usually 10–30′ Lat/Long) based on a physical process. Thus, an RCM is fed by the global output of GCMs to provide the boundary conditions and global weather input for downscaling. In this project, we used three RCMs, i.e., HadRM3, HIRHAM3, and RACMO2 (Hewitt 2004), which were fed by three different GCMs, i.e., HadCM3, ECHAM5, and Arpège. These RCMs represented a

wide range of future climate projections. All of the RCM scenarios were interpolated to the same spatial resolution of 30 arc-seconds (~ 1 km) for the 30-year mean monthly temperature and precipitation values. These monthly values were used to calculate the 19 bioclimatic variables in Worldclim for the 2080 time period (see Appendix S4).

Modeling and projection

Bioclimatic envelope models are sensitive to the mathematical functions used to describe species distributions (Araújo et al. 2005; Araújo and New 2007). We quantified the exposure of species to climate change by using an ensemble of various model projections, which yielded a lower mean error than that of any of the constituent individual forecasts (Thuiller 2003; Araújo and New 2007).

Three alternative techniques were used to model the current presence of each single species: generalized linear models (GLMs), generalized additive models (GAMs), and classification and regression tree (CART) analysis. (1) GLM (McCullagh and Nelder 1989): GLMs were built, before applying backward and forward stepwise variable selection procedures based on Akaike's information criterion (Akaike 1974) to select the most significant variables. The model fit was evaluated using the adjusted D^2 according to Weisberg (1980). The agreement between predictions and observations was assessed using the standard area under the curve (AUC) measure based on the receiver operating characteristic plot (Fielding and Bell 1997). Only projections from models where AUC > 0.7 (Swets 1988) were considered in subsequent analyses in order to avoid using poorly calibrated models. We also evaluated the model accuracy using Cohen's kappa (k; Cohen 1960). (2) GAM (Hastie and Tibshirani 1990): GAMS are nonparametric extensions of GLMs, which are more data-driven than GLMs, where they allow both linear and complex additive responses shapes (Pöyry et al. 2008). A stepwise variable selection procedure was also performed, where the model fit was evaluated using the percentage deviance. AUC and k were calculated as for the GLMs, where the models with AUC < 0.7 were discarded. (3) CART (Breiman et al. 1984): CART is a procedure that employs a 10-fold cross-validation to select the best trade-off between the number of leaves in the tree and the explained deviance. CART is used less commonly than the two previous methods, but it is accurate and useful (Thuiller 2003). Trees were pruned to their optimal size using the complexity parameter (Venables and Ripley 2002) and models were evaluated using Cohen's k (Cohen 1960). If k < 0.4 (Araújo et al. 2005), only GLM and GAM were considered to build the ensemble map.

For each species, we used the initial number of presence records (Appendix S2) and 200 pseudo-absences selected randomly across the study area between these points with a probability of occurrence ≤0.2 (Chefaoui and Lobo 2008). Randomly selected pseudo-absences yield the most reliable distribution models (Barbet-Massin et al. 2012). The species presence input data ranged from 20 to 159 points (Appendix S2).

Not all of the five climatic variables were used when fitting models for species with less than 50 presence points. To avoid over-parameterization, we employed a rule-of-thumb where we included one explanatory climatic variable for each 10 presence points. All three models (GLM, GAM, and CART) were run for each species and the calibrated models were then used to project the species distributions. The likelihood of occurrence was projected for individual species based on present-day modeled climate data (Ninyerola et al. 2005) and the future climate in 2080 using the A1B scenario with three RCMs.

Finally, an ensemble projection map was developed for each species by combining the single output climate suitability maps. The likelihood under current conditions was the

average of the projected maps (obtained from the three algorithms), whereas the likelihood under future conditions was the average of nine combinations (three algorithms and three possible scenarios). This allowed us to assess the projected uncertainty due to the variability attributable to statistical methods and the modeled climate.

To produce binary maps of the current and future climate suitability, the ensemble maps for each species were reclassified into presence/absence values. We tested two different threshold likelihood values, i.e., 0.5, which has been used widely in many studies (i.e., Manel et al. 1999; Bailey et al. 2002), but this option has received many objections from various researchers (Osborne et al. 2001; Liu et al. 2005), so we also used a threshold 0.7 to discriminate presences and absences. Both obtained very similar results for the proportional range shifts, so the more conservative threshold of 0.7 was fixed. Binary maps of the modeled current and future distributions were used to calculate species-specific impact metrics, as described in Table 2.

Species traits

Potentially important lichen species traits were considered and classified as "functional" or "ecological" traits. Data were obtained from bibliographic sources (except the current distribution) (Table 1), as follows.

Functional traits: (1) Species thallus size (mm): average maximum diameter of the thallus, where L = large (diameter >5 mm) and S = small (diameter ≤5 mm). This threshold size split the species data into two balanced groups, which were similar to the micro- and macrolichen groups. Data were used from different studies (i.e. Burgaz and Martínez 2003; Aragón et al. 2005; Otálora et al. 2008; Carballal et al. 2010; Prieto et al. 2010; Múñiz and Hladún 2011; etc.). Thallus size is related to the water-holding capacity and/or maintenance cost (Gauslaa and Solhaug 1998; Fos et al. 1999). (2) Growth form: this factor describes the main growth forms of lichens (classified according to Asplund and Wardle 2013). The species studied were grouped into: Cr = crustose, S = squamulose, Fr = fruticose, and Fo = foliose. Lichen morphology is related to the water uptake and water-holding capacity. For example, crustose lichens are expected to resist drought events because of their desiccation tolerance, whereas the foliose and fruticose growth forms are more sensitive to desiccation (Büdel and Scheidegger 2008; Giordani et al. 2012; Nascimbene and Marini 2015). (3) Photobiont type: primary photobiont in a symbiosis as a two-level-factor: G = green-algae and C = cyanobacteria. Only the primary photobiont

Table 2 Impact metrics. List of variables and their calculation

Variable	Description	Unit
Current distribution	Suitable climatic area under current conditions. (Threshold likelihood = 70%)	km^2
Future distribution	Suitable climatic area under future conditions. (Threshold likelihood = 70%)	km^2
Exposure	Future distribution-current distribution	km^2
Relative exposure	(Exposure/current distribution) × 100	%
Gain	Suitable areas under future conditions (net gain/current distribution) × 100	%
Loss	Suitable areas under current conditions (net loss/current distribution) × 100	%
Shift	(Net gain + net loss)/(current distribution + future distribution) × 100	%

was considered for tripartite lichens (more than one photobiont). The photobiont type is related to lichen physiology. Cyanolichens depend entirely on liquid water for positive carbon gain (Lange et al. 1986), whereas green-algae lichens and tripartite lichens are only activated by humid air (Nash III 2008). Furthermore, the thallus hydration values for net photosynthesis are also different, where photobionts play an important role in the water-holding capacity (Merinero et al. 2014). The functional trait values obtained for each species from bibliographic sources are shown in Table 1.

Ecological attributes: (4) Modeled current distribution: the suitable climatic area (km^2) calculated under current conditions (we used the modeled current distribution because voucher data may under-represent the actual distributions due to sampling bias). We treated the modeled current distribution range as an attribute that represented the wider or narrower distribution area of each species. Widely distributed species with less strict environmental requirements may have a greater ability to expand their range boundaries or habitat niches, and thus they may be more resistant to climate change (Angert et al. 2011; Kharouba et al. 2013). (5) Substrate type (Asplund and Wardle 2013): the substrate type on which a lichen species can grow, E = epiphytic or corticolous, T = terricolous, and Sx = saxicolous. Not all of the available substrates have the same ecological implications. Thus, saxicolous lichens are usually more exposed to drying out and terricolous lichens compete more directly with vascular plants for resources (i.e. Bruun et al. 2006; Baniya et al. 2014; Rai et al. 2015). In addition, epiphytes are strongly dependent on their host's dynamics (Shiver et al. 2011; Ellis et al. 2014) and their own response to climate change (Felicísimo et al. 2012) (Table 1).

Climate change impact evaluation

To evaluate the impacts of climate change on the lichen species, we calculated seven impact metrics to estimate specific distribution changes and the exposure to climate change (see Table 2 for descriptions of the variables).

The modeled current distribution and future distribution (km^2) were calculated as the aerial extent for both the modeled current and future conditions using binary consensus maps (likelihood threshold >70%). In the following, we refer to these as the current and future distributions for simplicity. Exposure was the difference between the future and current distribution. The values obtained were used to calculate the distribution variation as: ((future-current distribution)/current distribution)*100)), in order to determine the relative exposure to climate change. Thus, high negative relative exposure values indicate that a species is at a higher risk when affected by climate change, whereas higher positive values indicate lower risk.

Spatially explicit future and current distributions were overlapped by Geographic Information System to calculate the specific area gain or loss. Gain indicates that a species is less vulnerable to climate risk, where overlapping represents new climatic areas where the species might migrate (gain = (net gain/current distribution) * 100). Loss indicates the proportional area lost, where a larger value denotes higher species vulnerability (loss = (net loss/current distribution) * 100). The species distribution range shift was also calculated (shift = (net gain + net loss)/(current distribution + future distribution). A value closer to 100 indicates less overlap between the current and future distributions. This approach provides a measure of the distance a species might have to migrate.

Trait–impact relationships

We used GLMs to test for associations between each trait/attribute and each impact metric. For factors with more than two levels, we used the lm and Tukey HSD test in R version 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria). Five traits and attributes were tested as explanatory variables (see Table 1) and the response variables were the seven impact metrics (described in Table 2), except for the current distribution, which was used as a proxy of the distribution range breadth.

To avoid multicollinearity, we ensured that all the predictor variables had correlations < 0.7. The residuals obtained from the GLMs were generally uniformly distributed.

The current and future distributions were square root-transformed to satisfy the model assumption of normality. The response variables shift and exposure were normally distributed, and thus "identity" was used as the link function. Relative exposure, gain, and loss had trimodal distributions, so we could not directly test the effects of species traits on them. However, we analyzed the effects of traits on gain using the subsample of species with positive exposure values (future distribution > current distribution). Gain was natural log-transformed and we used the link function "identity." Similarly, loss was analyzed using the subsample of species with negative exposure values. We analyzed the absolute value of **loss** using link = "logit".

Results

The model accuracy varied depending on the statistic used (Appendix S2). The AUC values were within an acceptable range (GAMs: $0.76 < AUC < 0.95$; GLMs: $0.78 < AUC < 0.97$) and the k values were also adequate [GAMs: $0.34 < k < 0.87$; GLMs: $0.37 < k < 0.83$; CART: $0 < k < 0.95$, excluding CART models where $k < 0.4$ (Appendix S2)]. The models explained 23–100% of the variance in the lichen distribution using GAMs, where the D^2 values (GLMs) varied between 0.22 and 0.77 (Appendix S2).

Projected potential areas and calculated range shifts

Our results showed the variability in the species distributions under current and future conditions. The distributions under current climatic conditions varied from 5440 km^2 for *Staurolemma omphalarioides* to an almost ten times larger range for *Chaenotheca chrysocephala* (49,127 km^2) (Table 1). The mean value of the current distribution was 20,541 km^2, which decreased by more than 30% under future conditions. The relative exposure values were negative for most of the species (31 out of 41) and quite high (mean = -21.97%, Table 1). The general results indicated a projected loss of bioclimatic space for most of the species.

We observed that the 41 species tended to fall into three natural groups according to our impact metrics. We considered the first group to be highly vulnerable because they had a high loss (<70%), no gain, and negative relative exposure (Table 1). The seven taxa in this group comprised *Peltigera elisabethae*, *P. hymenina*, *P. leucophlebia*, *P. membranacea*, *P. polydactylon*, *P. venosa*, and *Solorina saccata*. *Peltigera elisabethae* (Fig. 1e) was an extreme case, which was restricted to some areas of the Cordillera Cantábrica and the Pyrenees under future conditions. The second group comprised 10 species ("moderately vulnerable") with positive relative exposure values and a considerable gain in most cases
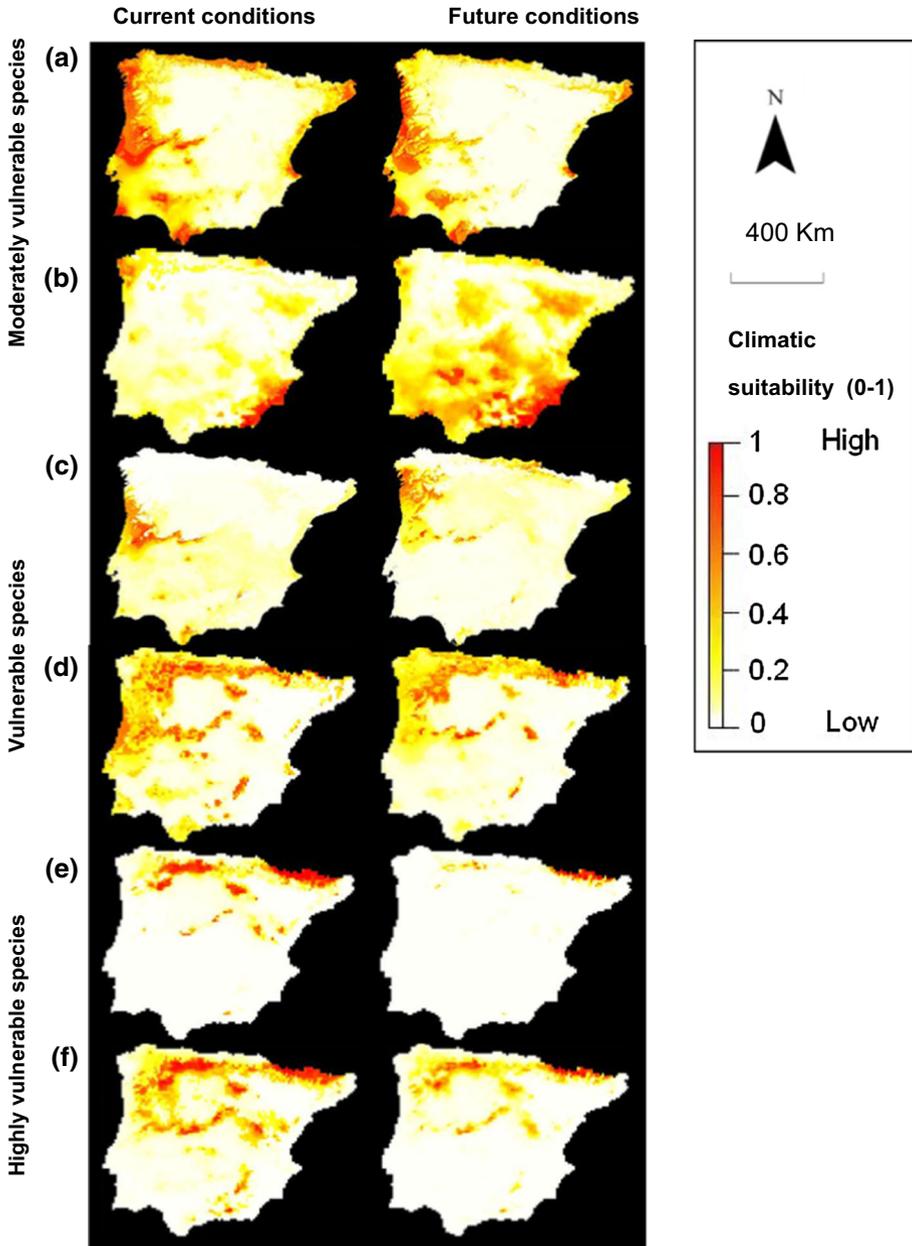
Fig. 1 Climatic suitability maps. Moderately vulnerable species: **a** *Cladonia mediterranea,* **b** *Solenopsora holophaea*; vulnerable species with different responses: **c** *Staurolemma omphalarioides,* **d** *Lobaria pulmonaria*; highly vulnerable species: **e** *Peltigera elisabethae,* **f** *Solorina saccata*

(*Buellia cedricola, Calicium glaucellum, Cladonia mediterranea* (Fig. 1a), *Fuscopannaria ignobilis, Leptogium furfuraceum, Lobarina scrobiculata, Peltigera neckeri, Pyrrhospora lusitanica, Solenopsora holophaea,* and *Waynea adscendens*). Finally, the remaining 24

species comprised a group of "vulnerable" species with different responses, where they all had high loss values (loss >50%) and a negative relative exposure with variable gains (gain values = 0.29–57.83%). This largest group of species mainly lost climatic space to a different extent, such as *Lobaria pulmonaria* (Fig. 1d) with a reduced distribution (relative exposure = −66.57%, loss = 92.57%, shift = 89.76%; see Table 1), and *Staurolemma omphalarioides* (Fig. 1c), the distribution of which exhibited a clear northward displacement (also see Table 1, shift = 99.73%) but it was not reduced due to distribution gains (gain = 44.67%, Table 1).

The shift values showed that future climatic conditions led to distribution displacements in all species (Table 1). The future and current distribution areas of species such as *Staurolemma omphalarioides,* which had a very high shift value (99.73%) (also see Fig. 1c), had almost no overlap.

Impacts and traits/attributes

Growth form was the only trait with no effect on any of the impact metrics considered. None of the traits/attributes affected the shift response variable.

Species thallus size was the trait that had the strongest relationship with the climate change impact metrics. Thus, smaller species will have a higher future distribution, higher exposure, and lower habitat loss. Photobiont type was another notable functional trait. Green-algae lichens had significantly higher gain values when tracking suitable climatic conditions (Table 3).

Among the ecological attributes, substrate type was related to the future distribution. Terricolous lichens had smaller distributions under future conditions compared with saxicolous and epiphytic lichens. The modeled current distribution was also relevant when evaluating exposure because species with reduced current distributions tended to have higher exposure values (Table 3).

Table 3 GLM results for the effects of each trait on each impact metric

Impact metric	Trait	Level	Estimate ± SD	P value
Future distribution	Size	Intercept	84.92 ± 10.95	<0.001
		Small	41.42 ± 15.68	0.011
	Substrate type	Intercept	120.93 ± 10.68	<0.001
		Saxicolous	6.89 ± 27.23	0.814
		Terricolous	−45.04 ± 16.77	0.011
Exposure	Size	Intercept	−13,478 ± 2918	<0.001
		Small	13,965 ± 4177	0.001
	Current distribution	Intercept	53.52 ± 12.11	0.314
		Current distribution	−0.58 ± 0.23	0.015
Gain	Photobiont	Intercept	3.41 ± 0.28	<0.001
		Green-algae	1.45 ± 0.36	0.004
Loss	Size	Intercept	4.19 ± 0.22	<0.001
		Small	−0.79 ± 0.36	0.035

Only significant traits are shown. Current distribution = modeled current distribution

Discussion

Previous studies have noted that lichens are among the most sensitive organisms to climate change (Aptroot and van Herk 2007; Ellis 2013). Our study provides a general view of the projected impacts of climate change on lichens, including a high number of species from various genera with differences in their ecology, distribution area, and functional traits (but see Ellis et al. 2007a, b, 2014, Allen and Lendemer 2016). Our results strongly suggest a loss of bioclimatic space for most species (75% of species studied) but an increase for some (10 species). Our results also demonstrate that the relative exposure, susceptibility, and vulnerability are species-specific, but some general response patterns might be established according to different traits and attributes.

Overall, our results indicated geographical shifts for all of the species studied. Moreover, most of the predicted shifts involve a contraction of the distribution, thereby leading to reduced species ranges. Indeed, the mean distribution of the species considered decreased by 30% under future climate conditions, which is consistent with the declines in lichen occurrence determined by experimental studies following the simulated effects of climate change (Aptroot and van Herk 2007; Ellis et al. 2007a; Escolar et al. 2012; Allen and Lendemer 2016). Our results are in agreement with many previous studies in other groups of organisms (e.g., Root et al. 2003; Chen et al. 2011; Bellard et al. 2012). The convergence of these predictions in terms of reduced distribution areas or even species losses in many different organisms support the robustness of this general trend, and thus it might be interpreted as a major threat to biodiversity.

However, climate change could also have positive effects on bioclimatic ranges, especially in Mediterranean species such as *Buellia cedricola* and *Cladonia mediterranea*, as well as in *Pyrrhospora lusitanica*, *Solenopsora holophaea*, and *Waynea adscendens* with a Mediterranean Atlantic distribution. Moreover, species such as *B. cedricola, S. holophaea*, and *W. adscendens* currently have a restricted world distribution (Global Biodiversity Information Facility; www.gbif.org, accessed on 28/09/2016), but their future distribution ranges will increase in the Iberian Peninsula by more than 170%, thereby suggesting that these species will have a wider world distribution area in the future. According to our study, 10 species expanded their distributions, including those mentioned earlier, as well as other species that we did not expect to have increased ranges in the future. For instance, *Peltigera neckeri* has a general Holarctic distribution but it mainly occurs in the Mediterranean region in the Iberian Peninsula (Burgaz and Martínez 2003). It was the only *Peltigera* species considered in this study with an increased distribution area in the future. In addition, *Calicium glaucellum* has a temperate to boreal montane global distribution but it is more frequent in the meso- and supramediterranean belts of the Mediterranean region in the Iberian Peninsula (Muñiz and Hladún 2011). Mild temperate species such as *Leptogium furfuraceum* or *Lobarina scrobiculata* will also increase their distribution area, where *L. scrobiculata* is a species in the genus *Lobaria* s. lat. that is better suited to the summer drought with the Mediterranean climate (Burgaz and Martínez 2003).

The climate change predictions for the Iberian Peninsula indicate increases in temperature and reduced precipitation, so the species with current Mediterranean distribution will have better conditions in the future and their distribution areas will increase. Long-term monitoring studies have shown that warm-temperate lichens have increased their European distributional ranges, whereas species specific to cold and wet environments have decreased or disappeared (e.g., Herk et al. 2002). Ellis et al. (2007b) also found an

increase in response to future climate change in the potential range of *Lecanora populi-cola*, a lichen species in northern Britain.

In addition, another group of species will lose more than 70% of their current modeled distribution area, most of which are large macrolichens with cyanobacteria as their photobionts. Decreases in these species will lead to great biomass losses in the forests where they grow, thereby affecting nutrient cycles and the provision of food and habitats for animals (Sillett et al. 2000; Edman et al. 2008; Ellis 2012). For instance, among the 12 *Peltigera* species analyzed, nine with a Holarctic distribution will lose more than 70% of their area. This was an expected result given the ecological characteristics of these species, as well as the loss of distribution area for species linked to high mountains, such as *Catapyrenium cinereum*, or *C. daedaleum* with a boreal montane to arctic alpine distribution (Table 2). Similar results were obtained by Allen and Lendemer (2016) in a study of the impact of climate change on endemic and high-elevation lichens in the Southern Appalachians, USA, where they found distributional losses of over 93% in all of the species they studied. However, surprisingly, our results indicate that species with a continental Mediterranean distribution (characterized by moderately humid summers and cold, dry winters) and an extremely restricted world distribution, such as *Cetraria crespoae* and *Pertusaria paramerae* (Crespo and Vězda 1985; Barreno and Vázquez 1981; Roux et al. 2003a, b; Halici et al. 2010; Muñiz et al. 2013), will also lose more than 70% of their current distribution area, which probably makes them the most vulnerable species considered in this study (Table 1).

Moreover, our analysis identified a significant relationship between the functional traits and ecological attributes of some lichen species and their responses to climate change impacts. Smaller species such as *Calicium glaucellum* or *Waynea adscendens* will respond better to future climatic conditions because they are less exposed, susceptible, and vulnerable. Several studies have shown that larger thalli such as those of *Peltigera*, *Nephroma*, and *Lobaria* species require greater water availability (Merinero et al. 2014), and a higher biomass could imply higher costs of maintenance as they occur on plants (Milla and Reich 2007).

Other traits were also related to the future distribution of species and their susceptibility to change. In terms of substrate type, terricolous lichens such as *Catapyrenium* species or *Placidium imbecillum* will have smaller future distributions compared with epiphytes. These results may accurately reflect the situation for soil lichens because lichens that grow directly on the soil respond more directly to climatic parameters (Escolar et al. 2012; Concostrina-Zubiri et al. 2014a).

As expected, green-algae lichens exhibited less susceptibility to climate change than cyanolichens. Among the lichens with enlarged distribution areas, green-algae lichens will undergo greater expansions under future climate conditions. Lichens with a green photobiont perform better under drier conditions (Lange et al. 1986); therefore, green-algae lichens will respond better in the drier conditions predicted for the Iberian Peninsula (IPCC 2007).

Species with small modeled current distributions had higher relative exposure values. These species are usually found in habitat types that are relatively rare at present in the Iberian Peninsula, where most of them grow in habitats with extreme Mediterranean conditions, which could become more common when climatic conditions change in the next few decades (IPCC 2007). *Cladonia mediterranea* (gain = 111.99%) and *Solenopsora holophaea* (gain = 174.75%) are mainly Mediterranean species with restricted distributions in Europe, where their bioclimatic niches are linked to warm and dry areas (Rubio-Salcedo et al. 2013). Ellis and Coppins (2006) also found an increase in

suitable areas for "southern species" (that require warmer temperatures and tolerate drought better) in Scotland. A species may be locally abundant in sandy coastal areas, rocks, and dunes, such as *Cladonia mediterranea*, for which the models predicted an increase in the distribution area, but these habitats are currently threatened and disturbed (Morillo and Gómez-Campo 2000; Cogoni et al. 2011), and they may be threatened more in the future due to the predicted rise in the sea level (Moreno et al. 2005). This example highlights how complex interactions between global change factors are not considered in these models and these interactions may decrease or increase the future extinction risk (Pereira et al. 2010).

Our approach provides a valuable tool for exploring how lichen species will respond to climate change in the Iberian Peninsula and how specific traits and attributes are associated with these responses. Nevertheless, these results should be interpreted with caution given the assumptions and limitations of this type of analysis (Thuiller 2003; Pearson and Dawson 2003; Zimmermann et al. 2010; Araújo and Peterson 2012; Ellis 2015). In addition, lichen species must cope with additional co-occurring threats, such as pollution (Giordani et al. 2002) and habitat destruction (Ellis et al. 2014), some of which may act in synergy with climate change (Bellard et al. 2012; Ellis et al. 2014). However, this type of study may help Spanish and Portuguese authorities to detect species that are more vulnerable to climate change in order to develop conservation measures that might prevent declines in their populations. For instance, extremely vulnerable species such as *Cetraria crespoae* and *Pertusaria paramerae* with a Mediterranean distribution are known from very few countries throughout the world and they will lose more than 70% of their modeled current distribution, possibly leading to the global extinction of these species.

Conclusions

This study provides useful estimates of the projected impacts of climate change on lichen species in southern Europe, which is a territory that will be affected greatly by climate change. Our results suggest a great loss of bioclimatic space, with some exceptions for species linked to drier and warmer areas. Moreover, focusing on the traits of lichen species may be valuable for determining their distribution patterns. We found that species thallus size, substrate type, and photobiont type were important lichen traits related to general responses to climate change, while the modeled current distribution and substrate type were important ecological attributes. Lichens species are sensitive to climate but they are also sensitive to pollution, urbanization, forest stand age, their host's dynamics, and other factors (McCune et al. 1997; Ellis 2012; Ellis et al. 2014). Thus, all of these factors might determine the distributions of lichen species as well as factors such as biotic interactions or their specific dispersal capacity (Lawrey 1991; Muñoz et al. 2004).

References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723

Alam MA (2014) Growth chamber experiments on lichens. Temperature and humidity regimes rapidly shape growth rates and carbohydrate contents. Master Thesis. Norwegian University of Life Sciences

Allen JL, Lendemer JC (2016) Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. Biodivers Conserv 25:555–568

Angert LA, Crozier LG, Rissler LE, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? Ecol Lett 14:677–689

Aptroot A, van Herk CM (2002) Lichens and global warming. Int Lichenol Newsl 35:57–58

Aptroot A, van Herk CM (2007) Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. Environ Pollut 146:293–298

Aragón G, Otálora MAG (2004) Ecological and chorological novelties of the genus *Leptogium* in the Iberian Peninsula. Nova Hedwig 78:353–366

Aragón G, Sarrión FJ, Martínez I (2004) Epiphytic lichens on *Juniperus oxycedrus* in the Iberian Peninsula. Nova Hedwig 78:45–56

Aragón G, Otálora MAG, Martínez I (2005) New data of the genus *Leptogium* (ascomycetes lichenized) in the Iberian Peninsula. Nova Hedwig 80:199–226

Aragón G, Martínez I, Izquierdo P, Belinchón R, Escudero A (2010) Effects of forest management on epiphytic lichen diversity in Mediterranean forests. Appl Veg Sci 13:183–194

Aragón G, Martínez I, García A (2012) Loss of epiphytic diversity along a latitudinal gradient in southern Europe. Sci Total Environ 426:188–195

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Araújo MB, Peterson T (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93:1527–1539

Araújo MB, Pearson R, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. Glob Change Biol 11:1–10

Asplund J, Wardle DA (2013) The impact of secondary compounds and functional characteristics on lichen palatability and decomposition. J Ecol 101:689–700

Bailey SA, Haines-Young RH, Watkins C (2002) Species presence in fragmented landscapes: modelling of species requirements at the national level. Biol Conserv 108:307–316

Baniya CB, Rai H, Upreti DK (2014) Terricolous lichens in Himalayas: patterns of species richness along elevation gradient. In: Rai H, Upreti DK (eds) Terricolous lichens in India. Springer, New York, pp 33–52

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Electing pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3:327–338

Barreno E, Vázquez VM (1981) *Coelocaulon crespoae* Barreno & Vázquez sp. nova (Lichenes). Notas sobre la flora liquénica de brezales españoles. Lazaroa 3:235–246

Barrera-Escoda A, Gonçalves M, Guerreiro D, Cuniellera J, Baldasano JM (2014) Projections of temperature and precipitation extremes in the North-Western Mediterranean Basin by dynamical downscaling of climate scenarios at high-resolution (1971–2050). Clim Change 122:567–582

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Benito MG, Sánchez de Dios R, Sainz HO (2008) Effects of climate change on the distribution of Iberian trees species. Appl Veg Sci 11:169–178

Branquinho C, Matos P, Pinho P (2015) Lichens as ecological indicators to track atmospheric changes: future challenges. In: Lindenmayer D, Barton P, Pierson J (eds) Indicators and surrogates of biodiversity and environmental change. CSIRO Publishing, CRC Press, Melbourne

Breiman L, Friedman JH, Olshen RA et al (1984) Classification and regression trees. Chapman & Hall, New York

Bruun HH, Moen J, Virtanen R, Grytnes J-A, Oksanen L, Angerbjörn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. J Veg Sci 17:37–46

Büdel B, Scheidegger C (2008) Thallus morphology and anatomy. In: Nash TH III (ed) Lichen biology. Cambridge University Press, Cambridge, pp 40–68

Burgaz AR, Ahti T (2009) Flora Liquenológica Ibérica. In: Cladoniaceae, Vol 4. Sociedad Española de Liquenología, SEL, Madrid

Burgaz AR, Martínez I (2003) Flora liquenológica ibérica. Peltigerales: lobariaceae, nephromataceae, peltigeraceae. Sociedad Española de Liquenología, SEL, Murcia

Busby JR (1991) BIOCLIM a bioclimate analysis and prediction system. Plant Prot Q 6:8–9

Carballal R, Paz-Bermúdez G, López de Silanes ME, Pérez Valcárcel C (2010) Flora liquenológica ibérica. Pannariaceae. Sociedad Española de Liquenología, SEL, Pontevedra

Carter GM, Stolen ED, Breininger DR (2006) A rapid approach to modeling species–habitat relationships. Biol Conserv 127:237–244

Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. Ecol Model 210:478–486

Chen I, Hill JK, Ohlemüller R, Roy DB et al (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Cogoni A, Brundu G, Zedda L (2011) Diversity and ecology of terricolous bryophyte and lichen communities in coastal areas of Sardinia (Italy). Nova Hedwig 92:159–175

Cohen J (1960) A coefficient of agreement for nominal scales. Educ Psychol Meas 20:37–46

Colesie C, Green TGA, Haferkamp I, Büdel B (2014) Habitat stress initiates changes in composition, CO_2 gas exchange and C-allocation as life traits in biological soil crusts. ISME J 8:2104–2115

Comisión de Coordinación de Políticas de Cambio Climático (2007) El cambio climático en España. Estado de situación. Documento Resumen. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid

Concostrina-Zubiri L, Pescador DS, Martínez I, Escudero A (2014a) Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodivers Conserv 23:1757–1770

Concostrina-Zubiri L, Martínez I, Rabasa SG, Escudero A (2014b) The influence of environmental factors on biological soil crust: from a community perspective to a species level. J Veg Sci 25:503–513

Cornelissen JHC, Lang SI, Soudzilovskia NA et al (2007) Comparative cryptogam ecology, a review of bryophyte and lichen traits that drive biogeochemistry. Ann Bot London 99:987–1001

Costa M, Morla C, Sáinz H (eds) (2005) Los montes ibéricos, una interpretación geobotánica. Editorial Planeta, Barcelona

Crespo A, Vězda A (1985) *Pertusaria paramerae* sp. nov., un liquen epífito de los sabinares españoles. Anales Jard Bot Madrid 41:251–255

Diamond SE, Frame AM, Martin R, Buckley LB (2011) Species' traits predict phenological responses to climate change in butterflies. Ecology 92:1005–1012

Edman M, Eriksson M, Villard MA (2008) Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*. J Appl Ecol 45:26–33

Eldridge DJ, Rosentreter R (1999) Morphological groups, a framework for monitoring microphytic crusts in arid landscapes. J Arid Environ 41:11–25

Ellis CJ (2012) Lichen epiphyte diversity: a species, community and trait-based review. Perspect Plant Ecol 14:131–152

Ellis CJ (2013) A risk-based model of climate change threat: hazard, exposure and vulnerability in the ecology of lichen epiphytes. Botany 91:1–11

Ellis CJ (2015) Ancient woodland indicators signal the climate change risk for dispersal-limited species. Ecol Indic 53:106–114

Ellis CJ, Coppins BJ (2006) Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. J Biogeogr 33:1643–1656

Ellis CJ, Coppins BJ, Dawson TP, Seaward MRD (2007a) Response of British lichens to climate change scenarios, trends and uncertainties in the projected impact for contrasting biogeographic groups. Biol Conserv 140:217–235

Ellis CJ, Coppins BJ, Dawson TP (2007b) Predicted response of lichen epiphyte *Lecanora populicola* to climate change scenarios in clean-air region of Northern Britain. Biol Conserv 135:396–404

Ellis CJ, Eaton S, Theodoropoulos M, Coppins BJ, Seaward MRD, Simkin S (2014) Response of epiphytic lichens to 21st Century climate change and tree disease scenarios. Biol Conserv 180:153–164

Escolar C, Martínez I, Bowker MA, Maestre FT (2012) Warming reduces the growth and diversity of biological soil crust in a semi-arid environment, implications for ecosystem. Philos Trans R Soc B 367:3087–3099

European Environment Agency (2009) Biogeographical regions in Europe. Website http://www.eea.europa.edu. Accessed 25 June 2016

Felicísimo AM, Muñoz J, Mateo RG, Villalba CJ (2012) Vulnerabilidad de la flora y vegetación españolas ante el cambio climático. Ecosistemas 21:1–6. doi:10.7818/ECOS.2012.21-3.01

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Fos S, Deltoro VI, Calatayud A, Barreno E (1999) Changes in water economy in relation to anatomical and morphological characteristics during thallus development in *Parmelia acetabulum*. Lichenologist 31:375–387. doi:10.1006/lich.1999.0215

Gauslaa Y, Solhaug KA (1998) The significance of thallus size for the water economy of the cyanobacterial old forest lichen *Degelia plumbea*. Oecologia 116:76–84

Gauslaa Y, Solhaug KA (1999) High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria* – interaction of irradiance, exposure duration and high temperature. J Exp Bot 50:697–705. doi:10.1093/jxb/50.334.697

Giordani P, Incerti G (2008) The influence of climate on the distribution of lichens, a case study in a borderline area (Liguria, Nw Italy). Plant Ecol 2:257–272

Giordani P, Brunialti G, Alleteo D (2002) Effects of atmospheric pollution on lichen biodiversity (LB) in a Mediterranean region (Liguria, northwest Italy). Environ Pollut 118:53–64

Giordani P, Brunialti G, Bacaro G, Nascimbene J (2012) Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. Ecol Indic 18:413–420

Giordani P, Incerti G, Rizzi G, Nimis PL, Modenesi P (2013) Functional traits of cryptogams in Mediterranean ecosystems are driven by water, light and substrate interactions. J Veg Sci 25:778–792

Green TGA, Sancho LG, Pintado A (2011) Ecophysiology of dessication/rehidration cycles in mosses and lichens. In: Luettge et al. (eds) Plant desiccation tolerance, Ecological studies 215. Springer, Berlin, pp 89–120

Guisan A, Thuiller W (2005) Predicting species distribution, offering more than simple habitat models. Ecol Lett 8:993–1009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Halici MG, Kocakaya M, Sweeney K, Fankhauser JD, Schmitt I (2010) *Pertusaria paramerae* (Pertusariales, Ascomycota), a species with variable secondary chemistry, and a new lichen record for Turkey. Nova Hedwig 91:223–230

Hamada H (1983) The effect of temperature on lichen substances in *Ramalina subbreviuscula* (lichens). Bot Mag Tokyo 96:121–126

Hastie TJ, Tibshirani R (1990) Generalised additive models. Chapman & Hall, London

Herk CM, Aptroot A, van Dobben HF (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. Lichenologist 34:141–154

Hewitt CD (2004) Ensembles-based predictions of climate changes and their impacts. EOS Trans Am Geophys Union 85:566

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

IPCC (2001) Climate change 2001: impacts, adaptation, and vulnerability. In: McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds) Contribution of working group II to the third assessment report of the intergovernmental panel on climate change. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, New York

IPCC (2007) Climate change 2007: The scientific basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Contributions of working group I to the fourth assessment report of the intergovernmental panel on climate change: the physical science basis. Cambridge University Press, Cambridge

Kharouba HM, McCune JL, Thuiller W, Huntley B (2013) Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. Ecography 36:657–664

Lakatos M, Rascher U, Büdel B (2006) Functional characteristics of corticolous lichens in the understory of a tropical lowland. New Phytol 172:679–695

Lange OL, Kilian E, Ziegler H (1986) Water vapor uptake and photosynthesis of lichens, performance differences in species with green and blue–green algae as phycobionts. Oecologia 71:104–110

Lavorel S, Garnier F (2002) Predicting changes in community composition and ecosystem functioning from plant traits, revisiting the Holy Grail. Funct Ecol 16:545–556

Lawrey JD (1991) Biotic interactions in lichen community development: a review. Lichenologist 23:205–214

Lisewski V, Ellis JC (2010) Epiphyte sensitivity to a cross-scale interaction between habitat quality and macroclimate, an opportunity for range-edge conservation. Biodivers Conserv 19:3935–3949

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distribution. Ecography 28:385–393

Manel S, Dias JM, Ormerod SJ (1999) Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. Ecol Modell 120:337–347

Martínez I, Burgaz AR, Vitikainen O, Escudero A (2003) Distribution pattern of the genus *Peltigera* Willd. Lichenologist 35:301–323

Martínez I, Flores T, Aragón G, Otálora MAG, Rubio-Salcedo M (2014) What factors influence the occurrence of the genus *Degelia* (a threatened lichen) in central Spain? Fungal Ecol 11:50–59

Matos P, Pinho P, Aragón G, Martínez I, Nunes A, Soares AMVM, Branquinho C (2015) Lichen traits responding to aridity. J Ecol 103:451–458

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman & Hall, London

McCune B, Dey J, Peck J, Heiman K, Will-Wolf S (1997) Regional gradients in lichen communities of the southeast United States. Bryologist 100:145–158

McPherson JM, Jetz W (2007) Effects of species ́ecology on the accuracy of distribution models. Ecography 30:135–151. doi:10.1111/j.2006.0906-7590.04823.x

Merinero S, Hilmo O, Gauslaa Y (2014) Size is a main driver for hydration traits in cyano- and cephalo-lichens of boreal rainforest canopies. Fungal Ecol 7:59–66

Met Office UK (2011) Climate:observations, projections and impacts. Spain. Met Office and the Met Office Logo, United Kingdom

Milla R, Reich PB (2007) The scaling of leaf area and mass, the cost of light interception increases with leaf size. P R Soc B 274:2109–2114

Moreno JM (coord.) et al (2005) Principales conclusiones de la evaluación preliminar de los impactos en España por efecto del cambio climático. Oficina Española de Cambio Climático, Ministerio de Medio Ambiente, Madrid

Morillo C, Gómez-Campo C (2000) Conservation in Spain 1980–2000. Biol Conserv 95:165–174

Muñiz D, Hladún N (2011) Calicioides. Sociedad Española de Liquenología. SEL, Barcelona

Muñiz D, Llop E, Hladun N (2013) *Sphinctrina paramerae*, a new Mediterranean lichenicolous species with non-septate spores. Lichenologist 45:137–143

Muñoz J, Felicísimo AM, Cabezas F, Burgaz AR, Martínez I (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science 304:1144–1147

Nakicenovic N, Swart R (2000) Special report on emission scenarios. Cambridge University Press, Cambridge

Nascimbene J, Marini L (2015) Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. J Biogeogr 42:1222–1232

Nash TH III (ed) (2008) Lichen biology, 2nd edn. Cambridge University Press, London

Nimis PL, Martellos S (2008) *ITALIC* the information system on Italian lichens version 4.0. http://dbiodbs.univ.trieste.it/italic/italic03

Ninyerola M, Pons X, Roure JM (2005) Atlas Climático Digital de la Península Ibérica. Universidad Autónoma de Barcelona, Barcelona

Osborne PE, Alonso JC, Bryant RG (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. J Appl Ecol 38:458–471

Otálora MAG, Martínez I, Molina CM, Aragón G, Lutzoni F (2008) Phylogenetic relationships and taxonomy of the *Leptogium lichenoides* group (Collemataceae, Ascomycota) in Europe. Taxon 57:907–921

Otálora MAG, Martínez I, Aragón G, Molina MC, Lutzoni F (2010) Disentangling the *Collema-Leptogium* complex through a molecular phylogenetic study of the Collemataceae (Peltigerales, lichen-forming Ascomycota). Mycologia 102:279–290

Otálora MA, Belinchón R, Prieto M, Aragón G, Izquierdo P, Martínez I (2015) The threatened epiphytic lichen *Lobaria pulmonaria* in the Iberian Peninsula: genetic diversity and structure across a latitudinal gradient. Fungal Biol 119:802–811

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species, are bioclimate envelope models useful? Global Ecol Biogeogr 12:361–371

Pereira HM, Leadley PW, Proença V et al (2010) Scenarios for global biodiversity in the 21st CENTURY. Science 330:1496

Pérez FF, Boscolo R (eds) (2010) Clima en España: pasado, presente y future. Informe de evaluación del cambio climático regional. Red Temática CLIVAR-España. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid

Pinho P, Dias T, Cruz C, Sim-Tang Y, Sutton MA, Martins-Louçao MA, Maguas C, Branquinho C (2011) Using lichen functional diversity to assess the effects of atmospheric ammonia in Mediterranean woodlands. J App Ecol 48:1107–1116

Pisani T, Paoli L, Gaggi C, Pirintsos SA, Loppi S (2007) Effects of high temperature on epiphytic lichens: issues for consideration in a changing climate scenario. Plant Biosyst 141:164–169

Pöyry J, Luoto M, Heikkinen RK, Saarinen K (2008) Species traits are associated with the quality of bioclimatic models. Global Ecol Biogeogr 17:403–414

Prieto M, Aragón G, Martínez I (2010) The genus *Catapyrenium* s. lat. (Verrucariaceae) in the Iberian Peninsula and the Balearic Islands. Lichenologist 42:637–684

Prieto M, Martínez I, Aragón G, Gueidan C, Lutzoni F (2012) Molecular phylogeny of *Heteroplacidium, Placidium* and related catapyrenoid genera (Verrucariaceae, lichen-forming Ascomycota). Am J Bot 99:23–35

Rai H, Khare R, Baniya CB, Upreti DK, Gupta RK (2015) Elevational gradients of terricolous lichen species richness in the Western Himalaya. Biodivers Conserv 24:1155–1174

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Roux C, Bricaud O, Menard T, Gueidan C, Coste C, Navarro-Rosinés P (2003a) Champignons lichénisés et lichénicoles de la France méridionale (Corse comprise): espèces nouvelles et intéressantes. Bull Soc Linn Provence 54:125–141

Roux C, Signoret J, Masson D (2003b) Proposition d'une liste d'espèces de macrolichens à protéger en France. Association Française de Lichénologie, 33 pp

Rubio-Salcedo M, Martínez I, Carreño F, Escudero A (2013) Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species. J Nat Conserv 21:1–9

Seoane J, Carrascal LM (2008) Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. Glob Ecol Biogeogr 17:111–121

Shiver R, Cutler K, Doak DF (2011) Comparative demography of an epiphytic lichen, support for general life history patterns and solutions to common problems in demographic parameter estimation. Oecologia 170:137–146

Sillett SC, McCune B, Peck JE, Rambo TR, Ruchty A (2000) Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecol Appl 10:789–799

Søchting U (2004) Flavoparmelia caperata, a probable indicator of increased temperatures in Denmark. Graph Scr 15:53–56

Summers DM, Bryan BA, Crossman ND, Meyer WS (2012) Species vulnerability to climate change, impacts on spatial conservation priorities and species representation. Glob Change Biol 18:1365–2486

Swets J (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293

Thuiller W (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Glob Change Biol 9:1353–1362

Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Divers Distrib 12:49–60

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araújo MB (2011) Consequences of climate change on the tree of life in Europe. Nature 470:531–534

Venables WN, Ripley BD (2002) Modern applied statistics with s, 4th edn. Springer, New York

Vitikainen O (1994) Taxonomic revision of Peltigera (lichenized Ascomycotina) in Europe. Acta Bot Fenn 152:1–96

Weisberg S (1980) Applied Linear Regression. John Wiley and Sons, New York

Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. Ecol Lett 8:1138–1146

Zimmermann NE, Edwards TC, Graham CG, Pearman PB, Svenning JC (2010) New trends in species distribution modelling. Ecography 33:1–5