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Do protected areas represent species' optimal climatic conditions? A test using Iberian water beetles

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ABSTRACT

Aim To assess the effectiveness of protected area networks in representing the climatic niche of Iberian water beetle species.

Location Iberian Peninsula.

Methods We used distribution data from 133 endemic water beetle species in the Iberian Peninsula. Climatic potential distributions were estimated by applying a multidimensional-envelope procedure based on climatic data (both current and future) and observed occurrences. Mahalanobis distances were calculated to obtain continuous climatic suitability values within the climatic potential distribution. Two protected area networks were assessed: National Parks (NPs) and Natura 2000 (N_{2000}). The average climatic suitability value for the cells overlapping with protected areas was calculated and compared with the average value of 10,000 random samples from the same number of cells within their entire potential distribution, which allowed to identify species whose climatic niches were optimally or marginally represented.

Results Fifty-seven and 104 of the 107 considered taxa were represented with at least one occurrence in NPs and N_{2000}, respectively, and the climatic potential distributions of 93 and all 107 taxa overlapped with NPs and N_{2000}. While the climatic niches of 48 and 38 taxa were marginally represented in NPs and N_{2000}, the climatic niches of only 11 and 29 were optimally represented by these two protected area networks. When predicted future climatic conditions were considered, both the climatic suitability values and the number of species whose potential distribution was represented by protected areas decreased.

Main conclusions Although the representation of endemic Iberian taxa could be considered adequate, these results show that for most of them the protected networks tend to include areas with climatic conditions close to the species tolerance limit, and the expected climate change only worsened this scenario. Thus, current protected areas cannot be considered to guarantee the long-term survival of the species considered in this study.

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INTRODUCTION

Protected area networks should ultimately be designed to ensure the persistence of species and other valued ecosystem attributes. However, although protected areas play a key role in reducing biological diversity losses in conservation strategies (Chape *et al.*, 2005), they were often not selected to meet specific biodiversity objectives, and historical, socio-economic or aesthetic criteria have predominated in the choice of their locations (Pressey, 1994). Thus, assessing the effectiveness of existing reserve networks in representing different taxa is a relatively frequent task in biological

conservation research (e.g. Scott *et al.*, 2001; Abellán *et al.*, 2007; Sánchez-Fernández *et al.*, 2008a; Lawrence *et al.*, 2011). Using species-location records combined with cartographical data on protected areas, these assessments, known as gap analyses, provide information regarding the percentage of species (endemic, rare, etc.) represented in these protected areas (Scott *et al.*, 1993; Jennings, 2000; Margules *et al.*, 2002).

The absence of records for one species in a particular area does not necessarily imply that this zone is not of interest for the conservation of that species. For example, the absence of records might be indicative of a lack of survey efforts rather than an absence of the species. In the same way, some of the localities from where a species is absent can in fact be environmentally favourable places where dispersal limitations or local extinctions have prevented the presence of the species (Lobo *et al.*, 2010). In these cases, it is common to use species distribution models (SDM) to detect suitable areas, thereby suggesting zones where conservation actions should be focussed (Scott *et al.*, 2001; Cabeza *et al.*, 2004). We must note here the conceptual difference between potential and realized distributions (see Soberón & Peterson, 2005; Jiménez-Valverde *et al.*, 2008). While a potential distribution refers to the places where a species could live, a realized distribution tries to estimate where a species actually lives. Traditionally, SDM were used in conservation to predict possible occupied locations, that is, their main purpose was to estimate realized rather than potential distributions (Domínguez-Domínguez *et al.*, 2006; Elith & Leathwick, 2009; Marini *et al.*, 2010). However, the realized distribution of a species cannot be accurately estimated without knowing with confidence where it is absent (Lobo *et al.*, 2010). Most of the SDM geographical representations for hyperdiverse groups should thus be interpreted with caution when used to delimit protected areas (Ferrier, 2002; Loiselle *et al.*, 2003; Guisan & Thuiller, 2005; Cabeza *et al.*, 2010; Trisurat *et al.*, 2012), as they reflect an intermediate state between realized and potential distributions. In this study we show that the use of potential instead of realized distributions can also be useful for conservation purposes.

The presence of a species in a given protected area is not *per se* a guarantee of its long-term survival, as protected areas may include unviable populations (Margules & Pressey, 2000; Cabeza *et al.*, 2004). To assess the adequacy of a protected area, several authors have used proxies for population viability, such as the number of occurrences or populations, the total amount of habitats or the number of individuals (Cabeza & Moilanen, 2001). The probability of occurrence has also been used to determine site quality (Cabeza *et al.*, 2004), and in some cases, it has been transformed into an estimate of persistence using information on expected threats and vulnerability (Araújo & Williams, 2000; Williams & Araújo, 2000).

An unexplored alternative is the use of SDM intended to represent the potential distribution of a species to assess the extent to which protected areas are climatically suitable for it. The assumption is that the occurrence of adequate climatic conditions may maximize the likelihood of its future persistence if dispersal limitations or other contingent factors could be overcome. In this study, we aim to assess the extent to which protected areas may support the long-term survival of species by determining whether protected area networks contain either occurrence sites or parts of the climatic potential distribution, that are close to their climatic optimum. For this, we have used all available geographical information on species occurrences to derive partial representations of their climatic niches to estimate the most favourable areas from a climatic point of view, which are assumed to better support the persistence of their populations over time (Thomas *et al.*, 2008). We have also assessed potential suitability changes due to global change by projecting the climatic potential distributions into future scenarios.

Two different Iberian protected area networks [Natura 2000 and current National Parks (NPs)] and distributional data from the 133 aquatic Coleoptera species and subspecies endemic to the Iberian Peninsula were used. Aquatic Coleoptera were selected because they are one of the most diverse and best-known groups of aquatic invertebrates in the region and show a high level of endemicity (Ribera, 2000; Sánchez-Fernández *et al.*, 2008b). In addition, they have been proven to be good indicators of the wider diversity in aquatic ecosystems (Bilton *et al.*, 2006; Sánchez-Fernández *et al.*, 2006) and also useful when selecting priority conservation areas (Abellán *et al.*, 2005, 2007). Aquatic habitats are considered highly vulnerable ecosystems (Collen *et al.*, 2012) that are experiencing greater biodiversity loss than other habitats (Saunders *et al.*, 2002), especially in areas with a considerable anthropogenic impact, such as the Iberian Peninsula (Hernández-Manrique *et al.*, 2013).

METHODS

Biological and climatic data

Geographical data were compiled for the 133 endemic Iberian water beetle species and subspecies (Table S1 in Supporting Information). Endemic taxa were used due to their special conservation value, as all of their known range is included within the Iberian Peninsula, and because accurate information on their presence throughout their entire distributional range is available. Non-endemic species were not considered to reduce the risk of misrepresenting potential distributions and climatic niches, a common problem when only regional data are used (Sánchez-Fernández *et al.*, 2011). Distributional data were obtained from the ESACIB (Escarabajos Acuáticos Ibéricos) database (last updated in March 2012), which represents the most complete information available for a major group of freshwater invertebrates in the study area and includes all available geographical and biological data for water beetles from literature as well as museum and private collections, PhD thesis and other unpublished sources (the database is available upon request from

authors). The database currently contains over 60,000 records with associated location data [100 km^2 Universal Transverse Mercator (UTM) cells] for 510 species. Most database records (90%) are posterior to 1987. Only endemic taxa with records in at least five 100 km^2 UTM cells were considered for the analyses.

Current climatic data were obtained from WORLDCLIM, version 1.3 (http://www.worldclim.org; Hijmans *et al.*, 2005). WORLDCLIM contains climate data obtained from the interpolation of climate station records from 1950 to 2000. Seventeen bioclimatic variables were used at the same resolution as the biological data (100 km^2 UTM cells) as predictors: annual mean temperature, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, mean temperature of the wettest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter and precipitation of the coldest quarter. The assessment focussed solely on the climatic niche, and hence, other environmental factors were not included that could also potentially constrain the distribution of aquatic organisms (e.g. the physical–chemical properties of water bodies, such as pH and dissolved oxygen) because including these factors could limit the capacity of revealing the potential climate distribution. Furthermore, it is impossible to obtain representative measurements of these variables for thousands of 100 km^2 UTM cells.

Estimating climatic potential distributions

The potential distribution of a species can be briefly defined as the region in which the climatic conditions are suitable for its existence according to observed occurrences. Potential distributions can be represented by a multidimensional-envelope procedure (MDE), as this method is able to delimit locations with similar climatic conditions to those where the species actually occurs (see Soberón & Nakamura, 2009; Jiménez-Valverde *et al.*, 2011 for a more precise definition of the niche concept). The localities predicted as belonging to this potential distribution may be inhabited or not, but they constitute the best available hypothesis on the fundamental niche of a species based on empirical geographical evidence (the available presence data). Assuming that presence localities reflect a subset of the suitable conditions under which a species can maintain viable populations, MDE is an approach directed at maximizing the capacity to represent geographically the potential distribution of species when they are only based on distributional data (see Aragón *et al.*, 2010; Jiménez-Valverde *et al.*, 2011; Sánchez-Fernández *et al.*, 2011 for an application of this procedure).

In MDE, the maximum and minimum scores (extreme values) for all relevant climatic variables from the entire set of observed presence cells are first calculated for each species. Then, all grid cells with climatic values falling within the mentioned range are designated as suitable, and all cells outside it as unsuitable. In this way, the extreme values are used to derive a binary distributional hypothesis about the areas having climatically suitable conditions (climatic potential distribution), under the assumption that recorded occurrences reflect the spectrum of climatic conditions in which the species can survive and reproduce.

There are some uncertainties and limitations in the method used that could lead to an overestimation of the potential distribution. For example, MDE is very sensitive to outliers, does not take into consideration interactions among environmental factors, and only the boundary records along each environmental variable are used to define the limits of the ecological niche. However, other aspects could have an opposite effect, leading to an infra-estimation of the potential distribution. For example, the environmental conditions in the occupied localities can only provide a partial representation of the fundamental niche of the species, by not considering areas where a species has become extinct for reasons other than climatic ones or potentially suitable regions still not colonized due to limited dispersion. This is especially important when the current knowledge on the distribution of most species is likely to be incomplete, a common situation in insects. It must be noted that the models used to estimate potential distributions cannot be statistically validated by standard procedures (both calibration and discrimination), as the places deemed as suitable for the species may be inhabited or not, depending upon contingent factors such as biological interactions or dispersal limitations. In this sense, potential distributions can only be evaluated using new presence information, or preferably with either physiological data (Kearny, 2006) or translocation experiments (see Jiménez-Valverde *et al.*, 2008).

Because distributional simulations obtained by MDE are highly dependent on the number of selected predictors (Beaumont *et al.*, 2005), the minimum set of climatic variables needed to explain the occurrence of each species was estimated using an ecological-niche factor analysis (ENFA; Hirzel *et al.*, 2002; Basille *et al.*, 2008), with the Iberian Peninsula as the background area. This procedure compares the climatic data of presence localities against the climatic conditions found throughout the study area, thereby computing uncorrelated factors that can explain both species marginality (the distance between the species optimum and the average climatic conditions in the study area) and specialization (the ratio between the climate variance in the study area and variance associated with the focal species). Factors were retained or discarded based on their eigenvalues relative to a broken-stick distribution (Hirzel *et al.*, 2002). Climatic variables selected as predictors were those showing the highest correlation values (factor scores > 0.30) with the retained ENFA factors. The number of climatic predictors ranged from 2 to 6, depending on the species. A binary map with the climatic potential distribution for each of the considered taxa was obtained using the selected variables and a MDE procedure.

Climatic optimum distances

To obtain continuous climatic suitability values within the binary potential distribution, the Mahalanobis distance (a multidimensional non-Euclidean distance widely used in studies of spatial ecology; e.g. Farber & Kadmon, 2003; Etherington *et al.*, 2009) was calculated from each cell to the centroid of the hypervolume formed by the selected variables (mean values for each of the selected variables), with reference to species presence records. The same predictors previously selected by ENFA were used. This procedure has been previously proposed as a useful tool for estimating favourable areas for a species (e.g. Calenge *et al.*, 2008). Thus, the potential distribution of each taxa was represented by a map containing a continuous value of favourability (or climatic suitability) within their potential distribution ranging from 0 (low suitability) to 100 (high suitability). This procedure assumes that there are no significant biases in the occurrence data, so that the mean climatic values obtained for the species reflect conditions with a higher likelihood of collecting individuals. This assumption is not free of error as current knowledge on the distribution for most of these species could be incomplete and biased, which might affect the description of their climatic niche (Hortal *et al.*, 2008). The aquatic Coleoptera are, however, one of the best studied groups of insects in the Iberian peninsula, and our database can be considered comprehensive enough to minimize this effect. A rectilinear bioclimatic envelope model was used to estimate suitability values by Mahalanobis distances instead of directly using a Mahalanobian model, to avoid underestimating the area of suitable climatic space (Farber & Kadmon, 2003), and thereby obtaining a geographical representation closer to the potential than the realized distribution.

Predicted changes in potential distributions

Predicted future potential distributions were estimated following the procedure described earlier by using the same maximum and minimum scores (extreme values) for the relevant climatic variables, which had been estimated using current climate data and projecting those values into future climatic scenarios. A binary distributional hypothesis was obtained for the areas that were predicted to have suitable future climatic conditions. In the same way, continuous climatic suitability values were calculated within the binary future potential distribution. For this purpose, the Mahalanobis distance was determined as before, but in this case, it was measured from each cell of the future potential distribution to the same centroid of the hypervolume and calculated using current climate data.

Bioclimatic predictors for future scenarios (2080) were obtained from the CCCMA-CGCM2 climate model (Flato *et al.*, 2000) through the CIAT database (www.ccafs-climate. org, Ramirez & Jarvis, 2008). The A2 and B2 scenarios from the 4th assessment report of the intergovernmental panel on climate change (IPCC, 2007) were used. The A2 and B2 are not considered extremes scenarios: while scenario A2 assumes regional resiliency and adaptation, scenario B2 assumes local resiliency and adaptation. A2 is referred to as a more 'extreme' scenario, with a projected warming of the mean annual temperature of 3.8 ± 1.1 °C. B2, on the contrary, reflects a 'moderate' scenario, with an increase in the projected mean annual temperature in our study area of 2.5 ± 1.0 °C ($\pm$ standard deviation).

Protected areas and their effectiveness in representing climatic niches

The present study focussed on two different protected area networks found in the Iberian Peninsula: NPs and Natura 2000 (N_{2000}) (see Fig. 1). In the Iberian Peninsula (Spain and Portugal), a recognized global biodiversity hotspot (Brooks *et al.*, 2006), NPs (UICN category II) are at the core of national conservation policies and are committed to preserving the best representation of its natural heritage (Morillo & Gómez-Campo, 2000). On the other hand, the N_{2000} network forms the mainstay of biodiversity conservation policies in Europe. The network's aim is to assure the long-term survival of Europe's most valuable and threatened species and habitats. It includes Special Areas of Conservation (SAC) designated by Member States under the Habitats Directive (92/43/EEC), and also incorporates Special Protection Areas (SPAs) which are designated under the Birds Directive (79/409/EEC). Natura 2000 is not a system of strict nature reserves from where all human activities are excluded. Although the network certainly includes nature reserves, most of the land is likely to remain in private hands and the emphasis is on ensuring that future management will continue to be sustainable, both ecologically and economically. Four GIS data layers (SACs and SPAs for Spain and Portugal) supplied by national conservation agencies were edited and combined to produce a single layer of current Natura 2000 network areas in the Iberian Peninsula.

The present study determines (1) the occurrence of individual species (known distribution) and (2) the individual potential distribution maps of each species. Subsequently, these maps were overlapped with both protected areas networks using ArcGIS 9.3 (ESRI, Redlands, CA, USA). A cell was considered protected when at least 50% of its area was within a NPs or N_{2000} site (Fig. 1). This threshold can be considered appropriate, as most aquatic habitats are highly influenced by processes occurring in their catchments. Nevertheless, to assess the sensitivity of the results to the choice of this threshold, alternative values (1%, 25%, 75% and 90%) were also considered. Protected areas covering less than the selected cut-off percentage of a grid cell were not considered. The climatic suitability values from the occurrence cells within the protected areas were then compared with the values of the cells outside using nonparametric Mann–Whitney *U*-tests.
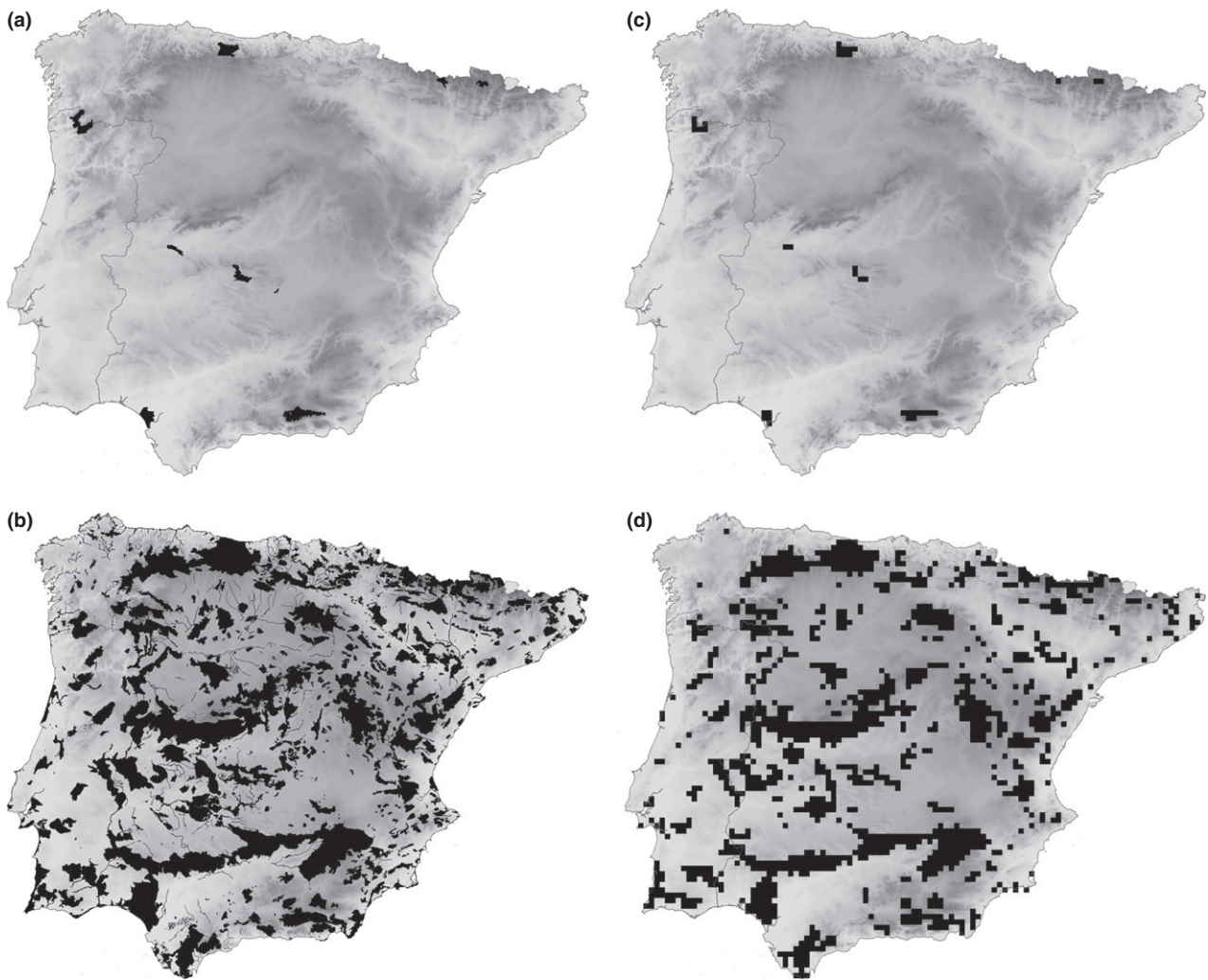
Figure 1 Study area (Iberian Peninsula) showing the two different protected area networks considered (a) Current National Parks (NPs), (b) Natura 2000 (N_{2000}) and the cells considered as protected by National Park (c) or Natura 2000 network (d) at a threshold of 50% coverage by each protected area network.

Similarly, after determining how many cells belonging to the potential distribution of each species overlap with NPs or N_{2000} sites, the average value of climatic suitability for these protected grid cells (ACSp) was calculated. This value was then compared with the average value of 10,000 random samples of the same number of cells extracted from their entire potential distribution (ACSr) using the software R v. 2.13 (R Development Core Team, 2011). The proportion of random samples with higher or lower average suitability values than ACSp allowed to obtain a significance value. When more than 95% of the random samples have higher climatic suitability values than ACSp ($P > 0.95$), one can hypothesize that the protected areas represent parts of their potential distributions with lower climatic favourability values than the remaining potential distribution area (i.e. they are species whose climatic niches are marginally represented in protected areas). Similarly, when < 5% of the random samples from the potential distribution show higher climatic

suitability values than ACSp ($P < 0.05$), it is assumed that protected areas represent parts of their potential distribution with higher climatic suitability than expected at random (i.e. they are species whose climatic niches are optimally represented). The same procedure was repeated using potential distribution and climatic favourability as estimated for the predicted future climatic conditions.

Finally, nonparametric Mann–Whitney U-tests were performed to estimate whether the characteristics of areas inhabited by taxa whose climatic niche was not represented or represented worse than at random differed significantly from those areas inhabited by the remaining taxa. Different variables related with species occurrences were compared: number of occurrences (10 km^2 × 10 km^2 UTM cells) per taxa, mean altitude, range of altitude, mean annual temperature, annual precipitation and percentage of natural and anthropogenic (urban areas and intensive irrigated crops) land use (see Lobo et al., 2011 and Hernández-Manrique et al., 2013 for more details).

RESULTS

Representation of species' occurrences

Among the 133 currently recognized endemic Iberian species and subspecies of aquatic Coleoptera (grouped in what follows under the term 'species' for simplicity), 107 had more than five records in the ESACIB database and were included in the study (Table S1). A total of 57 and 104 of these 107 species were represented (with at least one occurrence) in NPs and N_{2000}, respectively. As expected, the level of species representation varied considerably when other thresholds were used to consider a cell as protected, especially regarding species' coverage in NPs (see Fig. S1).

Differences between the mean climatic suitability of occurrences within the NPs and N_{2000} and the values of the occurrences outside these protected area networks were significant for 10 and 19 species, respectively (Mann–Whitney U-test; $P < 0.05$) (Table S2). In the first case, climatic suitability values of the occurrence sites in NPs were significantly lower than those outside of NPs for these 10 species. However, in the second case, the Natura 2000 network include 15 species whose occurrence sites display climatic suitability values significantly higher than those outside this network, and four species whose occurrence sites display climatic suitability values significantly lower than those outside (Table S2).

Representation of species' potential distributions

Part of the potential distributions of 93 and 107 species (86.9% and 100%) overlapped with NPs and N_{2000}, respectively (Table 1). There were 14 species (13.1%) whose climatically favourable areas (and logically, all of their occurrence sites) did not overlap with any NPs (see Table 1 and Fig. S2).

The climatic niches of 48 and 38 species were marginally represented in NPs and N_{2000}, respectively. Only for 11 and 29 species, the climatic niche was optimally represented in the two protected area networks (see Table 1, Table S3 and Fig. 2 for an example of each case).

A general decrease in climatic favourability was found within the protected areas when considering future scenarios, and these results were consistent across the different thresholds used to consider a cell as protected (Fig. 3). For both B2 and A2 scenarios, we found (1) a decrease in the number of species whose potential distribution was represented in both protected area networks; (2) a decrease in the number of marginally represented species; and (3) an increase in the number of optimally represented species in both protected area networks (Tables 1 and S4). Scenario A2 predicted no overlap with any protected area for the potential distribution of 10 species. Seven of which are high-priority taxa according to Sánchez-Fernández *et al.* (2008a) (Table S5). The climatically favourable areas for five of these endemics (*Deronectes fosteri*, *Deronectes wewalkai*, *Hydraena lucasi*, *Hydraena monstruosipes* and *Hydroporus constantini*) were estimated to

Table 1 Number (and percentage) of species' potential distribution (PD) represented in National Parks (NPs) and Natura 2000 networks; and number (and percentage) of species for which the protected areas represent parts of their potential distribution with lower (or higher) climatic suitability than expected at random (i.e. species which climatic niche is marginally SMR- or optimally SOR-represented). These data were calculated for three potential distributions estimated for each species, one using current climate conditions (present) and the rest using two future climatic scenarios (A2 and B2) obtained from the model CGCM for the year 2080

|	NPs	Natura 2000
PD		
Present	93 (86.9)	107 (100)
CGCM A2	83 (77.6)	97 (90.7)
CGCM B2	80 (74.8)	104 (97.2)
SMR		
Present	48 (44.9)	38 (35.5)
CGCM A2	21 (19.6)	29 (27.1)
CGCM B2	18 (16.8)	35 (32.7)
SOR		
Present	11 (10.3)	29 (27.1)
CGCM A2	16 (15)	25 (23.4)
CGCM B2	23 (21.5)	34 (31.8)

disappear not only from protected areas, but also from the entire Iberian Peninsula.

How are the areas inhabited by the marginally represented species?

The areas inhabited by species whose climatic niche (current climate conditions) was not or only marginally represented by N_{2000} ($n_1 = 38$) showed a significantly higher percentage of anthropogenic land use ($U = 946$, $P < 0.05$) and a higher mean annual temperature ($U = 1005$, $P < 0.05$) than those areas inhabited by the remaining species ($n_2 = 69$). In the case of NPs, only the percentage of anthropogenic land use was significantly higher ($U = 1086$, $P < 0.05$) in the areas inhabited by species whose climatic niche was not or marginally represented ($n_1 = 61$) than those areas inhabited by the remaining species ($n_2 = 46$). However, no differences were detected in the number of occurrences or in the variables related to topography.

DISCUSSION

Our results show that representation of endemic Iberian species in the protected areas is relatively good, considering both actual occurrences and potential distributions. However, it should be noted that a species was considered as represented when there was a single occurrence in a 100 km² that overlapped with any protected area. As a consequence, the overlapping threshold had a large effect on the estimated representation of species in the network. When focussing on
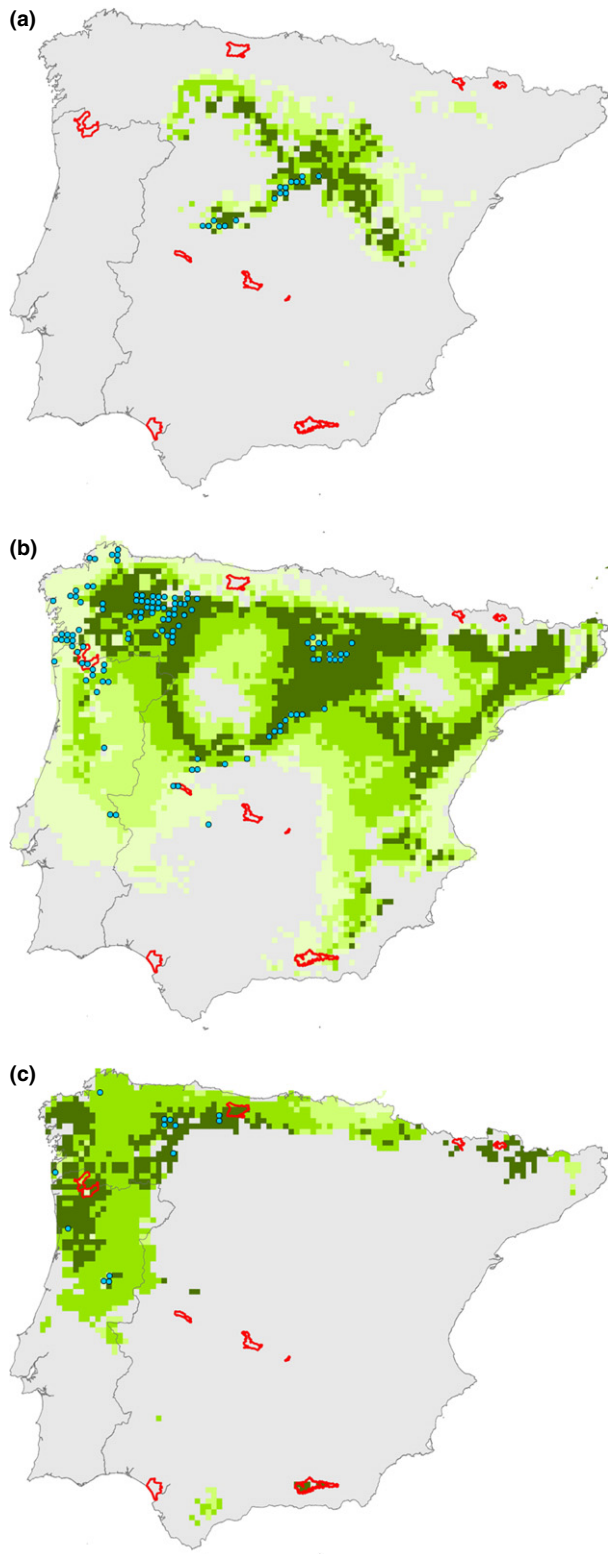
Figure 2 Three examples of varying effectiveness of the Iberian National Parks (NPs) network in representing species' climatic conditions. Maps show the value of climatic favourability within the potential distribution. These values are labelled in quartiles from dark green (high suitability) to light green (low suitability). Blue dots indicate species occurrences and red lines, the boundaries of Iberian NPs. (a) *Deronectes wewalkai*, a species whose known occurrences and potential distribution are not represented in the NPs network; (b) *Hydraena iberica*, a species whose climatic niche is marginally represented, that is, protected areas contain parts of their potential distribution with lower climatic suitability than expected at random; and (c) *Hydroporus paganettianus*, a species whose climatic niche is optimally represented, that is, protected areas contain parts of their potential distribution with higher climatic suitability than expected at random.

were counted as included in a NPs when protected cells were considered to be covered by just 1% of a protected area, but not when a threshold of 90% of coverage was used. When considering potential distributions, this number decreased to a quarter of the species (25%). These results highlight the importance of the surrounding areas of NPs for conserving biodiversity (Gaston *et al.*, 2001). The average climatic suitability value for areas of the potential distribution overlapping with the protected networks was relatively high, and their values were independent of the threshold used to consider a cell as protected both for current and future climate conditions (Fig. 3).

Although representation of the considered species in protected areas was relatively good, their climatic niche was often only marginally represented. This is especially relevant when taking into account that most of the species whose climatic niches are marginally represented in protected areas (both NPs and Natura 2000 network) are also high-priority taxa for conservation according to Sánchez-Fernández *et al.* (2008a). Hence, such inefficiency means losing opportunities to protect a very valuable aspect of biodiversity. To be successful, conservation plans must go beyond the mere representation of extant biodiversity and ensure its persistence over time by accommodating ecological, evolutionary and sociopolitical processes (Sarkar *et al.*, 2006). As noted by Williams & Araújo (2000), 'ultimately it is not how many species have been recorded within a set of areas that is important for conservation, but how many will persist there for the future'. These results demonstrated that the protected networks tend to mostly represent areas with climatic conditions close to the tolerance limit for most of the species, so that although they could be a guarantee for their short-term survival, that may not be the case in the future (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Araújo & Rahbek, 2006). When considering future climate scenarios, the favourability for most of species was estimated to be lower than under current climate conditions. However, this decline in climatic favourability appears to be more pronounced outside than within protected areas.

their occurrence sites, approximately one-third of the species (32%) might be considered as represented or unrepresented in a NPs depending on the threshold selected to identify a cell as overlapping with a protected area (i.e. as 'protected', see Araújo, 2004 for a similar effect). Thus, these species
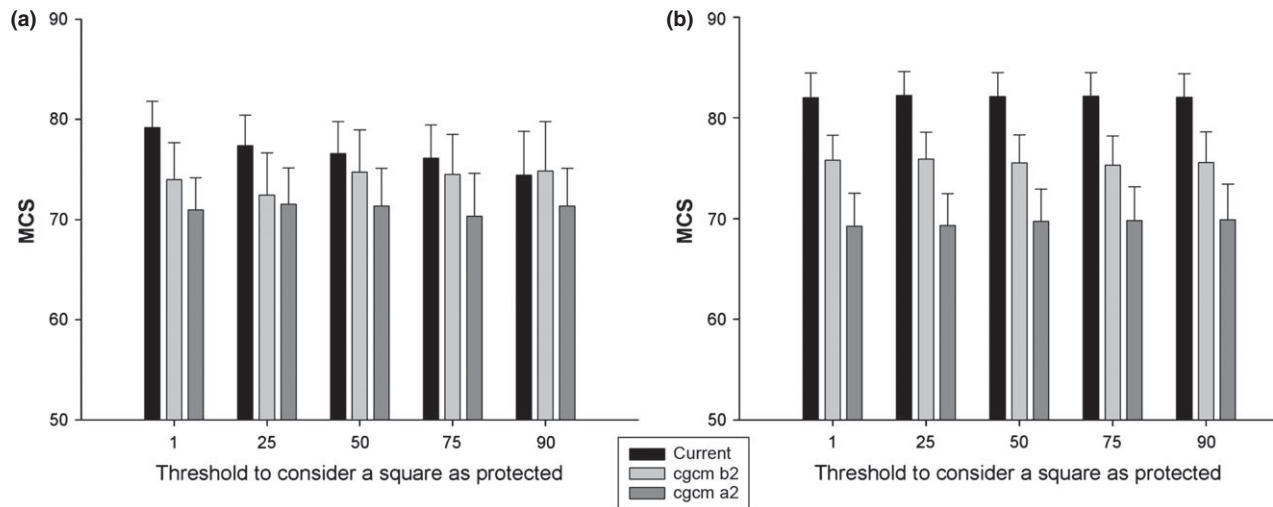
Figure 3 Average climatic suitability (ACS) of the potential distributions overlapping with both National Parks (a) and Natura 2000 networks (b) using different thresholds to consider a cell as protected. Potential distributions were estimated by the multidimensional-envelope procedure for current (black bars) and future climatic conditions [model CGCM; scenarios B2 (light grey bars) and A2 (dark grey bars)].

The rationale of this approach is that the higher the climatic suitability for a species in a protected area, the greater their probability of long-term survival (Cabeza & Moilanen, 2001). However, the generality of the link between persistence and climatic suitability remains untested, mainly due to the paucity of data regarding the species' climatic tolerances. Under these circumstances, it is worth noting that estimated climatic niches and potential distributions can be narrower than actual values (Sánchez-Fernández *et al.*, 2011), thus diminishing the estimated representativeness of protected areas. In the absence of more accurate climatic niche estimations based on experimental evidence, the authors advocate using a precautionary principle by employing potential distributions as reflected by the available empirical distributional evidence. However, such a procedure is especially hazardous when considering the potential distribution of narrow range endemic species. In the Iberian Peninsula, there are often ancient endemic species with low dispersal ability (see e.g. Ribera *et al.*, 2010, 2011; Hidalgo-Galiana & Ribera, 2011). It is likely that these species have strong dispersal constraints, which complicates the colonization of new, climatically suitable locations. It may be thus expected that these species will experience further difficulties in coping with rapid climate change (Sánchez-Fernández *et al.*, 2012). The influence of these species has been minimized in this study by not considering those present in less than five 100 km^2 UTM cells (see Methods), thus excluding most of the very narrow range endemics. In any case, the aim of this study was not to propose new reserve networks for species conservation using the probability of persistence, but to assess the effectiveness of existing networks in representing the species' climatic niches.

Our results show that protected areas do not represent the climatic conditions typical of mountain species (generally wetter and colder) better than those inhabiting lowland areas or valleys. Despite their apparent under-representation of warm and wet conditions, both protected area networks cover rather well the full spectrum of Iberian climatic conditions (Fig. 4) and not only areas at a high altitude and with a high slope, as could be expected. There were also no differences between rare or common species (as measured by the number of occurrences), so the climatic conditions of the rare species were not better represented than the climatic conditions of the more widely distributed species (as in e.g. Nóbrega & De Marco, 2011).

The information generated in this study could be useful in assigning conservation priorities to some species, granting a higher vulnerability value to those marginally or unrepresented in the protected areas and promoting specific
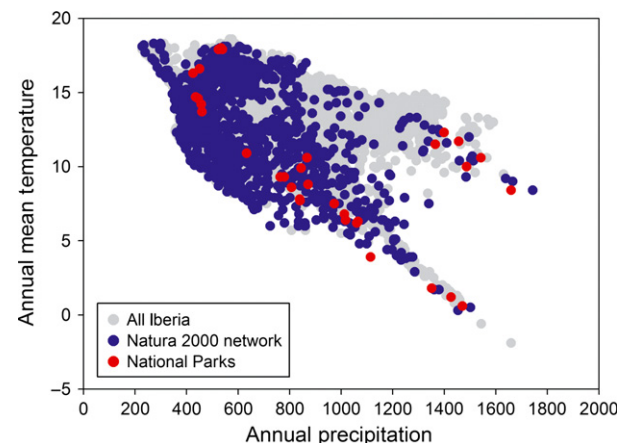
Figure 4 Climatic conditions of the cells considered as protected (with an overlapping threshold of 50%) in relation to the climatic conditions of the entire Iberian Peninsula.

conservation measures such as reintroductions or, in extreme cases, even translocations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Percentage of species represented in the National Parks and Natura 2000 networks (considering current occurrences).

Figure S2 Percentage of species with current and future favourable climatic conditions represented in the National Parks and Natura 2000 networks.

Table S1 List of species used indicating the code.

Table S2 Comparison for each species between the climatic suitability values from the occurrence cells within and outside these protected area networks.

Table S3 Comparison between the average value of climatic suitability for the cells of the potential climatic distribution of each species overlapping with each protected areas network and the average value of 10,000 random samples of the same number of cells extracted from their whole potential distribution (current climate conditions).

Table S4 Comparison between the average value of climatic suitability for the potential climatic distribution cells (estimated using the climatic scenario B2 of the model CGCM for the year 2080) for each species overlapping with each protected areas network and the average value of 10,000 random samples of the same number of cells extracted from their entire potential distribution.

Table S5 Comparison between the average value of climatic suitability for the cells of the potential climatic distribution (estimated using the climatic scenario A2 of the model CGCM for the year 2080) for each species overlapping with each protected areas network and the average value of 10,000 random samples of the same number of cells extracted from their whole potential distribution.

BIOSKETCH

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