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A probability-based approach to match species with reserves when data are at different resolutions

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ABSTRACT

Gap analysis is a protocol for assessing the extent to which valued biodiversity attributes are represented within protected areas. Such analysis involves overlaying the distribution of biodiversity features (e.g. species) with protected areas, but the protocol entails arbitrary assumptions that affect the outcome of the assessments. In particular, since species' distributions are usually mapped at a coarser resolution than protected areas, rules have to be defined to match the two data layers. Typically, a grid cell is considered protected if a given proportion is covered by protected areas. Because the effectiveness of protected areas is dependent on the definition of such arbitrary proportions (i.e., thresholds), errors of commission and omission in the level of species' representation are bound to exist. We propose an alternative approach whereby the contribution of a cell for the representation of species is defined as the expected value of a hyper-geometric random variable. We compare the conventional approach based on fixed thresholds with this new probability-based approach for both static and dynamic conservation scenarios, using a virtual dataset and a 100-plant-species' dataset for Iberian Peninsula. Results support the view that traditional fixed thresholds yield inconsistent results. Because species present different distributional patterns coinciding differently with protected areas, species-specific and time-specific thresholds should be used. Our approach enables to easily obtain these more adequate threshold values, thus offering a promising method for gap analyses. Future studies should seek to evaluate the performance of this method empirically in different conservation planning contexts.

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1. Introduction

Protected areas (hereafter termed reserves) are the cornerstone of *in situ* conservation strategies. Given their significance for biodiversity conservation, it is important to assess how well they meet their goals (Margules and Pressey, 2000). Gap analysis is a procedure to assess reserve representativeness (Scott et al., 1991) that aim to ensure that a viable collection of biological attributes (e.g., species) is protected from disturbances. Information on species' representation within reserves is used to identify gaps that may be filled through the establishment of new areas for conservation.

The implementation of gap analysis is commonly supported by geographical information systems, which facilitate the overlay of

maps of species' distributions with maps of reserves. At national to continental scales, species and reserve data are often recorded at different resolutions. Species' data are available as occurrence records on regular grid cells, while reserves are typically represented by polygons (e.g., data from the World Database on Protected Areas). To match both types of data, arbitrary thresholds are used for deciding when reserves of varying size and position should be considered present or absent from a particular grid cell (Hopkinson et al., 2000). These thresholds vary from any coverage greater than zero to more conservative choices, where greater proportions of the grid cells need to be covered by reserves in order for the grid cell to be considered "protected". Although conceptually simple, the rules used for matching species' distributions and reserve-coverage data affect the assessment of species' conservation status in reserves to a variable but usually not negligible extent.

Araújo (2004) was the first to warn against the impacts of thresholds on gap analysis assessments. He provided evidence that assessments measuring the degree of species' representations in

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Table 1

Overview of gap analysis studies where cut-off threshold values were applied to reserve data. Only papers published after 2004 were reviewed because Araújo (2004) produced a similar review for the period prior to 2004: reference: bibliographic reference; region: geographical focus of the studies; resolution: grid cell extent; protected area type: type of protected areas (PAs); criteria for protected area grid-assignment: criteria used to assign grid cells as protected or not; taxonomic data: taxonomic scope of the studies; grid-based data type: type of original data for taxonomic layers.

Reference	Region	Resolution	Protected areas type	Criteria for protected areas grid-assignment	Taxonomic data	Grid-based data type
Araújo et al. (2007)	Iberian Peninsula	50 × 50 km cells	National PAs	2%, 5%, 10% and 20%-cover thresholds	Amphibians, reptiles, birds, mammals and plants	Presence from sampling records
Burgess et al. (2005)	Sub-Saharan Africa	1 × 1° cells	National PAs and forest conservation areas	10%, 25%, 33% and 50%-cover thresholds	Plants	Presence/absence from range maps
De Klerk et al. (2004)	Sub Saharan Africa	1 × 1° cells	National PAs	10%, 25% 33% and 50%-cover thresholds	Afrotropical birds	Presence from sampling records
Estrada et al. (2008)	Andalusia (Spain)	10 × 10 km cells	Natural Conservation areas Network of Andalusia	25%-cover	Terrestrial mammals	Favourability values (fuzzy classification)
Fjeldsa et al. (2004)	Sub-Saharan Africa	1 × 1° cells	National PAs	5%, 10%, 25%, 33% and 50%-cover thresholds	Mammals	Presence from sampling records
Freemark et al. (2006)	British Columbia	640 km ² hexagons	Provincial PAs	Omitted	Threatened birds	Presence/absence from range maps
Hannah et al. (2007)	Mexico (MX), Cape Floristic Region, South Africa (CFR) and Europe (EU)	10 × 10 km (MX); 1.8 km ² (CFR); 50 km ² (EU)	National PAs	Omitted	Birds and mammals (MX); Proteacea plants (CFR), Plants (EU)	Presence/absence after a threshold value on probabilities
López-López et al. (2007)	Castellón Province, Spain	1 × 1 km cells	Important Bird Areas	Omitted	Golden eagle	Probability values (3 classes)
Maiorano et al. (2006)	Italy	2 × 2 km cells	National PAs	10%-cover threshold	Terrestrial vertebrates	Presence/absence after a threshold value on probabilities
Martinez et al. (2006)	Spain	10 × 10 km cells	Natura 2000	Omitted	Lichens	Presence/absence after a threshold value on probabilities
Papes and Gaubert (2007)	Africa and Asia	5 × 5 km cells	Formal and proposed IUCN PAs	Omitted	Viverrid mammals	Presence/absence after a threshold value on probabilities
Rondinini et al. (2005)	Africa	1 km ² cells	Existing system of PAs	Omitted	Amphibians and mammals	Probability values (3 classes)
Sánchez-Fernández et al. (2008)	Iberian Peninsula and Balearics	10' × 10' cells	Natura 2000	25%-cover threshold	Water beetles	Presence from sampling records
Stoner et al. (2007)	Tanzania	5 × 5 km and 10 × 10 km cells	National parks, game conservation areas, partially protected game-controlled areas	Omitted	Large herbivores	Presence from sampling records
Thomaes et al. (2008)	Belgium	5 × 5 km cells	Natura 2000	0–10%; 10–50% and 51–100%-cover thresholds	Saproxylic stag beetle	Presence/absence after a threshold value on probabilities
Traba et al. (2007)	Spain	10 × 10 km cells	Natural Protected Areas and Special Protected Areas under EU Birds Directive	20%-cover threshold	Birds	Presence from sampling records
Trisurat (2007)	Thailand	200 × 200 m cells	National PAs	Omitted	Vegetation types	Presence/absence from range maps

reserves were contingent on the threshold used to assign reserves to grid cells and that little (biological) guidance existed for the selection of a reliable threshold. Araújo (2004) concluded that careful examination of the impacts of using different threshold values when mapping reserves should be performed. However, most subsequent gap analyses failed to provide justifications for the chosen thresholds, and in some cases, even omitted to report them (for some examples of the threshold-based approaches used in gap analyses after 2004, see Table 1).

Although the sensitivity of gap analysis to varying thresholds has been demonstrated, the solutions to solve the problem remain elusive. Araújo (2004) suggested an approach to circumvent the arbitrariness of threshold choices based on an analysis of species' accumulation curves. He proposed that a threshold of 50% would be adequate for the particular studied system. However, the use of thresholds (single, "optimal", or a range of values) presents conceptual weaknesses. First, common threshold applications use a fixed value to map reserves, but different species may require different thresholds, and this cannot be assessed with species' accumulation curves that are, by definition, calculated from the complete species' pool used in the analysis. For example, if a restricted-range species is mostly distributed in small and isolated reserves, then conservative threshold choices (i.e., filtering out grid cells with low reserve-coverage) may not adequately quantify this species protection.

Second, because reserve size and density vary from region to region, reserve-coverage in grid cells is likely to be biased to lower or higher values depending on the region. In the same way, adopting a fixed threshold on evaluations based on maps produced under different resolutions (i.e., grid cell extents) is likely to deliver different sets of protected grid cells, which would lead to ambiguity when comparing biodiversity representation within reserves.

Third, the use of thresholds impedes the use of all available information on reserve-coverage. Thresholds convert the continuous information on grid cell reserve-coverage into binary classifications of fully protected or unprotected. Such conversions are prone to high rates of commission and omission errors that accumulate across the set of grid cells under analysis (Rondinini et al., 2006; Whittaker et al., 2005).

Furthermore, apart from these limitations, threshold values on reserve data are not amenable to use in less common analytical designs. There are cases where species' distribution data come from statistical modeling frameworks where species' probabilities of occurrence are obtained for each grid cell. In such situations, statistically-informed cut-off values are applied to define presence/absence of species in each grid cell (Liu et al., 2005). Because this threshold-like procedure on species data is also flawed by significant error rates (e.g., Araújo et al., 2005), adopting a two-threshold approach in gap analysis may increase uncertainties.

Another issue that has been ignored is the effect of the choice of thresholds when species' distributions change with time, for example, as a response to climate change. As mentioned above, since threshold values impact species differently depending on how species' distributions and reserves relate, changes in species' distribu-

tions by means of dynamic threats (e.g., climate change) are likely to be inconsistently treated by threshold values. Therefore, the use of approaches capable of responding to the above-mentioned weaknesses is critical for achieving more robust solutions in gap analyses assessments.

Here, we propose a novel approach to circumvent the use of thresholds in gap analyses. Rather than using a threshold to convert reserves into either present or absent, the proportion of grid cells that is covered by areas with conservation status is taken into account. A probabilistic framework is then developed that estimates how likely species are represented in reserves within every grid cell. We use virtual and plant-species' distribution data in the Iberian Peninsula to compare levels of species' representation in reserves obtained with our probability-based approach and different thresholds. We also seek to determine if comparisons of levels of species' representation in reserves with random areas differ when assessed with conventional threshold approaches versus the proposed methodology. By using species' distribution modeling outputs (i.e., probabilities of occurrence) for the present and the future, we discuss the robustness of various approaches when assessing reserve representativeness under climate change.

2. Material and methods

2.1. Virtual data

We produced a small virtual dataset to illustrate how the threshold approach differs from a threshold-free approach in evaluating species' representation in reserves. Probabilities of occurrence (s_i) for three hypothetical species (sp_A , sp_B , sp_C) in each one of ten grid cells (i) ordered by non-increasing values of reserve-coverage (r_i) are shown in Table 2. Range sizes for the hypothetical species and total area with reserves are obtained by summing s_i and r_i for all i , respectively. Species were simulated to represent a variety of patterns such that one species had a similar probability of occurrence across the protected grid cells (sp_A); one species had a biased distribution towards grid cells with higher protected coverage (sp_B); and one species had a biased distribution towards grid cells with lower protected coverage (sp_C).

2.2. The Iberian Peninsula dataset

We used 100 plant-species' distributions (Table S1, Supplementary material) from a larger pool of 1298 European plant species modeled for another study (Araújo et al., submitted for publication). The species set was randomly selected following two conditions: (1) species should have at least 20 registered occurrences in the Iberian Peninsula (approximately 1% of the analyzed area); and (2) a wide variety of sizes of the species' European ranges, taken as the proportion of the total 50° grid cells in analysis where a species occurs, should be represented.

Probabilities of occurrence of each species in each 10° Iberian Peninsula grid cell were obtained from models investigating corre-

Table 2

Data for an illustrative example. Probability of occurrence (s_i) for three hypothetical species (sp_A , sp_B , sp_C) in each of 10 cells (i) ordered by non-increasing values of the fraction of reserve-coverage (r_i). Species' range sizes and total protected area (Range) are obtained by summing s_i and r_i , respectively. Species were simulated to represent a variety of distributions: a species with a similar probability of occurrence values across the protected grid cells (sp_A); a species with a biased distribution towards grid cells with higher reserve fractions (sp_B); and a species with a biased distribution towards grid cells with smaller reserve fractions (sp_C).

i		1	2	3	4	5	6	7	8	9	10	Range
r_i		0.99	0.77	0.60	0.47	0.36	0.28	0.22	0.17	0.14	0.00	4.0
s_i	sp_A	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.00	1.0
	sp_B	0.25	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.0
	sp_C	0.00	0.00	0.00	0.00	0.25	0.10	0.20	0.10	0.25	0.10	1.0

lations of species' presences/absences at European level with climate predictors for a baseline period (i.e., averaging predictors for 1961–1991) and 2080 (i.e., averaging predictors for 2051–2080) (Araújo et al., submitted for publication). Probabilities were filtered by downscaled recorded occurrences of species in the baseline period (i.e., atlas records). Where species were not recorded, probabilities were set to zero. With such approach, we reduced commission errors associated with projections of species' distributions in areas where they were not recorded, thereby adopting a conservative and precautionary approach for conservation assessments.

The Iberian Peninsula reserve data were also extracted from the analysis performed by Araújo et al. (submitted for publication) in which the proportion of each grid cell area within reserves was computed (Fig. S1, Supplementary material). Grid cells were considered protected if the fraction of the protected area equaled or exceeded a threshold value R . A sequential set of 11 area-proportional threshold values were chosen, ranging from a small residual value above zero to 1 (0^+ , 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90 and 1), to define 11 grid-based binary maps of Iberian Peninsula reserves (Fig. S2, Supplementary material).

2.3. Measuring species' representation levels in reserves

Conservation assessments are typically performed in relation to previously defined targets (Rondinini and Chioza, 2010). Targets are commonly specified as the total area (in square kilometers) or the proportion of the total area of a biodiversity feature's distribution that should be in a reserve. Because our analysis takes place with species with different range sizes here we consider the proportional target for species' representation in reserves (i.e. values in the interval $[0, 1]$).

We propose to compute a species' representation index in reserves (SRI) with the expression below, which is flexible enough to accommodate different transformations of data (by means of the intervenient f and g functions):

$$SRI = \frac{\sum_{i=1}^N f(r_i) \cdot g(s_i)}{\sum_{i=1}^N g(s_i)} \quad (1)$$

where N is the number of grid cells; s_i is probability of occurrence for the species in grid cell i and r_i is the fraction of grid cell i considered protected. The choice of f and g determines a particular approach for assessing species' representation in reserves. For the case when both species and reserve data are binary-transformed after using S and R as thresholds, respectively (i.e., a two-threshold approach), $f(r_i) = 1$ when $r_i \geq R$ and 0 otherwise, and $g(s_i) = 1$ when $s_i \geq S$ and 0 otherwise. Because it only generates binary layers of species and reserve data, this case is comparable to commonplace grid-based gap analyses, in which recorded data on species are used instead of modeled data. In this circumstance, $g(s_i) = 1$ in places where a species occurs and $g(s_i) = 0$ where it does not occur. When species' probabilities of occurrence are used instead (preferably corrected for commission errors) and only reserve data are binary-transformed (i.e., a one-threshold approach), $f(r_i)$ follows the two-threshold approach and g is the identity function (i.e., $g(s_i) = s_i$).

With the two-threshold approach the SRI is calculated as the proportion of grid cells where a species is assumed to occur that coincides with reserves. Under the one-threshold approach the SRI is obtained by taking the sum of species' probabilities of occurrence across the grid cells assumed to be protected divided by the sum of species' probabilities of occurrence across all analyzed grid cells.

When data allows, we advocate to measure species' representation in reserves simply taking f and g in Eq. (1) as identity functions, i.e., $SRI = \sum_{i=1}^N r_i \cdot s_i / \sum_{i=1}^N s_i$. We term this proposal the

continuous approach. Below we give a probabilistic support for the interpretation of the continuous SRI as the sum, across all grid cells, of the expected relative area of the region that is simultaneously suitable for the species and under some protection status.

Consider a random experiment where: (i) a grid cell i is split into M squares with equal area; (ii) $M \cdot r_i$ squares are covered with reserves; and (iii) $M \cdot s_i$ squares are extracted, without replacement, among the M squares to represent the territory occupied by the species. If X is a random variable representing the number of squares marked in step (ii) among those squares selected in step (iii), then this experiment can be viewed as follows. If a grid cell is divided in M squares, $M \cdot r_i$ of them protected and $M - M \cdot r_i$ not protected then X counts those squares from the $M \cdot s_i$ squares that are protected (see Fig. S3, Supplementary material). Accordingly, X follows a hyper-geometric distribution with parameters M , $M \cdot r_i$ and $M \cdot s_i$ and an expected value equal to $M \cdot r_i \cdot s_i$. The random variable X/M represents the proportion of squares in grid cell i that are simultaneously protected and occupied by the species. Therefore, its expected value is $E(X/M) = r_i \cdot s_i$. We propose to use this value as a predictor of the fraction of the grid cell in the intersection of the territory covered by reserves and occupied by the species. This value represents the contribution of grid cell i to the representation of the species in the protected territory (i.e., the parcels in the numerator of Eq. (1)). The variance of X/M can also be derived using $Var(X/M) = s_i \cdot r_i (1 - r_i)(1 - s_i)/(M - 1)$. For large values of M , $Var(X/M) \approx 0$, thus making $E(X/M) = r_i \cdot s_i$ a precise measure for the proportion of the area in grid cell i that is simultaneously protected and occupied by the species.

There is a relation between threshold-based and continuous SRI . The SRI for the one-threshold approach is a stepwise (decreasing) function of thresholds R , ranging between 0 and 1. Therefore, the continuous SRI lays in some minimal interval $[a, b]$ bounded by two threshold-based SRI values. In general, determining the thresholds R corresponding to a and b , requires the knowledge of s_i . However, for species that are equally distributed across partially-protected grid cells (e.g., sp_A Table 2), it is possible to analytically determine the thresholds R^* for which the two approaches converge, without knowing s_i . To show this, let us assume that the grid cells are ordered by non-increasing r_i values (i.e., $r_1 \geq r_2 \geq \dots \geq r_N$). In doing so, there is an integer $0 \leq K^* \leq N$ such that (with the convention $s_0 = r_0 = 0$) $\sum_{i=0}^{K^*} s_i \leq \sum_{i=0}^{K^*} r_i \cdot s_i < \sum_{i=0}^{K^*+1} s_i$, and therefore, $R^* = r_{K^*}$. For species that are equally distributed, i.e., $s_i = s$, $\sum_{i=0}^{K^*} s_i = sK^*$ and $\sum_{i=0}^N r_i s_i = s \sum_{i=0}^N r_i$, and therefore $K^* = \lfloor \sum_{i=0}^N r_i \rfloor$.

We used the virtual data set to illustrate the mechanics of the one-threshold and continuous approaches as well as how they generate the SRI . We also used the Iberian Peninsula example to illustrate differences obtained with both approaches using a large number of species with varying distributional patterns. Analyses were performed for the baseline (present time) and 2080 periods.

2.4. Randomization tests

The degree to which reserve networks represent species better than expected by chance alone is often assessed under gap analyses frameworks (e.g., Araújo et al., 2007). Here we tested how the performance of the threshold-based and continuous approaches varied against a null model obtained by randomly selecting reserves. Randomizations included the selection of an equal number of cells as the protected grid cells. For threshold-based approaches, this means randomly selecting a number of grid cells equal to the number of protected grid cells obtained with thresholds. For the continuous approach, because the full range of reserve-coverage information is maintained in the analysis, an equivalent randomization test is produced by redistributing the s_i values within the N grid cells.

Table 3

The percent of species' ranges within reserves (SRI) for the example in Table 1 in which several threshold values (R) and the continuous approach were applied.

	SRI (%)							Continuous
	$R = 0.90$	$R = 0.75$	$R = 0.60$	$R = 0.45$	$R = 0.30$	$R = 0.20$	$R = 0.10$	
sp_A	11.0	22.0	33.0	44.0	55.0	77.0	100	44.0
sp_B	25.0	50.0	100	100	100	100	100	74.0
sp_C	0.0	0.0	0.0	0.0	25.0	55.0	90.0	21.4

For the virtual-data example ($N = 10$), we performed all possible permutations of s_i values ($10!$ permutations), thus producing an exact rank of species' representation values (SRI) to compare the performances of reserves produced with the threshold-based and the continuous approaches. For each species in the Iberian case study, we conducted 9999 permutations for each one of the chosen thresholds and for the continuous approach.

For each species, the SRI values obtained using the real reserve networks (produced with different threshold values and with the continuous approach) were then compared with those obtained using the corresponding random set of reserves. We performed one-tail tests by counting the number of permuted outcomes in which the SRI was lower (or higher) than the real SRI. Specifically, we were interested in checking whether the real SRI was greater than the 95th percentile (or lower than the 5th percentile) of the SRI values obtained from a random selection of grid cells. Analyses were performed for the baseline period and 2080.

3. Results

3.1. Measuring species' representation levels in reserves

3.1.1. Virtual data

For the three virtual species, representation levels within virtual reserves differed when a set of threshold values and the continuous approximation were applied (Table 3).

When $R = 0.10$, all the grid cells with some fraction of reserve land were assumed to be completely protected, and therefore all the range of sp_A , sp_B and most of the range of sp_C were assumed to be within reserves. Otherwise, if $R = 0.60$, then 33% of the sp_A distribution, 100% of the sp_B distribution and 0% of the sp_C distribution coincided with reserves. Therefore, a detailed analysis proved that the one-threshold approach is unstable, producing SRI values that are highly contingent on the particular threshold used. For example, species sp_C is completely distributed within grid cells with low protected fractions ($r_i \leq 0.36$). When one optimistically assumed a small threshold value, for example, $R = 0.10$ or $R = 0.20$, then a large fraction of the species's distribution was predicted to be within a reserve, which did not seem realistic given the small sizes of reserves. Conversely, when we assumed a strict threshold value, $R > 0.36$, then no sp_C distribution was predicted to coincide with reserves, although the species occurs in grid cells in some of the protected areas. The continuous approach weights the species' probabilities of occurrence in grid cell i with reserve-coverage at i Eq. (1). In doing so, the SRI values were 44% for sp_A distribution, 74% for sp_B distribution and 21% for sp_C distribution. These values seem consistent with an intuitive perception of the species' distributions. We examined the sensitivity of species' representation levels in reserves to a more extensive set of R values (Fig. 1). Note that sensitivity differs from species to species depending on how the species are distributed across the protected grid cells. Because sp_A approximates an evenly distributed species, the analytical formula for R^* could be applied across partially-protected grid cells. In our example, $K^* = 3.96 \approx 4.00$; this means that both approaches produced very similar SRI values (SRI = 44.0%) for sp_A when a threshold $R = r_4 = 0.47$ was considered (or any R

in the interval [0.36; 0.47]). For sp_B , an approximated R^* was in the interval [0.60; 0.77], while for sp_C was in the interval [0.28; 0.36] (see Table 3).

3.1.2. The Iberian Peninsula dataset

The proportion of the Iberian Peninsula that was considered protected varied according to the different threshold values used to assign reserves to grid cells (Fig. S2, Supplementary material). For the most liberal scenario ($R = 0^+$) in which all partially-protected grid cells were assumed to be fully protected, 27.6% of the Iberian Peninsula was considered protected. When applying the more conservative threshold ($R = 1$), where grid cells that were fully covered by reserves were actually considered to be protected, the percentage of the Iberian Peninsula area that was considered to be protected decreased to 0.4%. The real figure, obtained with polygonal reserve mapping, was 4.55%, which would correspond to the area covered when choosing a threshold value between 0.5 and 0.6.

Variations in threshold values also caused perceived levels of species' representation in reserves to vary accordingly. For the baseline period, the averaged SRI taken across species varied from 39.5% to 0.6% for $R = 0^+$ and $R = 1$, respectively (Fig. 2), with species exhibiting different sensitivities to threshold values depending on their occupancy patterns. For the more liberal $R = 0^+$, *Aconitum burnatii* (sp68), *Cystopteris montana* (sp7) and *Cardamine bellidifolia* (sp90) were predicted to have more than three quarters of their Iberian range within reserves (97.7%, 85.6% and 75.8%, respectively), while *Silene uniflora* (sp52), *Malcolmia triloba* (sp86) and *Camelina microcarpa* (sp94), the species with lower SRIs, were predicted to have 18.0%, 19.2% and 20.9%, respectively, of their Iberian range within reserves.

When gap analysis is undertaken using the more conservative threshold $R = 1$, the three species that previously had the highest

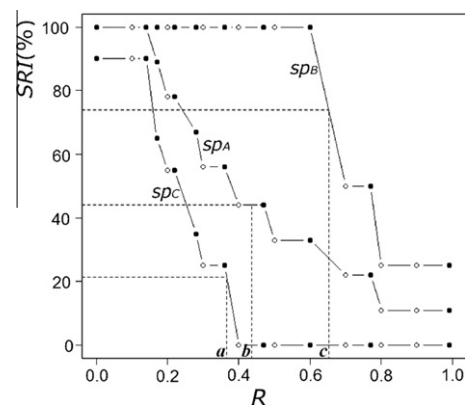


Fig. 1. Representation levels within reserves (SRI) for the three species (sp_A , sp_B , sp_C) in the hypothetical example (Table 2) after using several threshold values (R): open dots for an *ad hoc* sequence of increasing values: 0^+ , 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90 and 1; black dots for values equal to the fraction of reserve-coverage in grid cells: Table 2). Threshold values producing representation values equivalent to the continuous approach (R^*) are represented by a, b and c for sp_A , sp_B and sp_C , respectively.

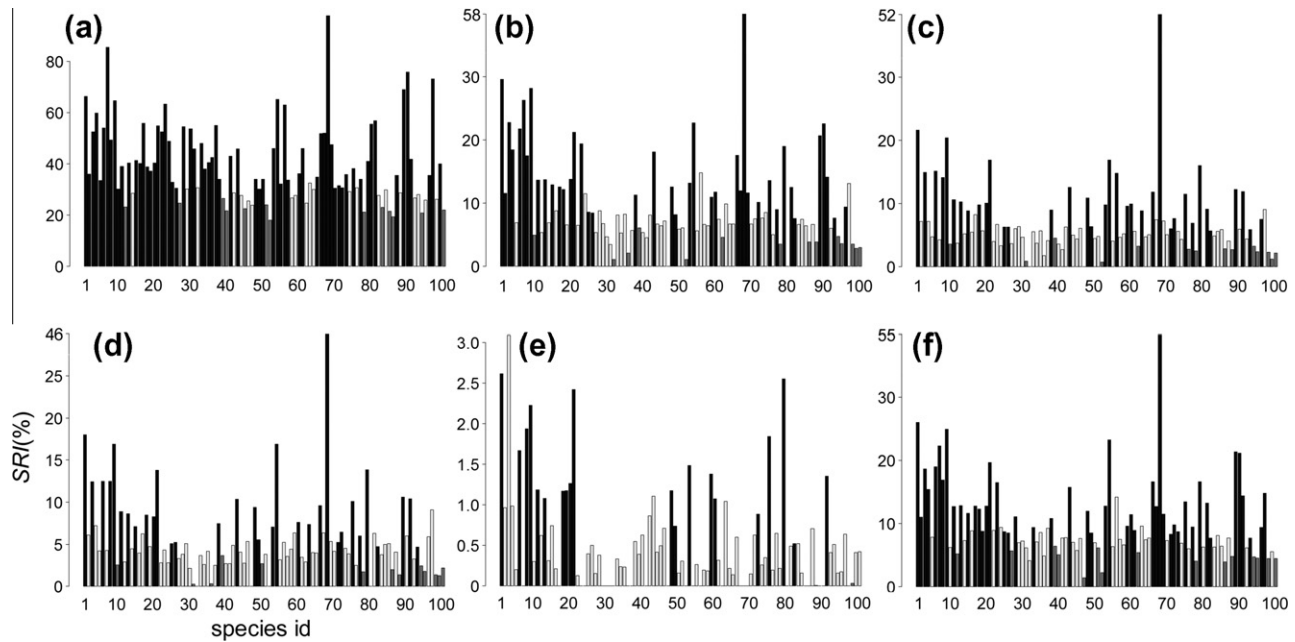


Fig. 2. Species' representation levels (*SRI*) within Iberian Peninsula reserves for the baseline period. *SRI* values were obtained using the one-threshold approach applying five different threshold values to reserve data, (a) $R = 0^+$, (b) $R = 0.40$, (c) $R = 0.50$, (d) $R = 0.60$, (e) $R = 1$ and (f) the continuous approach. Darker-grey bars indicate species with higher *SRI* values than 95% of a set of 1000 random areas, medium-grey bars indicate species with lower *SRI* values than 95% of random areas, lighter-grey bars indicate species whose *SRI* values are not significantly different from the random areas.

SRI were predicted to have no Iberian range within reserves, while species predicted to have a greater representation were *Equisetum sylvaticum* (sp3: 3.1%), *Selaginella selaginoides* (sp1: 2.6%) and *Corydalis cava* (sp79: 2.6%). In addition, 22 other species had no representation in reserves.

Across the sequence of the analyzed thresholds, there was no clear consistency in species' rankings with respect to their levels of representation within reserves (Fig. 2). *Aconitum burnatii* (sp68) appeared different from other species because it has a considerably higher *SRI* across all but the highest of the analyzed thresholds. This species has a restricted-range in two regions on the NE and SE of the Iberian Peninsula (Fig. S4, Supplementary material) coinciding with protected areas. Moreover, grid cells where this species is expected to be better represented (i.e., having higher probability of occurrence) coincide with grid cells with a greater reserve-coverage that were converted to "protected" grid cells using most of the threshold applications, except for the most conservative one ($R = 1$) (Fig. S2, Supplementary material).

Within the range of threshold values, the majority of species' *SRI* curves followed very closely the accumulated frequency of reserve-coverage in Iberian Peninsula (Fig. S5, Supplementary material). Because *SRI* co-vary with the occurrence of reserves across grid cells after application of a threshold, this pattern is likely to signal the species that have approximately equal probabilities of occurrence in the partially-protected grid cells where they are predicted to occur (similar to *sp_A* in Fig. 1 and *Ceratophyllum demersum* in Fig. S4, Supplementary material), including both species with wide and restricted-ranges (Table S1, Supplementary material). There were also species whose *SRI* departed from this trend, exhibiting *SRI* curves constantly over the reserve-coverage cumulative frequency curve (e.g., *Aconitum burnatii* in Fig. S4, Supplementary material) or constantly below the reserve-coverage cumulative frequency curve (e.g., *Fumaria gaillardotii* in Fig. S4, Supplementary material). Species that follow these patterns (similar to *sp_B* or *sp_C* in Fig. 1, respectively) are characterized by distributions biased towards higher and lower reserve-coverage across grid cells, respectively. Species with restricted-ranges are more sensitive to

variations in threshold values. This translates into step patterns in the *SRI* curves. Flat sections originate when a range of threshold values does not change the protection status of the grid cells where the species has high probabilities to occur, while abrupt deflections reflect substantial changes in the protection status of grid cells where species are very likely to occur.

The threshold values that resulted in *SRI* similar to those obtained with the continuous approach differed by species (Table S2a, Supplementary material). These values varied from 0.14 for *Sagina nodosa* (sp47) to 0.55 for *Silene behen* (sp56), with a mode between 0.35 and 0.40 (Fig. S6, Supplementary material).

For 2080, there were no radical shifts in expected species' representations within the Iberian reserves when compared to the baseline period. With $R = 0^+$, the three species with the highest *SRI* and the three species with the lowest were the same in 2080 and in the baseline period. Moreover, these species exhibited similar *SRI* for the both periods. With $R = 1$, the three species with the highest *SRI* were *Silene boryi* (sp53: 3.2%), *Corydalis cava* (sp79: 3.1%) and *Ranunculus hederaceus* (sp75: 2.4%). As in the baseline period, 25 species were predicted to have no representation in reserves (Table S2b, Supplementary material). For intermediate threshold values (Fig. S5, Table S2b, Supplementary material), *SRI* varied in the same way as observed for the baseline period. Most species followed the cumulative reserve-coverage curve, indicating that they are distributed equally among all the partially-conserved grid cells. With the predicted shifts resulting from climate modifications in the Iberian Peninsula for 2080, portions of species' distributions in reserves are expected to change. Consequently, the relationship between *SRI* variation and threshold values is also expected to change. In fact, from the 100 plant species in the analysis, the sensitivities to threshold values for 27 species differed between the baseline period and 2080 (Fig. S5, Supplementary material). From these, 22 species had R^* that significantly differed between the baseline and 2080 (Fig. 3). *Silene behen* (sp56) had the most pronounced difference ($R^* = 0.55$ in the baseline and $R^* = 0.31$ in 2080). Overall, R^* values obtained for 2080 differed significantly from the R^* values for the baseline period (Wilcoxon signed-rank test:

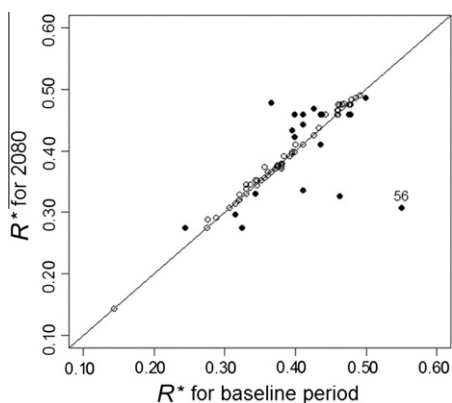


Fig. 3. Threshold values that generate SRI values close to the SRI values obtained using the continuous approach (R^*) for the baseline period and 2080. Results are shown for 100 plant species in the Iberian Peninsula. The diagonal line represents similar values of R^* for both periods. Open circles identify species with similar values of R^* in both periods. Solid circles identify outlier species. A large difference between R^* in the baseline and 2080 periods is expected for *Silene behen* (sp56).

$W = 485$, P -value < 0.05). For 2080, *Sagina nodosa* (sp47) had the lowest R^* ($R^* = 0.14$), while *Corydalis cava* had the highest value (sp79: $R^* = 0.49$) (Fig. S6, Table S2b, Supplementary material).

3.2. Randomization tests

3.2.1. Virtual data

We analyzed how different thresholds determine different appraisals of the performance of a virtual reserve when compared to random sets of areas with equivalent sizes. Species sp_A is characterized by a perfectly balanced distribution of probabilities across grid cells with different extents of reserve-coverage. In this case, any redistribution of the s_i across the N grid cells resulted in an SRI smaller than or equal to the real value for both approaches (Table 4).

Species sp_B has higher probabilities of occurrence in grid cells with larger reserve-coverage and is absent from seven grid cells where $r_i < 0.60$. Therefore, for thresholds resulting in seven or fewer grid cells protected ($R > 0.17$), the minimum value for the SRI taken from permutations was $SRI = 0$, which corresponded to the species' representation in the grid cells where it is absent. Similarly, for threshold values that produced a reserve system composed of three or more grid cells ($R \leq 0.60$), the permutation retrieving the highest SRI ($SRI = 100\%$) corresponded to the selec-

tion of grid cells $i = 1, 2$ and 3 , which were the only grid cells where the species is expected to occur with $s_i > 0$. For this species, all thresholds except for $R = 0.90$ produced reserve systems with higher representation than at least 95% of the selected random sets with equivalently sized grid cells. In the continuous approach species are also better represented in reserves than expected by chance. The minimum species representation level in reserves was obtained with permutations where the reserve-coverage of grid cell $i = 10$ ($r_i = 0$) was assigned to the grid cells where the species has a greater probability of occurrence ($i = 3$) and when the two other grid cells with a smaller reserve extent ($i = 8$ and 9) were assigned to the other grid cells where the species occurs with a probability of 0.25. In this case, $SRI = 0.17 \times 0.25 + 0.10 \times 0.25 + 0.00 \times 0.50 \times 100 = 7.8\%$. The higher permuted SRI value occurred when the grid cell with a larger reserve-coverage ($i = 1$) was assigned to the grid cell where the species occurs with a higher probability ($i = 3$), while the two other grid cells with elevated reserve-coverage ($i = 2$ and 3) were assigned to $i = 1$ and 2 . In this case, $SRI = 0.99 \times 0.50 + 0.77 \times 0.25 + 0.60 \times 0.25 \times 100 = 83.8\%$.

In contrast to sp_B , the distribution of sp_C is biased towards grid cells with smaller reserve-coverage. When conservative to moderate threshold values ($R > 0.30$) were used sp_C appeared less represented in reserves than in random selected areas. The continuous approach produced the same result because the majority of the permutations redistributed grid cells with elevated r_i in the grid cells where the species occurs with some probability. That is by aligning grid cells 1–4 with non-zero species' probabilities, high values of reserve-coverage weighted the species' local probability of occurrence, producing higher SRI than in the real distribution.

3.2.2. The Iberian Peninsula dataset

In the Iberian Peninsula dataset, randomization tests for the baseline and 2080 periods applied across the thresholds indicated better species' representation in Iberian Peninsula reserves than in 95% of equivalent random choices of grid cells for most of the analyzed species (Fig. 2; Tables S2a and S2b, Supplementary material). This was particularly true for the more optimistic threshold value ($R = 0^+$). In fact, like sp_A in the virtual-data example (Table 2), most of the plant species in the analysis have approximately equitable distributions along the partially-conserved grid cells (Fig. S5, Supplementary material), which make them better represented in reserves than expected by chance for most of the threshold values (P -value < 0.05). There was a general trend where increasing threshold values led to poorer performing reserves. However, some species presented distinct patterns being less represented in reserves, even when using $R = 0^+$, than in most of the equivalent

Table 4

Permutation assessments for the illustrative example presented in Table 2 and continued in Table 3. All possible redistributions of reserve-coverage values (r_i) across species' probabilities of occurrence (s_i) are compared to the real (Real) percent of species' range sizes within reserves (SRI) using several threshold values (R) and the continuous approach. The distribution of SRI values obtained from permutations is summarized by minimum (min) and maximum (max) SRI values and by the percentage of permutation events generating higher (% higher) and lower (% lower) SRI values than the real SRI.

		$R = 0.90$	$R = 0.75$	$R = 0.60$	$R = 0.45$	$R = 0.30$	$R = 0.20$	$R = 0.10$	Continuous
sp_A	Real SRI	11.1	22.2	33.3	44.4	55.5	77.7	100	44.0
	min-max	0.0–11.1	11.1–22.2	22.2–33.3	33.3–44.4	44.4–55.5	66.6–77.7	88.8–100	33.4–44.4
	% higher	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]
	% lower	10.0	20.0	30.0	40.0	50.0	70.0	90.0	90.0
sp_B	Real SRI	25.0	50.0	100	100	100	100	100	74.0
	min-max	0.0–50.0	0.0–75.0	0.0–100	0.0–100	0.0–100	0.0–100	50.0–100	7.8–83.8
	% higher	10.0	4.4 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	2.2 [*]
	% lower	70.0	77.8	99.2	96.7	91.7	70.8	30.0	97.5
sp_C	Real SRI	0.0	0.0	0.0	0.0	25.0	55.0	90.0	21.4
	min-max	0.0–25.0	0.0–50.0	0.0–70.0	0.0–80.0	10.0–90.0	30.0–100	75.0–100	15.5–67.1
	% higher	60.0	86.7	96.7	99.5	92.9	76.7	40.0	98.4
	% lower	0.0 [*]	0.0 [*]	0.0 [*]	0.0 [*]	6.3	11.7	30.0	1.6 [*]

^{*} Combinations of species and approaches for which reserves perform better (in % higher) or worse (in % lower) than 95% of the possible permutations.

random sets (Fig. 2; Tables S2a and S2b, Supplementary material). In contrast, one-fifth of the species continued to be better represented in reserves, that were produced with the more stringent threshold value ($R = 1$), than expected by chance.

With the continuous approach the Iberian reserves were expected to perform better than expected by chance for about half of the species and to perform worst for one tenth of the species. This result was similar for the baseline period and 2080, although for 29 species levels of significance varied (i.e., P -values; see Tables S2a and S2b, Supplementary material). Similarly for some species, reserve systems obtained using equivalent thresholds (R^*) performed differently from the continuous approach. Once again, differences came only from levels of significance.

4. Discussion

Uncertainty in conservation planning arises from a variety of sources such as information gaps, natural system dynamics, several descriptive modeling architectures and contextual misunderstandings (Elith et al., 2002; Regan et al., 2009). Here we assessed a particular source of uncertainty influencing the interpretation and adequate implementation of gap analysis in conservation planning: the decision as to whether grid cells should be considered fully conserved when reserves only partially cover the grid cells being analyzed. The common approach to circumvent such a problem is to choose an arbitrary and fixed threshold that converts the grid cell into being either protected or unprotected. However thresholds affect the perception of whether species are to be considered well represented or underrepresented in reserves (see Fig 2). In this study, we propose an approach to estimate species' representation in reserves that circumvents problems associated with the use of arbitrary thresholds to match species with reserves.

As discussed above, the definition of SRI given by Eq. (1) accommodates conventional threshold approaches, where just one or both of the species and reserve datasets are converted to a binary classification system (i.e., presence/absence). However, the major benefit of the proposed SRI is its capacity to use the full breadth of information (i.e., continuous data) regarding species' distributions and reserve-coverage (i.e., the continuous approach). By avoiding thresholds and calculating the proportion of the grid cell i where a species range coincides with reserves, $r_i \cdot s_i$, we can also estimate the proportion of the grid cell where species range is not confined in reserves, $(1 - r_i) \cdot s_i$. Assuming that a species has a uniform probability of occurrence inside grid cell i , these proportions can be directly read as the probabilities of occurrence inside and outside reserves. Such inferences may then be used in the context of probability-based reserve selection algorithms (Cabeza et al., 2004; Polasky et al., 2000; Williams and Araújo, 2002). Importantly, the suggested approach presents low variance, and is thus a robust measure to be used in gap analysis.

Several target-based conservation programs are based upon population viability analysis (Cabeza and Moilanen, 2001; Rondinini and Chioza, 2010) in which demographic data (e.g., abundance) are used as a proxy of species' persistence in reserves (Faith et al., 2003; Godet et al., 2007; Grouios and Manne, 2009). To assess a species representation level in reserves, given abundances a_i of the species in each grid cell i , Eq. (1) can be used with s_i replaced by a_i . As for occurrence data, the continuous approach consists of taking f and g as the identity function with the following probabilistic interpretation: $a_i \cdot r_i$ is the expected value of the random variable representing the number of individuals (assumed to be randomly located in the grid cell) occurring in the reserve, which has a binomial distribution with parameters a_i and r_i .

Because reserves are often actively managed to minimize threats (Gaston et al., 2002), species are more likely to be present, to be abundant and to have higher rates of increase within reserves than in equivalent sized unprotected areas (Caro et al., 2009; Hopkinson et al., 2000). To incorporate in SRI such non-independence between species' conservation achievement and the degree of protection of the grid cells, we can use function f (with values ranging in $[0, 1]$) in Eq. (1) to weight reserves against non-protected areas. This gives

$$SRI = \frac{\sum_{i=1}^N f(r_i) \cdot s_i}{\sum_{i=1}^N s_i} \quad (2)$$

Values of $f(r_i) > r_i$ ($f(r_i) < r_i$) would contribute to increase (decrease) SRI , expressing that the species tends to favor (avoid) reserves over unprotected areas. This has the following probabilistic interpretation. Each parcel in the numerator can be interpreted as the product of the species probability of occurrence in grid cell i , s_i , by the conditional probability that the species is in the reserved area given that it occurs in the grid cell, $f(r_i)$. This product is precisely the probability that the species is represented in the grid cell's protected fraction. If reserves have no effect on the presence of species, the conditional probability $f(r_i)$ is simply the fraction of grid cell i under protection, i.e., $f(r_i) = r_i$. If the species tend to favor (avoid) reserves over unprotected areas, then the conditional probability $f(r_i)$ is greater (lower, resp.) than r_i . Interestingly, this interpretation also relates threshold-based approaches with the continuous application. If a specific threshold R generates a SRI higher than the one obtained by the continuous approach, then it is implicitly assumed that the species is attracted by reserve systems. If the choice of the threshold produces a lower SRI than the one from the continuous application, an undesirable effect of reserves on species is assumed. If the SRI obtained by the threshold and the continuous approaches converge (R^*), then a neutral effect of reserves is accepted.

Dynamic threats do probably intervene in the redistribution of species. Species are likely to change their distributions towards newly suitable regions, and therefore their representation levels in static reserves are likely to be altered (Heller and Zavaleta, 2009). Assessments of trends in reserve representativeness are therefore adequate to anticipate such changes (Dockerty et al., 2003; Hole et al., 2009; Kharouba and Kerr, 2010; Leroux et al., 2007). However, this dynamic component of biodiversity does not fit the common use of fixed thresholds for matching species with reserves in different timeframes. Here, we have seen that R^* is likely to change as species change their distributions in time (Fig. 3; Tables S2a and S2b, Supplementary material). Therefore, while it seems incorrect to maintain the same threshold value to assess a species occurrence in reserves over time, the definition of two arbitrary and uninformed threshold values would also probably make the analysis flawed. For many species, the quantification of suitability gains and losses within reserves depends on the threshold selected. For example, *Cystopteris montana* (sp7) and *Ulmus glabra* (sp21) appear to be winners from the baseline period to 2080 when applying $R = 0.40$, while when applying $R = 0.50$, they appear to be losers (Fig. 4; Table S2c, Supplementary material). In contrast, *Malcolmia ramosissima* (sp87) is predicted to be a loser species when $R = 0.40$ and a winner species when $R = 0.50$. A species-specific threshold-like that implicitly defined by the continuous approach seems to be more adequate because it uses (consistently) the full breath of distributional information for each species in order to derive species' suitability trends in reserves (Araújo et al., submitted for publication).

The performance of quantitative conservation plans is constrained by the quality of input data (Cabeza and Moilanen, 2001; Grand et al., 2007; Meir et al., 2004). Conventional thresh-

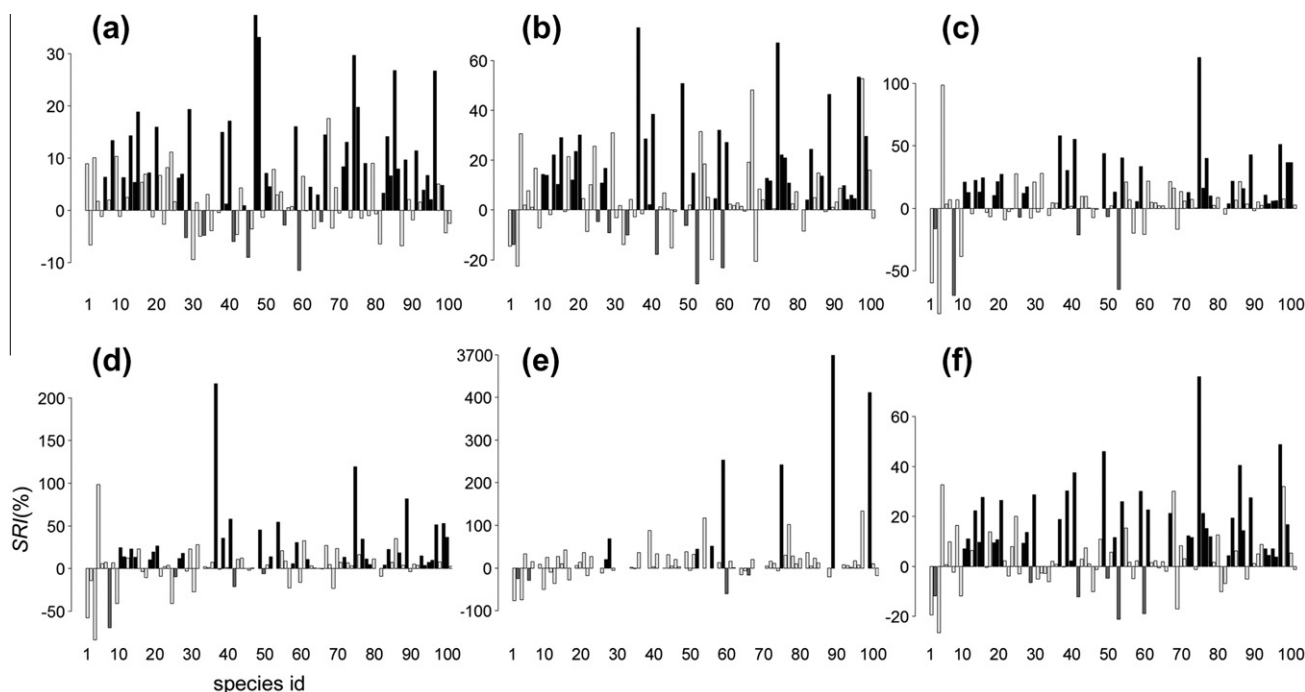


Fig. 4. Analysis of the percentage variation in species' representation in reserves (SRI%) from the baseline period to 2080 using the one-threshold approach applying five different threshold values to reserve data, (a) $R = 0^*$, (b) $R = 0.40$, (c) $R = 0.50$, (d) $R = 0.60$, (e) $R = 1$ and (f) the continuous approach. Darker-grey bars indicate species with higher SRI variation than 95% of a set of 1000 random areas, medium-grey bars indicate species with lower SRI variation than 95% of random areas, lighter-grey bars indicate species whose SRI variation is not significantly different from random areas.

old-based assessments of species' representations in reserves are prone to distributional errors (i.e., omission and commission errors, Rondinini et al., 2006) as grid cells are assumed totally protected or not protected at all. As more grid cells are analyzed in regional assessments, these errors are likely to accumulate, leading to flawed results on reserve representativeness. Some species will appear less represented in reserves than they actually are, while others will be erroneously assumed to be over-represented. Reserve selection algorithms based on these analyses are likely to produce costly, inefficient solutions (Wilson et al., 2009). The continuous approach presented here produces a fine-tuned quantitative assessment of species' representation within reserves when using grid-data and it thus deflates omission and commission errors.

5. Conclusions

We demonstrated that conservation planning is sensitive to errors arising from arbitrary decisions used to match species' distributions and reserve data that are originally mapped at different resolutions. These errors are seldom quantified leading to inefficiencies in the analysis of reserve performance. Here we present an approach that directly uses the full breadth of available data for species' distributions and reserve-coverage, in order to match species with reserves in a more effective and rigorous manner. Our approach has several advantages: (1) it allows to use species' probabilities of occurrence (i.e., [0, 1] rather than binary data) and reserve-coverage (i.e., continuous approach); (2) it can work with species' abundance data instead of probabilities of occurrence; (3) it allows to specify, for each species, the (equivalent) threshold R^* for which threshold-based and continuous approaches coincide; (4) it handles situations when species are more (or less) likely to occur in reserves (i.e., reserve attractiveness); (5) it provides an interpretation of the threshold-based outcomes in terms

of the species' reserve attractiveness, by comparison with the continuous approach; and finally (6) it is easy to compute.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.11.011.

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