Modeling the potential area of occupancy at fine resolution may reduce uncertainty in species range estimates

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ARTICLE INFO

ABSTRACT

Area of Occupancy (AOO), is a measure of species geographical ranges commonly used for species red listing. In most cases, AOO is estimated using reported localities of species distributions at coarse grain resolution, providing measures subjected to uncertainties of data quality and spatial resolution. To illustrate the ability of fine-resolution species distribution models for obtaining new measures of species ranges and their impact in conservation planning, we estimate the potential AOO of an endangered species in alpine environments. We use field occurrences of relict *Empetrum nigrum* and maximum entropy modeling to assess whether different sampling (expert versus systematic surveys) may affect AOO estimates based on habitat suitability maps, and the differences between such measurements and traditional coarse-grid methods. Fine-scale models performed robustly and were not influenced by survey protocols, providing similar habitat suitability outputs with high spatial agreement. Model-based estimates of potential AOO were significantly smaller than AOO measures obtained from coarse-scale grids, even if the first were obtained from conservative thresholds based on the Minimal Predicted Area (MPA). As defined here, the potential AOO provides spatially-explicit measures of species ranges which are permanent in the time and scarcely affected by sampling bias. The overestimation of these measures may be reduced using higher thresholds of habitat suitability, but standard rules as the MPA permit comparable measures among species. We conclude that estimates of AOO based on fine-resolution distribution models are more robust tools for risk assessment than traditional systems, allowing a better understanding of species ranges at habitat level.

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1. Introduction

Assessing the spatial distribution of rare species is one of the main questions to be solved for conservation planning and management (Rondinini et al., 2006). Distribution data is crucial for measuring the size of species' geographic ranges by using Extent of Occurrence (EOO) and Area of Occupancy (AOO), which are globally accepted as surrogates of extinction risk under IUCN Red List Criteria (Miller et al., 2007; Gaston and Fuller, 2009). The AOO was initially interpreted as the result of the exclusion, inside the EOO (the region encompassing all localities where a species has been recorded), of all the non-suitable habitats and those not occupied by a species (Gaston, 1994). Such a definition is supported by the assumption that suitable habitats for a species may be not completely occupied; remaining as potential areas for colonization or inaccessible areas by historical or competition reasons (Gibson

et al., 2007). Thus, the AOO may be conceptually divided into (i) the real AOO, including the localities where one species exists; and (ii) the potential AOO, including all suitable areas for the species. Although the IUCN (2001) considers that either the known, inferred or projected sites of occurrence could be used for the calculation of species ranges, the conservation assessment of rare species is commonly restricted to the known and real AOO, according to the localities reported for one species until one specific date (IUCN, 2001). This measure is subjected to uncertainties of species data (Akçakaya et al., 2000; Joseph and Possingham, 2008) and strongly depends on the spatial resolution of distribution maps and the scale of reference (Hartley and Kunin, 2003; Gaston and Fuller, 2009). However, estimating the potential AOO could provide more robust measures, providing inferred sites of species occurrence less sensitive to sampling effort and scale, but its applicability in conservation planning has been scarcely studied.

The ideal approach for estimating the potential AOO of any species should take into account its ecological requirements, in order to predict suitable areas where the species would be present. For this, one of the most promising tools developed during the last

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decades are species distribution models (SDMs) which are based on the statistical description of the environmental niche which allows species to survive (sensu Soberón, 2007). SDMs have been used for estimating species ranges such as EOO (Sérgio et al., 2007; Brito et al., 2009) and AOO (Good et al., 2006; Boitani et al., 2008) according to the total number of grid cells where a given species is known. However, these estimates are commonly built at coarse grain resolution (here referred to >1 km of resolution) and species ranges are expected to be overestimated at habitat level (IUCN, 2001). In order to obtain more representative outputs, SDMs should consider specific habitat conditions at finer resolution (Wilson et al., 2005; Damien et al., 2008; Bartel and Sexton, 2009), but the way in which these models may be employed for estimating the potential AOO is still unexplored. Yet, the last version of IUCN Guidelines (IUCN, 2010) recommends to always transform habitat models to AOO estimates at the standardized scale of reference (i.e. 2 km × 2 km). However, the lack of studies comparing species ranges based on recorded presences at coarse resolution and model-based estimates at fine scales makes difficult to explore new measures of AOO.

Model-based estimates of AOO primarily depend on the robustness of distribution models. When applied at fine scales, uncertainties of SDMs are mainly related to the availability of accurate presence data and the environmental variables at fine grain resolution (Trivedi et al., 2008; Thuiller et al., 2008). Although modern GIS tools allow the management of accurate spatial data at fine scales, species occurrences are usually restricted to biodiversity databases or natural collections (Hernández and Navarro, 2007; Körner et al., 2007) which are biased or have poor resolution (Carter et al., 2006). Because of resources limitation, it is challenging to delineate cost-effective sampling campaigns for mapping the distribution of a large set of species, and conservation agencies commonly turn to expert surveys (conducted by field biologists, non-profit organizations, etc.) for monitoring endangered species (CNPS, 2001; Dittes and Guardino, 2002; Bañares et al., 2003). Expert surveys are fast and relatively cost-effective, but limited by the lack of adequate sampling design or the poor capability of some species to be detected in the field (Poon and Margules, 2004). As an alternative approach, systematic surveys are proposed as rigorous rules for optimizing field sampling efforts, for example using habitat models and adaptive sampling as a better alternative to random sampling methods (Hirzel and Guisan, 2002; Engler et al., 2004; Edwards et al., 2005). Because both expert and systematic surveys provide accurate presence data about local species distribution, they are potentially useful for estimating species ranges using SDMs at fine resolution. However, serious doubts could arise about which is the most cost-effective sampling strategy for species mapping, and their implications for measuring the potential AOO.

In this paper, we investigate how SDMs can be used for estimating the potential AOO of a rare species at fine scale. Our main aim is to evaluate possible uncertainties of model-based estimates of AOO at fine resolution, as an alternative to traditional methods based on coarse-scale grid occurrences. As a real case of conservation concern, we study the distribution of Empetrum nigrum in Spain, where this species is endangered, since few populations survive in alpine refugia threat by human activities. Alpine plants are generally noted as priority species for conservation, but their distribution are difficult to assess at fine scales (Randin et al., 2009). In the example used to illustrate this study, we test whether different survey procedures, expert and systematic surveys, could affect the ability of different SDMs to (i) perform accurate models at fine scale, (ii) obtain realistic AOO estimates in comparison with coarse-scale methods based on occurrence grids and (iii) provide robust measurements for risk assessment and conservation management.

2. Methods

2.1. Study case

E. nigrum L. subsp. nigrum (hereafter E. nigrum) is a dwarf shrub widely distributed in boreal environments of the northern hemisphere, but restricted to few localities in alpine and subalpine shrub-formations of the southern European Mountains. In Spain, relict and threatened populations of the species are living in snow-belt topographical refuges in just one locality of the Cantabrian Range (Jiménez-Alfaro et al., 2006) where the species is a conservation priority with biogeographical concern (Jiménez-Alfaro et al., 2010). At the start of this study, the species distribution was known in three mountain summits of a Pleistocene-glacial site (extent = 125 km^2) currently used as a ski resort (San Isidro and Fuentes de Invierno resorts). Main threats affecting the species are related to the alteration of its occupancy area due to the skiing infrastructures, which have to support more than 200,000 visitors by year. Since conservation planning of the study area needs to be combined with the recreational use of the resort, accurate maps indicating the potential distribution of the species and possible priority areas for its conservation are required.

2.2. Modeling framework

We designed a two-step protocol that integrates expert and systematic surveys to obtain two data sets of occurrences, which were used to perform SDMs and to estimate the potential AOO of E. nigrum. Since we expected to have a low number of occurrences, we used presence-only algorithms instead of presence/absence methods to reduce the number of occurrences needed for model calibration (Zaniewski et al., 2002; Elith et al., 2006; Tsoar et al., 2007). Among different possibilities, we chose Maximum Entropy algorithm (Phillips et al., 2006) because it have been successfully test in contrast to other methods, being specially recommended when a low number of presences (<30) are available (Elith et al., 2006; Gibson et al., 2007; Pearson et al., 2007). All models were calibrated above 1600 m of altitude, because the target species is restricted to (sub)alpine habitats, and this altitude corresponds to the timberline in the study area.

A Digital Elevation Model (DEM) at 15 m × 15 m of resolution was obtained from regional cartography (Principate of Asturias and Castilla y León regions, scale 1:10,000) and a set of topographical variables were derived using Arc GIS 9.2 (Esri Inc., Redlands CA, USA). We used topographical variables instead of climatic data because (1) main factors affecting local distribution of plants in alpine snow-beds are related to slope and solar exposure (Körner, 2003), (2) these variables can be correlated to climate conditions at fine scales (Mackey and Lindenmayer, 2001) and (3) topographic variables can be more easily obtained and more reliable than climatic variables in alpine (or subalpine) environments (Sánchez Palomares et al., 1999). According to the known ecology of the species, the variables finally used for modeling are related to snow-melt habitats (Table 1). Co-linearity between the explanatory variables was relatively low ($R^2 < 0.6$) as revealed by linear regression analysis conducted through pair-wise comparisons.

2.3. Sampling

We performed a first survey for mapping extant populations of E. nigrum under the project "Spanish National Atlas of Endangered Plants" (Iriondo, 2011), which field methodology consisted on expert surveys conducted within 0.5 km × 0.5 km grid units on previously known localities of target species. In order to detect the maximum number of sites with the occurrences of E. nigrum, we

Table 1
Explanatory variables used to fit species distribution models for *Empetrum nigrum* and absolute ranges for the study area. All variables were derived from a Digital Elevation Model (DEM) at 15 m × 15 m resolution, and included as continuous environmental variables in MaxEnt software (Phillips et al., 2006).

Variable	Min–Max	Description
Altitude	1570–2150	Elevation (m) derived from DEM
Slope	0–75	Slope degrees generated from DEM
Radiation	1496–7466	Annual global solar radiation (WM^2) derived from altitude, exposure and solar trajectory
Curvature	−73 to 86	Indirect variable related to flow accumulation, reflecting concavity (<0) or convexity (>0)
Aspect (Northness)	−1 to 1	Cos (aspect)*sen (slope)
Aspect (Easterness)	−1 to 1	Sen (aspect)*sen (slope)

used distribution data provided by literature and herbarium specimens to design field itineraries based on field expert criteria and the known habitat of the species. Five one-day campaigns were carried out around the summits where the plant had been reported before, mapping the populations that we found with a GPS receptor (Garmin e-trex, mean estimate error = 5 m). To estimate the real (known) AOO of the species, presence locations were subsequently transformed into discrete polygons using the Minimal Polygon Convex method (IUCN, 2001) and a minimal separation of 15 m between polygons. Isolated subpopulations with one or few individuals and only one GPS reference were mapped as a circle with 3 m of diameter. Since spatial autocorrelation may be a serious limitation for SDMs (Vaughan and Ormerod, 2003; Segurado et al., 2006) we used the occupancy polygons previously defined to randomly select a maximum number of presence points with the condition of avoiding spatial correlation for the selected environmental variables. Spatial correlation was test through the Moran (I) statistic implemented in ArcGIS, and measured along different set of points randomly selected at different minimal distances. The set with a maximum number of non-correlated points was used as training data to calibrate the models.

In a second step, we designed a stratified sampling based on the probability of presence predict for *E nigrum* in the study area with the first set of occurrence data (Guisan et al., 2006). The aim of this systematic survey was to detect more populations of the species and to obtain an ecologically more representative number of occurrences for computing a second set of distribution models. We focused the field work on the areas that had been non prospected during the first campaign, using 500 points randomly stratified along the probability values (minimal distance = 100 m) to design sampling itineraries. We used a GPS receptor to follow such itineraries, collecting presence and absence data. New populations of *E. nigrum* were mapped in the same way that first sampling and the new occurrences were test again for spatial autocorrelation. New (not auto-correlated) presence data was used to perform the second set of models.

2.4. Model comparison

We evaluated the ability of the two survey protocols for computing accurate models using the standard area under the curve (AUC) measure of a receiver-operating characteristic (ROC) plot (Fielding and Bell, 1997). Models calibrated with the expert survey were evaluated with the data obtained during the systematic survey, using all new presences and an equal random number of absences. On the other hand, models derived from systematic survey were evaluated using a cross-validation procedure, dividing the total number of occurrences in five different sub-subsets. Five model replicates were run for each one of the presence-only

methods, using the 80% of occurrences for calibration and different sub-sets (20%) for validation. Mean AUC was used to compare the performance of the five models.

We compared the sensitivity of the two modeling situations for measuring the AOO under different thresholds of habitat suitability (HS), according to the total area estimated for equally partitions of predicted values from 0.1, 0.2,... up to 0.9. To obtain an equal measurement of the AOO to be compared between models, we calculated the Minimal Predicted Area (MPA), i.e. the minimal suitable area predicted for the 100% of the presences used for model calibration (see Engler et al., 2004; Guisan et al., 2006). We used the probability threshold that corresponded with the MPA to establish the potential AOO for *E. nigrum* (i.e. suitable but not necessarily occupied areas, Gaston and Fuller, 2009) with the assumption that it includes the minimal area where the species is projected to exist. In this way, for a given number of point occurrences used for calibration and the suitability values provided by the model to each point (e.g., minimum = 0.18; maximum = 0.98) we would calculate the total areas including predicted values equal of higher than 0.18. We compared these model-based measurements with standard AOO estimates based on coarse-scale grids, using the same occurrence data and three different grid sizes: (a) 2 km × 2 km, recommended as a general scale of reference by the IUCN (2010); (b) 1 km × 1 km, considered a fine scale measurement for rare plants (Guisan et al., 2007) and (c) 0.5 km × 0.5 km, a more accurate grid of reference used for the Spanish Atlas for Threatened Plants (Iriondo, 2011).

To assess possible divergences between different survey protocols in conservation planning, we test the spatial correlation of the predicted HS above the MPA threshold. We used a random set of 1000 points to calculate pair-wise correlations of the models using linear regression. We also test how potential conservation areas based on SDMs at fine resolution would spatially differ, calculating the spatial agreement between models using pair-wise comparisons of the AOO. For this, we summarized binary GIS layers of the models assigning values = 1 for priority areas (above the MPA threshold); and = 0 for not priority (below the MPA). We then calculated the total area considered as conservation areas in the two scenarios (sum value = 2). The percentage of this area in relation to the total area predicted by at least one of the layers (sum value = 1) was considered as the spatial agreement (in%) between models.

3. Results

3.1. Species distribution and modeling

The expert survey allowed us to detect extant populations of *E. nigrum* in the mountain summits where the species had been previously reported. A total number of 25 occupancy polygons were mapped (total area = 4.2 hectares; mean = 1.8; Standard Deviation, SD ± 3.8). From 113 presence points obtained in the field, a total number of 18 were finally selected for model calibration. We detected a minimal distance of 90 m between points to avoid spatial correlation with the selected explanatory variables (Moran I values between 0.04 and 0.10). Model-based, adaptive sampling was conducted over two areas detected with high probability of occurrences for *E. nigrum*, in which two new and previously unknown populations were recorded (Fig. 2). In addition, the systematic survey provided 32 new occurrences and 5 polygons (total area = 3.9 hectares; mean = 0.8; SD ± 1.5). As a result, the second data set included 32 non auto-correlated occurrences, from a total number of 145.

The predictive power of the two models computed was high (AUC > 0.8) with systematic survey performing better than expert survey (Table 2). The variables with a higher contribution to the
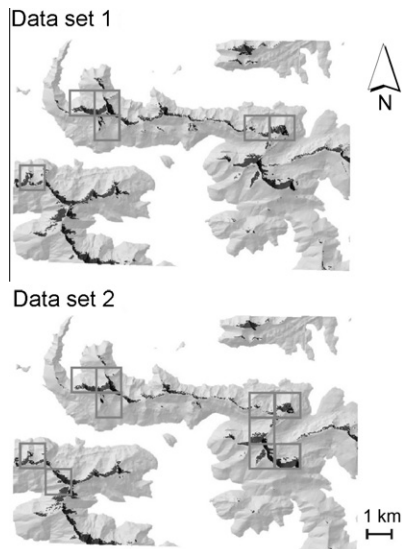
Fig. 1. Potential area of occupancy estimated for *Empetrum nigrum* along its known distribution area in Spain, using two data sets obtained from expert (Data set 1) and systematic (Data set 2) surveys. Dark colors show model-based estimates using maximum entropy algorithm and the minimal predicted area as probability threshold. Grid (gray) cells represent the AOO that would be measured using the occurrence of the species in 1 km × 1 km grids.
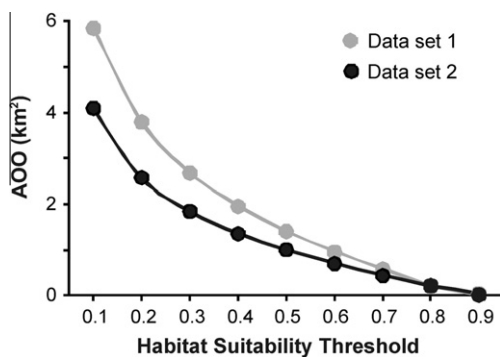

Fig. 2. Sensitivity of species distribution models to different thresholds of habitat suitability, according to the total Area of Occupancy (AOO) measured when using presence data obtained from expert (Data set 1) and systematic (Data set 2) surveys.

Fig. 3. Total estimates of Area of Occupancy (AOO) for *Empetrum nigrum* in Spain, according to different survey protocols (Data set 1 and 2) and alternative measurements of model-based methods (based on fine-resolution models and the minimal predicted area) and coarse-scale grids (based on reported localities) at different accuracy.

analysis allowed the comparison of the AOO that could be estimated under the two situations. We found some differences between the two survey protocols, providing the expert survey higher AOO estimates at low-medium ($P < 0.6$) suitability values than systematic survey. However, minor differences were found in the AOO estimated for high ($P > 0.8$) thresholds, and the MPA provided a similar measurement of the AOO under both situations (Table 2). In agreement with these results, the use of model outputs for selecting potential conservation areas revealed few differences between survey protocols. Linear correlation of habitat suitability values was positively significant between the two models ($R^2 = 0.86$; $P < 0.001$) and the comparison of the spatial agreement between the AOO (all predicted area above the MPA threshold) was high (75%) as reflected by suitability maps (Fig. 1).

Model-based estimates of AOO were generally lower than those provided by coarse grain resolution methods at different scales, especially when using the higher number of presences provided by the systematic survey, to which the differences varied from 2 to 3 orders of magnitude (Fig. 3). Nevertheless, the most relevant difference between model-based and coarse-scale estimates was that in the first case AOO did not increase with the second data set (even decreased from 4.8 to 4.1 km^2), while the other methods provided significantly higher estimates because of the higher number of localities (grids) considered. As an obvious effect of the scale, the higher differences between model-based and coarse-grain estimates existed when comparing the grid with a lower resolution (i.e., 2 km × 2 km grid).

4. Discussion

Our study shows that AOO estimates differ largely between SDMs at fine resolution and standard approaches based on distribution data at coarse scale. Furthermore, different sampling procedures provide similar measures of the potential AOO, suggesting model-based AOO reduces uncertainty of species range estimates.

resulting models (first and second data sets) were altitude (54.9% and 60.6%) and radiation (40.2% and 35.4%). The mean probability of occurrence predicted for the points used in model calibration was similar for the first (Mean = 0.63; SD ± 0.24) and second (Mean = 0.62; SD ± 0.26) data sets. The MPA threshold was relatively low in both cases, although the total area predicted as suitable for *E. nigrum* was always lower than the 8% of the study area (Table 2). The range of habitat suitability above the MPA threshold was similar in the two models, with a mean probability of 0.39 in the expert survey (SD ± 0.21; min. = 0.14; max = 0.95) and 0.34 in the systematic survey (SD ± 0.22; min. = 0.10; max = 0.98). Accordingly, maps of habitat suitability (Fig. 1) were rather similar for the two models, and both reporting the highest altitudes and northern exposures as the most suitable areas for the species.

3.2. AOO estimates

For the two data sets, estimates of the potential AOO similarly decreased at higher habitat suitability thresholds (Fig. 2). Since the MPA threshold was rather similar and low, the sensitivity
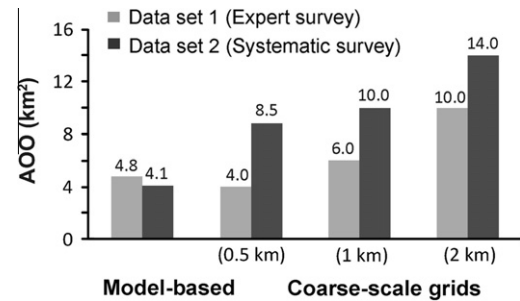
Table 2
Results of MaxEnt models according to different number of occurrences (*n*) obtained by expert and systematic surveys. MPA indicates the threshold of probability used for defining the minimal predicted area. AUC is an estimate of the model accuracy based on the area under the curve (see text).

Data	n	MPA	Study area (%)	AUC
Expert survey	18	0.142	7.54	0.883[a]
Systematic survey	32	0.104	6.27	0.939 (±0.064)[b]

[a] ROC curves calculated using an independent set with 14 presences and 14 absences.
[b] ROC curves calculated using cross-validation procedure with five subsets.

The main advantage of this approach is that it is spatially explicit, and derived estimates are based on suitable areas for the species (Fig. 1). This is a qualitative difference in relation to coarse-scale grid methods, which are strongly dependent of the number of localities where one species is known, and therefore the uncertainty of the measured AOO may be significant for conservation planning. On the contrary, we show that the uncertainty of model-based estimates is scarcely affected by survey protocols, and that therefore fine-resolution SMDs are able to obtain more robust measurements of the AOO. Considering financial restrictions for sampling rare species but the general availability of few, accurate occurrences (from monitoring surveys, herbarium collections, etc.) these systems may improve range estimates of species of conservation concern under relatively cost-effective procedures.

4.1. Modeling the potential AOO

One of the main constraints of SDMs for species mapping is the choice of a threshold to convert predicted values in potential distribution ranges (Gaston and Fuller, 2009). Although a plethora of probability thresholds could be used for different conservation purposes (Wilson et al., 2005) we preferred to use the Minimal Predicted Area (MPA) as a standard reference for measuring the potential AOO. This procedure has the advantage of maintaining zero omission errors in the localities used to calibrate the model (Pearson et al., 2007; Thorn et al., 2009) being an objective procedure that assumes the basic principle of the IUCN for estimating species ranges; that is, to include all the known locations (in this case, habitat suitability range) for a given species (IUCN, 2010). However, the MPA provides a conservative threshold expected to overestimate the AOO, considering as "suitable" many areas with low-medium probability of occurrence. Overestimation is a known limitation for calculating species ranges (Keith et al., 2000; Hernández and Navarro, 2007; Jetz et al., 2008) but no studies have previously assessed the influence of different thresholds for estimating the potential AOO.

We found that model-based estimates based on the MPA threshold are generally lower than coarse-scale grid methods (Fig. 3). However, all methods are rather similar in comparison with the real (known) AOO measured for the species in the field, which was extremely low (=0.081 km^2). Lower and more accurate estimations of the potential AOO could be obtained using less conservative thresholds than the MPA, but it is difficult to establish an ideal threshold that would reflect the real AOO of the species. Although our results can be contingent on the particular data set, grain and extent of our analyses, we highlight that model-based estimates may be flexible enough to reduce the overestimation of the AOO according to different thresholds of habitat suitability. Other studies are still needed to assess the possible effect of different fine-scale resolutions (Guisan et al., 2007) in AOO estimates, although such differences are expected to be minor than the scale-area relationships described for coarse-scale grids (Hartley and Kunin, 2003). In any case, comparing model-based estimates at coarse grid resolution (1 km, 2 km or higher) has little practical sense for the assessment of new measures of AOO at habitat level, which is the main aim of this study.

We have assessed the ability of SDMs under different survey protocols using extremely few occurrences of a rare alpine plant, E. nigrum, living on easily predictable habitats. The high model accuracy obtained for E. nigrum is commonly expected when modeling species with small geographic ranges and limited environmental tolerances (Hernandez et al., 2006; Tsoar et al., 2007). Thus, the topographical variables used here can be considered robust proxies to reflect the environmental niche of E. nigrum, assuming the relationships of solar radiation and altitude for maintaining the snow-beds where the species inhabit (López-Moreno

et al., 2006). Although MaxEnt reflected potential bias of the expert survey, this presence-only method performs robustly even when using biased occurrence data at fine spatial resolution, which is in agreement with the good performance obtained by MaxEnt when modeling biased plant distribution at broad scales (Loiselle et al., 2008). Thus, the impact of the differences detected in the performance of the two data sets compared here does not compromise the ecological understanding of E. nigrum, and both models accurately map the potential distribution of the species in the study area. Despite we did not test other algorithms, we expect that, in similar situations, extremely few occurrences obtained from expert surveys are able to accurately model the environmental niche of rare plants, and presence-only methods may well be considered as robust methods for estimating the AOO at fine scales.

4.2. Implications for conservation

The failure to detect spatial occurrences of rare species is commonly noted as a serious limitation for direct (Mackenzie et al., 2005) and indirect (Vaughan and Ormerod, 2003; Guisan et al., 2006) estimates of range sizes. In this study, we use SDMs for modeling the potential AOO of an endangered species in a natural area subject to human alterations for which urgent conservation actions are required. Finding more occurrences of the species would increase significantly the AOO using traditional coarse-scale grids, while model-based AOO seems to be less dependent of new occurrences and therefore more permanent in the time. We suggest that this approach when conducted properly may be less sensitive to uncertainties than traditional procedures, and a better option for risk assessment at national or local level, because it is potentially less dependent of accuracy and completeness of field survey. However, the use of AOO model-based estimates for IUCN risk assessment must be taken with care because of current standardization requirements and scale-area relationships (IUCN, 2010). According to the AOO estimates based on the systematic survey (which could be considered the best one available for E. nigrum) the potential AOO of our study species represents only the 28% of the estimate provided by the grid area recommended by the IUCN (2 km × 2 km) using the same occurrences. This suggests that, under a hypothetical generalization of model-based methods, IUCN strategies should also consider the revision of the thresholds for categorization. It would be also necessary to use standard thresholds permitting comparison among different species, and the MPA could be an useful and easily applicable form. Nevertheless, multi-species studies are still needed to establish optimal model-based measurements at fine scales.

Another application of model-based estimates of potential AOO at fine resolution could be the design of conservation areas at habitat level (Brambilla et al., 2009). This is probably one of the main limitations of AOO measures based on coarse-scale grids, and therefore building fine scale models to solve particular, local population problems can be argued as one of the new frontiers on conservation practice. Considering the character of "essential area" assigned to the AOO (Keith et al., 2000) our study provides an example of permanent and spatially-explicit measurement of species ranges potentially useful for conservation planning. Our results also suggest that accurate models based on different sampling procedures may provide similar (correlated) models with relatively high spatial agreement at fine resolution, in contrast with the general limitations attributed to SDMs and spatial range measurements for conservation management at other scales (Johnson and Gillingham, 2005; Joseph and Possingham, 2008). We of course realize some limitations to these results. For example, the grain size we used (15 m × 15 m) may be not effective for reserve selection, and conservation managers could prefer to design priority areas according to medium or high values of habitat suitability,

or alternative criteria such as mixed approaches using predicted and known estimates (Carvalho et al., 2010). Although generalizations to other species or regions across the world are difficult to predict, we conclude that SDMs applied to fine resolution studies would be a significant contribution for rare species conservation in natural areas. In particular, the potential AOO may provide representative geographical ranges of rare species at habitat level, and a flexible tool for designing conservation actions under different decision-making approaches.

Acknowledgments

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