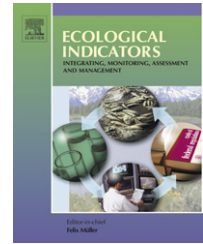


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Testing the effectiveness of discrete and continuous environmental diversity as a surrogate for species diversity

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ABSTRACT

Biodiversity surrogates are needed because detailed data on the distributions of species and communities is very limited. Among alternative surrogate strategies there is an environmental diversity (ED) framework, which uses the p -median model to sample environmental space as evenly as possible. The underlying idea is that such a sample would represent underlying species diversity well. However, tests of the effectiveness of ED as a surrogate for species diversity have been inconclusive, and there is a debate concerning the usefulness of different implementations of ED. In particular, it has been argued that tests of the ED framework are flawed because they used discrete algorithms (calculating the p -median from an observed environmental space), while continuous versions of ED should be preferred (i.e. calculating the p -median from a theoretical, continuously spaced, environmental space). Unfortunately, progress has been hampered by lack of independent testing of the two ED approaches. Here, we provide the first empirical test of the effectiveness of both continuous and discrete ED using European distributions of amphibians and reptiles. Analyses were implemented considering two different extents: (1) western Europe and (2) the Iberian Peninsula. In both cases, implementations of ED represented species at a lower rate than expected by chance ($P < 0.05$). Unlike suggested by some authors, the continuous ED was not consistently superior to the discrete form: continuous implementations of ED performed slightly better when fewer areas were selected and discrete ED performed better when the whole of the western European region was considered. Our results support findings that ED has only limited value as a surrogate for biodiversity and invite the interpretation that failure of ED is more likely to be related with oversimplification of assumptions underlying the model than to the particular p -median algorithm used.

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1. Introduction

Knowledge on the distribution of species is limited. Thence it is often the case that conservation planning requires the use of environmental surrogates for the distribution of biodiversity. Should such surrogates be effective, they could be used to design species sampling campaigns (Ferrier, 2002; Hortal and Lobo, 2005; Funk et al., 2005; Rocchini et al., 2005) or to locate networks of areas for the conservation of biodiversity (Faith and Walker, 1996; Faith et al., 2001; Trakhtenbrot and Kadmon, 2005; Sarkar et al., 2005; Bonn and Gaston, 2005; Heino and Mykra, 2006). One possible framework for using environmental data as a surrogate for biodiversity was proposed by Faith and Walker (1994, 1996). The framework proposes that if one selects conservation areas that include a greater number of different types of environments, then we would expect these areas to represent more species than if areas were selected with a more restricted number of types of environments (Austin and Margules, 1984; deVelice et al., 1988; Margules et al., 1988; Faith and Walker, 1996). If this surrogate framework was effective, then it should be particularly useful in poorly surveyed regions, because environmental data are readily accessible at low cost, whereas biological surveys are not.

The idea of sampling environmental pattern as surrogate strategy for biodiversity was termed environmental diversity (ED) by Faith and Walker (1994, 1996). The ED framework is based on the concept of complementarity proposed by Vane-Wright et al. (1991) and subsequently defined by Williams (2001) as a ‘property of sets of objects that exists when at least some of the objects (species) in one set (areas) differ from the objects (species) in another set (areas)’. Put simply, the complementarity principle states that if one selects areas with different species compositions [or different types of environments] one would attain full representation of species in these areas more rapidly than if areas were selected with redundant species compositions [or similar types of environments]. Drawing on a wealth of literature in geography and urban planning, the ED framework was formalised as a p -median model (Church and Sorensen, 1996; Church, 2002). The p -median is a specific location-allocation problem with a relatively simple rationale: if p sites are selected from a group of m demand sites, the location of these sites minimizes the sum of the distances between the demand sites and the p sites. This is a well-studied location-allocation problem in operational research, and a number of p -median models have been proposed to solve it (e.g. Mladenović et al., 2007). When applied to environmental space (as opposed to geographical space, which is where p -median models have been applied more often), solving the p -median problem is expected to be conceptually equivalent to maximising ED (Faith and Walker, 1996).

Even though the ED framework is logically intuitive, its usefulness has been questioned on the grounds that there is limited empirical evidence in support of the idea that maximizing environmental diversity in sets of areas would also maximize species diversity (for debate see Araújo et al., 2001, 2003, 2004; Faith, 2003; Faith et al., 2004). Proponents of the ED framework have argued that published tests are based on an inappropriate choice of the models used to solve the p -median problem. In particular, the authors argue that a ‘discrete’ form of ED rather than the [preferred] ‘continuous’

form have been utilized (Faith, 2003; Faith et al., 2004). According to these authors the continuous p -median (Faith and Walker, 1994, 1996) creates an equally stratified sampling of environmental gradients by allocating n regularly spaced ‘ideal’ demand points at regular distances throughout each environmental dimension. These n ideal points are used to represent the m original (i.e. real) demand sites: once p ‘ideal’ points that provide the better coverage of the environmental gradients are identified, the m ‘real’ sites placed nearest to each one of them are included within the group of selected sites (see Faith and Walker, 1994; Faith, 2003). In contrast, the discrete p -median form (Araújo et al., 2001, 2003, 2004; Hortal and Lobo, 2005) uses the available m sites as demand points instead of the n ‘ideal’ points regularly spaced in a theoretical space. Due to this, Faith et al. (2004) argued that the environmental description of the region provided by the discrete p -median could be limited, thus failing to represent the turnover of species produced by their responses to environment. Here, it is important to notice that classifying p -median models into discrete and continuous forms is a poor representation of the variety of models available to solve the minimum distance problems that are available in the spatial planning literature (e.g. Daskin, 1995; Moreno Jiménez, 2004; Mladenović et al., 2007); while the continuous p -median is similar to the MINISUM models, the discrete p -median form actually corresponds to most of the models available to solve the p -median location-allocation problem in such literature. In spite of this, we have chosen to retain the terminology used by Faith (2003) throughout the text to avoid introducing new terms and thus potentially diverting the discussion of substance to issues of semantics (e.g. Faith et al., 2004).

In contrast with the debate regarding the performance of different p -median algorithms, criticism of the ED framework is often related with the robustness of the underlying theory. The ED framework assumes that species distributions are at equilibrium with the current environmental conditions, i.e., species occur in all climatically suitable areas whilst being absent from all unsuitable ones, even though there is evidence this is not often the case (e.g. Araújo and Pearson, 2005; Araújo et al., 2008). It is also expected that species responses to environmental variables are unimodal: “Environmental diversity can be linked with ‘expected biodiversity’ at the species level by drawing on the model’s characterization of species’ responses to environmental continua or gradients as generally unimodal” (Faith and Walker, 1996, p. 421). Although species are indeed expected to respond to environmental variables following some sort of bell-shaped response curve, there are several factors that might modify this response (e.g. Austin et al., 1990; Thuiller et al., 2004). Although the basic assumptions of the ED formulation could be adapted to different situations (Faith and Walker, 1996; Faith, 2003; Faith et al., 2004), the idea that sampling environmental pattern would maximise species diversity in sets of areas is unavoidably linked with such species’ response model and with assumptions of equilibrium.

So far, independent testing of the ED framework has only been performed with the discrete p -median. These tests have shown that ED would often fail to represent species diversity at a rate higher than expected by chance (using the $P < 0.05$ threshold) (Araújo et al., 2001). The authors also showed that

species that were not represented with the ED framework were those most likely not to be at equilibrium with current environmental conditions (for additional discussion see Araújo and Pearson, 2005; Araújo et al., 2008). An interpretation was made that the failure of ED indicated the difficulty of the approach to represent species diversity when species distributions were highly affected by unaccounted historical factors (see also Araújo et al., 2003, 2004; Whittaker et al., 2005). In response to these interpretations, Faith (2003) and Faith et al. (2004) argued that unsuccessful recovery of species diversity with ED was due to use of the discrete ED rather than the preferred continuous version (see above). The debate has thus been polarised between those attributing the failure of ED to the inability of the approach to account for important [historical] determinants of species ranges, and those attributing the failure of ED to the characteristics of the location-allocation model used.

Here we provide a first test of the effectiveness using the ED framework to select conservation areas for European amphibian and reptile diversity that compares both the discrete and the continuous implementations of ED. In order to explore the sensitivity of ED to the spatial extent of the studied areas we perform the test using two regions: western Europe and the Iberian Peninsula.

2. Data

2.1. Species data

Species data included records of occurrence for 143 amphibian and reptile species (Gasc et al., 1997) within western Europe. The grid used was based on the Atlas Florae Europaeae (Lahti and Lampinen, 1999), with cell boundaries typically following the 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. The mapped area for Europe (2289 grid cells) includes western, northern and southern Europe, but excludes most of the eastern European countries (except for the Baltic States) where lower recording effort was less uniform and intensive. In the case of the Iberian Peninsula (Iberia), the 251 grid cells located south of the Pyrenees were used. For details on data conversion see Williams et al. (2000).

2.2. Climate data

A set of aggregated climate parameters were derived from an updated version of the CRU (Climate Research Unit at the University of East Anglia, UK) monthly climate data (New et al., 2000). The updated dataset provides monthly values for the years 1901–2000 in 10×10 min spatial resolution (Mitchell et al., 2004; Mitchell and Jones, 2005) and were used to calculate mean values of five different climate parameters for the period of 1961–1991. Variables included mean annual temperature within time slices ($^{\circ}\text{C}$), mean temperature of the coldest month ($^{\circ}\text{C}$), mean temperature of the warmest month ($^{\circ}\text{C}$), mean annual summed precipitation (mm), and mean sum of precipitation between July and September (mm). We also calculated growing season, defined as the temperature sum of all consecutive days with mean temperature greater than 5°C .

Choice of variables was made to reflect primary qualities of the climate that, on the basis of prior knowledge, have known roles in imposing physiological constraints upon the distributions of amphibian and reptile species (Carey and Alexander, 2003; Araújo et al., 2006; Whittaker et al., 2007).

2.3. Formulation of continuous and discrete ED forms

In a recent description of the ED framework, Faith et al. (2004; see references therein), described ED as a specific framework for using (1) distance (i.e. dissimilarity) measures and ordinations of environmental and/or biotic descriptors as surrogates for species diversity, and (2) p -median location-allocation procedures to select areas that represent as much variability as possible. ‘ p -median’ models are based on a continuous description of the environment, and attempt to avoid the problems of arbitrarily classifying environments into discrete entities when they are in effect continuous gradients. Faith and Walker (1996, p. 420) claim that: “The solution to this problem is to use the environmental descriptions of the areas to describe a continuum of variation among areas (...) by deriving a continuous environmental space (...) rather than a clustering...”. More specifically, the aim of these location-allocation procedures is to select a set of p sites (here, grid cells) that minimize the total sum of the distances between m demand sites (places available for protection) and p selected sites. Both discrete and continuous p -median procedures require two steps: (1) construct the matrix of distances between the studied demand points, and (2) select p sites according to a distance minimization criterion.

2.4. Distance matrices

The variation between a pair of sites can be quantified using dissimilarity measures. Therefore, the variability within a region can be described using a single distance matrix which contains all pairwise distances between the demand points present in the region. It is in this step of the ED calculation that discrete and continuous versions diverge. In the discrete ED, the distance matrix is developed using the scores of the environmental variables observed in each one of the m original sites that constitute the set of demand points in the selection process. In the continuous ED, a new set of n regularly spaced demand points is created using all environmental variables (see Faith and Walker, 1994, 1996; Faith, 2003; Faith et al., 2004), and the distance matrix is developed using these ‘ideal’ n demand points that represent the m original sites. Each original site m_i is assigned to the ideal demand point n_j located nearest to it (see Fig. 1).

We used the original pairwise distance-matrix for all p -median calculations (Hortal and Lobo, 2005) to avoid losses of information associated with transforming original matrix distances into ordination ranks. For both western Europe and the Iberian Peninsula we developed two different distance matrices using squared Euclidean distances:

- (1) Discrete ED (dED): the discrete matrices contain the distances among all m original grid cells. Therefore, these distance matrices are directly calculated from the original data, using the scores of all seven environmental variables

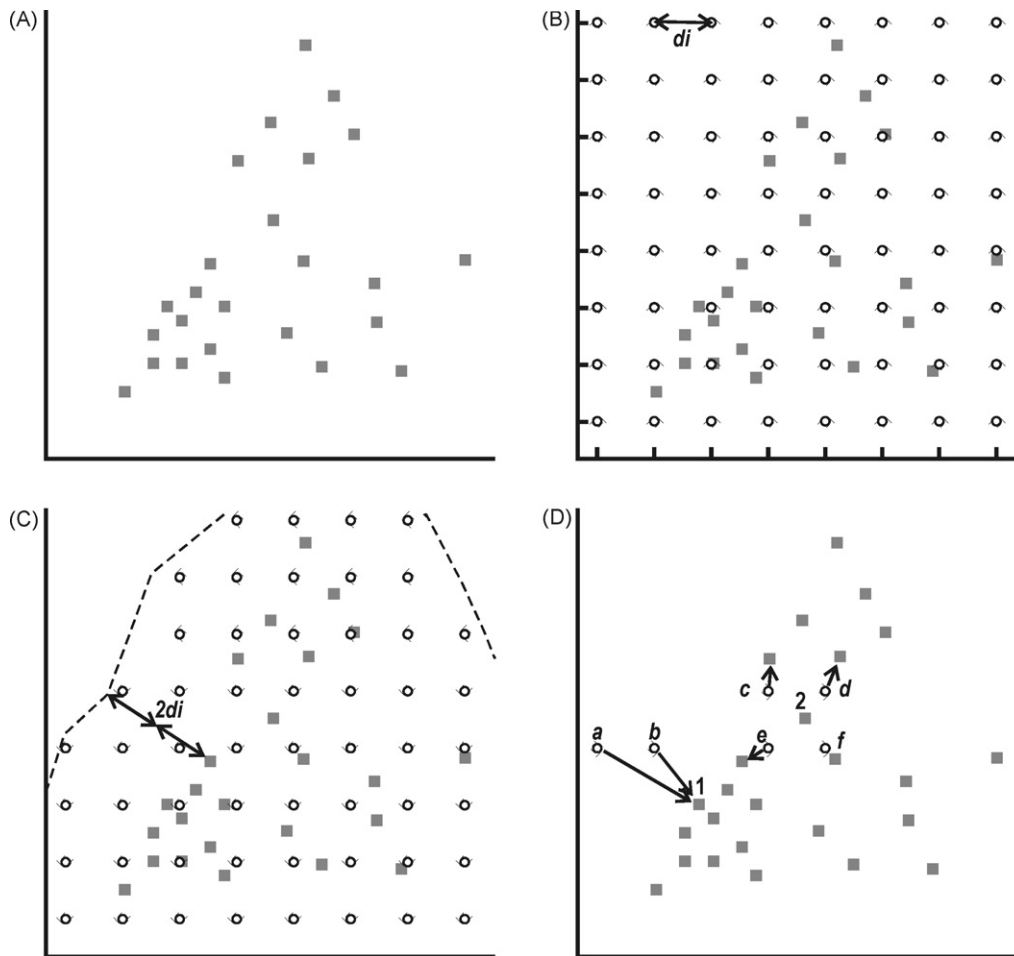


Fig. 1 – Allocation of points in a continuous ED formulation. (A) Two (or more) uncorrelated axes are obtained by means of an ordination technique (Grey squares are the ‘original sites’, which are the demand points in a discrete ED formulation). **(B)** Each one of these axes is divided into equal intervals (of distance d_i), and the points accounting for all the combinations of these intervals are located into the space defined by these axes (empty circles). **(C)** All the points outside the convex surface defined by the original sites are deleted. In our case, to avoid excluding the extremes of the environmental gradients (which could host assemblages different from the rest of the territory) we included also points placed near but outside the actual range of environmental conditions of the region (defined by the location of the original sites), when they were included in a buffer of two times d_i (discontinuous line). **(D)** The rest of the points (i.e. all empty circles remaining in C) are considered as ‘ideal’ demand points, and were assigned to the nearest ‘original site’ (i.e. once a demand point is selected, the nearest original site is included in the selection). Note that two different ideal demand points could be assigned to the same original site (e.g. points *a* and *b* in the figure are both assigned to site 1), and that several of the original sites could not be represented by demand points (e.g. the original site 2 has no assigned points, as *c*, *d*, *e* and *f* are located next to other four original sites).

at each grid cell m_i , and no prior ordination is needed to calculate them.

- (2) Continuous ED (cED): the continuous matrices contain the distances among a set of n ideal demand points, rather than among the original grid cells. These ideal demand points are placed regularly across the most important environmental gradients of the region, and the original m cells are assigned to them (see Fig. 1). Therefore, to create the ideal demand points it is first necessary to identify the main environmental gradients in the region. Here, this was achieved through an ordination that summarised seven environmental variables in the two axes that reduced

Table 1 – Results from the NMDS ordination analyses		
	Western Europe	Iberian Peninsula
Factor 1	50.71	78.47
Factor 2	19.25	14.83
Total	69.96	93.30

The factors obtained were used to develop the continuous ED formulations. Scores are reductions in stress for each factor, and total reduction in stress (in percentages).

‘stress’ in non-metric multidimensional scaling (NMDS) (see Table 1). Then, a number of n ideal demand points were located regularly across the space defined by these two axes (see method at Fig. 1). In order to obtain a comparable number of grid cells from those used to create the discrete matrices, we divided each axis in 50 intervals (in western Europe), and 16 intervals (in the Iberian Peninsula), generating 2500 and 256 demand points in step B of Fig. 1, respectively. After assigning each ideal demand point n_j to its nearest m_i grid cell (steps C and D of Fig. 1), $n = 1191$ and $n = 120$ grid cells were represented in the two distance matrices. It is thus assumed that the n ideal demand points associated to these grid cells summarize the variability in the grid cells not represented in the distance matrices.

We used squared instead of ‘simple’ Euclidean distances to maximize the distances between closely related sites, thereby avoiding an excessive aggregation of the sites. All matrix and ordination analyses were performed using Clustan Graphics package (Clustan Ltd., 2002).

2.5. Selection algorithm

p -Median models can be solved with optimal and heuristic (near-optimal) approaches. Optimal approaches are time consuming and require substantial computing power for dealing with large problems. Heuristic approaches can take at least two forms (see discussion in Araújo et al., 2001, 2003; Faith, 2003): (1) ‘greedy approaches’, which make a sequence of p location selections (i.e. they select p areas one by one in an iterative fashion); (2) more advanced system-wide search approaches, which produce a single suboptimal solution of a pre-determined number of p areas based on more complicated (and also time-consuming) heuristics that search within groups of areas instead of within areas one by one (see Mladenović et al., 2007 for a comprehensive review of these approaches). The differences between these two kinds of approaches result in different levels of optimality in the obtained selections. Although each of the consecutive selections in a greedy algorithm is optimal (given the distribution of the data and the selections already made), at each stage the algorithm only considers the remaining m (or n in the case of the continuous p -median) “vacant” demand points for the new selection; as a result, a sequence of optimal selections can result in a globally sub-optimal solution for the p areas. On the contrary, system-wide algorithms select these p areas from among the m vacant demand points as a group in a single step, resulting in a greater degree of optimality (see Araújo et al., 2003). Faith and Walker (1996) and Hortal and Lobo (2005) used greedy algorithms, while algorithms used by Densham and Rushton (1992), Church et al. (1996), and Araújo et al. (2001, 2004) pertain to the system-wide kind.

Given that results of greedy algorithms at each step are sensitive to the choices made in previous steps (Church and ReVelle, 1974), more complex algorithms would provide better results (see Church and Sorensen, 1996; Church et al., 1996; Araújo et al., 2003; Moreno Jiménez, 2004). Although one of these algorithms is available to us (Densham and Rushton, 1992), we decided to use a greedy algorithm to allow

comparison with the original ED implementation of the analytical framework proposed by Faith and Walker (1996). Therefore, we have selected areas using the greedy algorithm of Hortal and Lobo (2005) and repeated the selection a number of times to assess if different sub-optimal solutions would have resulted in markedly unstable solutions.

In each selection of p areas, the algorithm calculates, for each non-selected demand point m_i , the distance of all m non-selected demand points to the nearest selected one (S), if the point m_i is included in the group of selected items ($S + m_i$):

$$d_{m,s} = \min \text{dist}(m, S + m_i) \quad (1)$$

Then, the p -median score for each demand point m_i is calculated as the sum of all $d_{m,s}$:

$$p\text{-median}_i = \sum_{s=1}^m d_{m,s} \quad (2)$$

All the demand points with p -median scores included in the confidence interval defined by the minimum score plus the standard deviation are chosen:

$$\forall_i \in [(\min_{i=1}^m p\text{-median}_i), (\min_{i=1}^m p\text{-median}_i) + (\text{SD}_{i=1}^m p\text{-median}_i)] \quad (3)$$

Finally, when there are ties among the p areas selected in a given step (i.e. more than one demand point is chosen at any stage) one of these p areas is selected at random. In the case of the continuous ED, the n_j demand points assigned to the same m_i grid cell as the selected one (see Fig. 1) are also excluded from the selection procedure. This process is repeated iteratively after the inclusion of each new area p_i , up to the desired number of p areas. For a more detailed formulation and one example of the application of the algorithm see Appendix A.

2.6. Analyses

Because greedy algorithms (as any other heuristic algorithm) are bound to select different near-optimal solutions at each run, we performed 10 different runs for every matrix. A subset of grid cells (10 and 3 cells in the case of the western European and Iberian datasets, respectively) was selected at random to start each run. Therefore, in the results, we provide the mean and dispersion of the effectiveness of these 10 series of selections. We measured the effectiveness with which ED represents amphibian and reptile species at different levels of territorial coverage (from 11 to 250 grid cells [0.48–10.9%] in the case of western Europe, and 4 to 25 grid cells [1.59–9.96%] in the case of the Iberian Peninsula). We compared results with the mean and at the upper 5% level of the representation obtained with 1000 random selections (for details and discussion on the use randomization tests in conservation see Araújo et al., 2001, 2003, 2004; Faith, 2003; Faith et al., 2004).

To ascertain if the variability of the greedy selections could result in important differences in species representation between the solutions found, we examined their stability (i.e. the reduction in the standard deviation of the effectiveness of the selections as the number of grid cells selected

increases). It was assumed that p -median solutions would converge to a near-optimal solution after a number of iterations, and therefore the differences in their effectiveness would be reduced (i.e. the standard deviation will diminish and stabilize) (see also O’Dea et al., 2006).

3. Results

In all model runs, ED represented fewer species than expected by chance ($P < 0.05$). In western Europe the discrete and continuous ED selections performed so poorly that they represented fewer species than the mean level of species representation obtained with random simulations (Fig. 2). In the Iberian Peninsula, ED represented more species than the mean representation value obtained with random simulations, but the level of species representations was lower than expected by chance ($P < 0.05$, Fig. 2).

The effectiveness of discrete and continuous environmental ED was similar in both western Europe and Iberia. Nevertheless the continuous version of ED performed slightly better during the initial selections (Fig. 2): differences in species representation between these two ED approaches

were always smaller than 7% (median = 2.3% and 4.9% in western Europe and the Iberian Peninsula, respectively). When more than 4% of the studied areas were selected, the differences between the effectiveness of the two ED selections became irrelevant [median $< 0.3\%$ in western Europe (from 92 to 250 areas selected) and $< 1.2\%$ in the Iberian Peninsula (from 5 to 25 areas selected)]. All selections converged with relatively small territorial coverage (6% for the Iberian Peninsula and 5% for western Europe) (see Fig. 2).

4. Discussion

Our study supports the findings of previous studies that challenge the view that the ED framework always represents species at a rate higher than expected by chance. Whereas previous studies used the discrete version of ED, in this study we used both the discrete and the continuous implementations of ED. In doing so we address the criticism of Faith (2003) and Faith et al. (2004), that challenged previous tests on the grounds that discrete versions of ED had been used rather than the ‘preferred’ continuous version of ED. Our results show that the two versions of ED provide similar representation results,

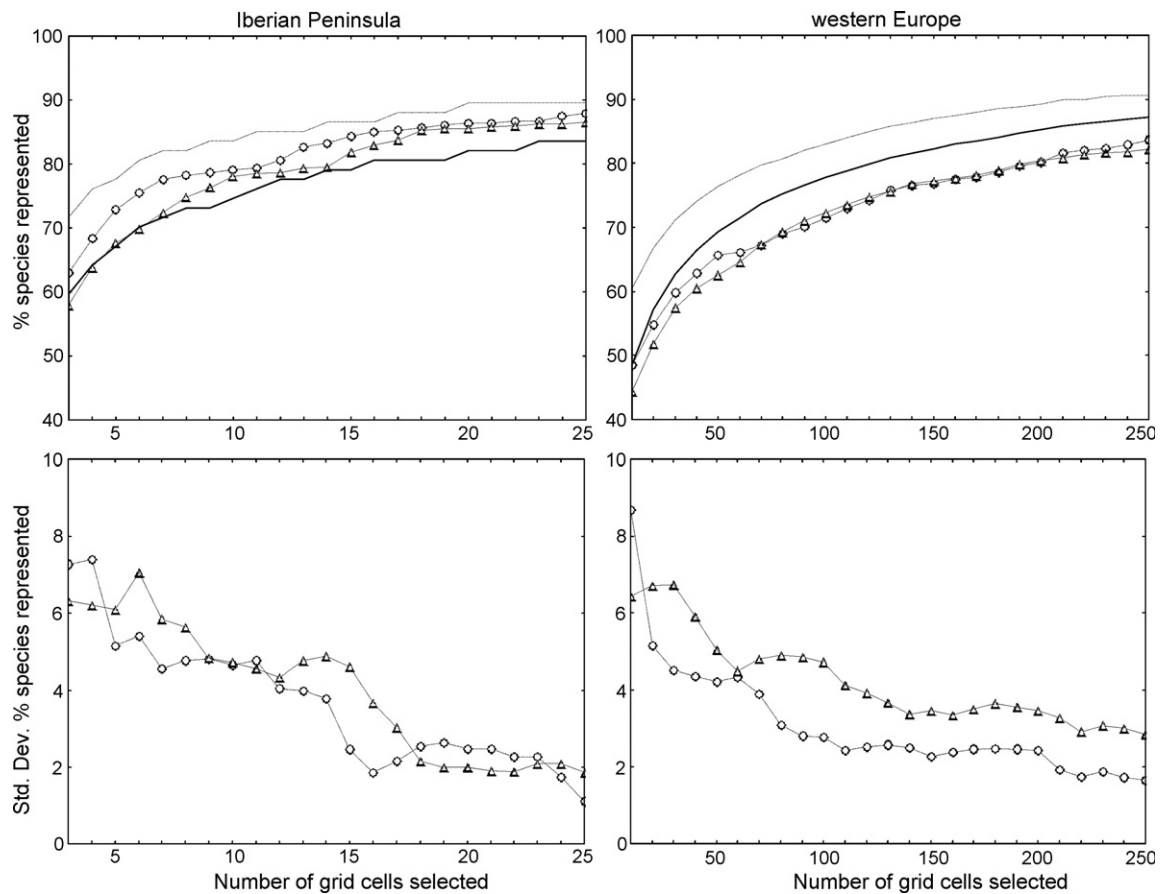


Fig. 2 – Results from the p -median selections. Upper graphs show the mean percentage of species represented in the 10 samples as the number of selected grid cells increases. The graphs below show the standard deviation of these ten samples. Continuous and discrete ED selections are shown as empty circles and dashed line and empty triangles and dotted line, respectively. The symbols in the western Europe graphs correspond to each tenth grid cell selected. The median and upper 5% tails of the species represented by 1000 random selections are shown as continuous line, and dots and lines, respectively.

i.e., similar numbers of species are represented when either method is used (Fig. 2). We hope these results will help move the field forward and lead to a more fruitful discussion of the circumstances that make ED more likely to succeed as a surrogacy strategy.

A first step for making progress is to deepen our understanding of the theoretical implications of ED and examine the consequences of using different implementations of the ED framework. In effect, the theoretical assumptions under the continuous and discrete forms of p -median correspond to two ways of representing continuous variables in a geographical space: field and object representations (see Cova and Goodchild, 2002). Briefly, *field representations* are spatially continuous representations of the studied phenomenon or variable, summarized either by a mathematical function, or by regularly allocated points, by equal-score lines (i.e. isopleths), or spatial tessellations (i.e. raster grids, or TIN polygons) that represent the scores of the variable in the geographical space. In contrast with *object representations* the scores of the studied variable are referred to as discrete objects defined in the geographical space (e.g. houses or land patches), defined as points, lines, polygons, or groups of grid cells in a raster environment. These two kinds of representations are conceptual perspectives rather than inherent qualities of geographical phenomena; therefore, any aspect of the geographical reality can be conceptualized and modelled using either one of the two approaches (Cova and Goodchild, 2002). The approach most suited to represent a given phenomenon depends on the purpose and context of the modelling exercise and might vary from case to case. The choice of the ED implementation might be contingent on the particular goals of the surrogacy strategy and the context in which it is developed; therefore, it might be difficult to establish *a priori* theoretical constraints for it.

The choice of the ED version implies slightly different assumptions about the response of the species to environmental gradients. The original theoretical formulation of ED (Faith and Walker, 1996; see also Faith et al., 2004) relies on two basic assumptions: firstly, that the breadth of environmental variation in a region matches the full breadth of species fundamental niches, which should be best described as a unimodal species response to the environment; secondly, that the centroids of the species distributions are randomly distributed in the environmental space. In the discrete p -median, the species responses are hypothetically represented by the environmental conditions available in the studied region. Faith et al. (2004) argued that, whilst continuous ED treats the environmental space as reflecting how turnover among species occurs, discrete ED disrupts such turnover by the geographic duplication of redundant p -median demand points. However, a logical implication of continuous ED assumptions is that the density of species would be homogeneously distributed along the gradient of environmental variation, regardless of the representation of these gradients in the geographic space (Araújo et al., 2003). This is in clear contradiction with the evidence that patterns of speciation and extinction are unevenly distributed in geographical space. Thus, Hortal and Lobo (2005) argued that such turnover would be better described using the actual conditions in the region

and the observed response of species assemblages to these conditions.

Beyond the discussion on the theoretical implications of the two ED frameworks, our results indicate that the spatial distributions of the species are measured with similar effectiveness by both implementations of ED. Providing that both continuous and discrete ED aim to describe the same phenomenon (geographic variations in species composition), it is expected that they might perform similarly. An implementation of ED will outperform the other if the assumptions underlying one of the two approaches provide a more adequate description of the species distribution patterns in the studied region. Interestingly, if some parts of the gradients are overrepresented due to the high similarity of some clumped real demand points (as argued by Faith et al., 2004), the effect on discrete p -median selections will be minimum; since solving the p -median problem involves summing distances of p areas to all unselected m demand points, such clusters of sites are virtually treated as being just one, and therefore once one site in the cluster is selected, the probability of selecting another one is highly diminished.

Significant differences between discrete and continuous ED appear only if there are important gaps in the coverage of the environmental gradients provided by the studied grid cells, such as in the first steps of the selection process. In our data, the redundancy in the demand points in the discrete p -median argued by Faith et al. (2004) has no effect on the coverage of the species turnover at least when more than a 4% of all the cells in the region have been selected (see Fig. 2). Below such area threshold, the continuous ED provided better species representation, although the difference between implementations of ED is typically less than 5%. Indeed, optimal complementary solutions are often clustered in the geographical space (e.g. Araújo et al., 2001; Cabeza, 2003; Cabeza et al., 2004), so the overdispersion of the sites produced by the continuous ED may not always be a desirable property of a framework for selection of conservation areas (as argued by Faith et al., 2004). Indeed, in our results the differences between the two forms, if any, are so small that there is no significant advantage in using either one form of ED or the other.

The non-environmental effects not considered by the ED framework are likely to affect both the continuous and discrete ED. The response of the species to environmental gradients is not only shaped by their basic requirements (i.e. their potential distributions), but also by other factors that modify these responses (see discussion in Lobo et al., 2006 and Araújo and Guisan, 2006). These factors include (1) the geographic extent (Whittaker et al., 2001; Willis and Whittaker, 2002) and geomorphologic configuration (Jetz and Rahbek, 2001) of the considered region and (2) past environmental conditions and other historical factors (Lobo et al., 2001; Hawkins et al., 2005; Svenning and Skov, 2005; Araújo et al., 2008). It follows that the performance of ED should be contingent on the size of environmental gradients measured (Araújo et al., 2004) and the importance of the historical factors governing current distributions of species (Araújo et al., 2001). Thus, the geographical extent in which ED is calculated should affect its effectiveness in sampling

species distributions. For example, if the distributions of species are more effectively explained by environmental surrogates in small areas, then a surrogate strategy that uses information of environmental variation at broader geographical extents will most likely fail to represent species diversity. Indeed, in small regional extents the importance of non-environmental factors is likely to be more important, and the distribution of the species is expected to be at a greater measurable degree of equilibrium with the current environmental gradients. When measuring species diversity at broader regional extents, the effects of environmental factors are likely to increase in importance, which could potentially increase the ability of ED to recover species diversity. However, our study does not provide a strong support for an effect of extent on ED effectiveness. Although the ED strategy was more effective at the smaller extent of the Iberian Peninsula, its performance was still worse than the expected by chance (Fig. 2). Indeed, the recent post-glacial colonization of Europe has not produced the gradual environmental response of amphibians and reptiles predicted by the ED model as formulated by Faith and Walker (1996) (Araújo and Pearson, 2005; Araújo et al., 2008). On the contrary, a more complex colonization pattern occurred, especially in the Mediterranean basin, where ED was less capable of representing amphibian and reptile diversity in the former Araújo et al. (2001) analysis (see also Araújo et al., 2003; Araújo and Pearson, 2005). As a result, ED selections perform worse than mean random selections in all the studied cases.

Surrogates are used when no complete data on the studied phenomenon are available. It follows that it is not possible to know their effectiveness *a priori*, since they are used in the absence of data. This implies that the choice of surrogates should be based on partial evaluations, such as the one presented here. An important condition for a surrogate is its generality, i.e., its ability to represent target features every time it is applied to. Therefore, any negative result of ED should be taken as conditional evidence of its lack of generality, and thus of its limited usefulness. Had we used other areas and other biological groups for this analysis, perhaps the results might have been different. For example, Araújo et al. (2001) found that discrete ED performed reasonably well for European plants, which are known to be in greater degree of equilibrium with the current environmental conditions than reptiles and amphibians. However, the low effectiveness of ED in this and other studies hampers its usefulness as a surrogacy strategy for overall biodiversity.

5. Concluding remarks

Biodiversity surrogates should be judged according to their ability to represent biodiversity targets. In this study, both the continuous and discrete implementations of ED were used to predict diversity among amphibian and reptile species. In both cases we found that ED would represent fewer species than expected by chance ($P < 0.05$). Similar results were found by Ferrier and Watson (1997) and Araújo et al. (2001, 2004), using slightly different implementations of the discrete ED

model. In theory, poor performance of ED could arise because of: (i) the shortfalls in the data used for evaluation (including false negatives, i.e., species present but unrecorded in some grid cells); (ii) the inability of ED to represent important drivers of the distribution of species diversity; and/or (iii) the failure of particular implementations of ED to sample adequately the environmental space. Whatever the source of the problems, evidence in support of ED as a general strategy for conservation planning remains limited. It is also unlikely that simpler environmental surrogacy strategies based on classifications (e.g. Trakhtenbrot and Kadmon, 2005; Sarkar et al., 2005; Bonn and Gaston, 2005; Heino and Mykra, 2006) would have general applicability since they are also prone to the same limitations of ED, namely the difficulty in accounting for important non-environmental factors affecting species distributions (e.g. human induced factors or historical effects).

Nonetheless, the ED framework could be still useful, for example, for stratifying samples in field surveys (see Hortal and Lobo, 2005; Funk et al., 2005; Rocchini et al., 2005) and as surrogates of forgone biodiversity values into trade-offs analyses of relatively small areas (e.g. continuous land patches or protected areas) (see Faith et al., 1996, 2003; Faith and Walker, 2002). However, formal evaluation of the performance of ED would also be required to assess its potential effectiveness in both tasks.

Acknowledgements

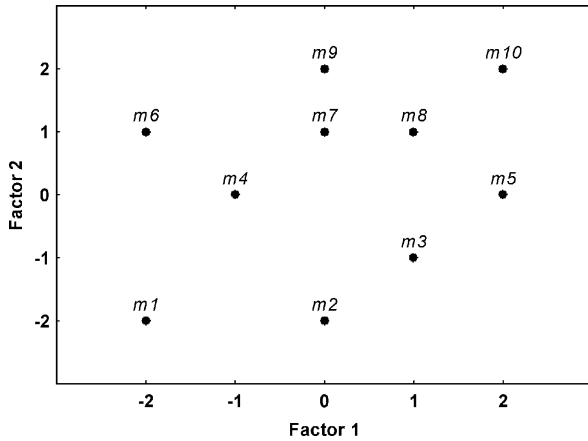
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Appendix A

Example of the application of the *p*-median greedy selection algorithm used by Hortal and Lobo (2005) and in this paper to some simple example data for the selection of three sites (*p*) from a hypothetical set of 10 sites (demand points, m_d or m_i), according to their environmental characteristics, described by two environmental factors (F1 and F2).

Sites	F1	F2
m_1	-2	-2
m_2	0	-2
m_3	1	-1
m_4	-1	0
m_5	2	0
m_6	-2	1
m_7	0	1
m_8	1	1
m_9	0	2
m_{10}	2	2

Location of the 10 original demand points in the environmental space defined by the two environmental factors.



Step 0: Create the distance matrix.

We calculate the triangular matrix of distances among sites. In this case, we use the squared Euclidean distance $D_{k,l} = (F1_k - F1_l)^2 + (F2_k - F2_l)^2$ to calculate the triangular matrix of distances.

	m_1	m_2	m_3	m_4	m_5	m_6	m_7	m_8	m_9	m_{10}
m_1	0									
m_2	4	0								
m_3	10	2	0							
m_4	5	5	5	0						
m_5	20	8	2	9	0					
m_6	9	13	13	2	17	0				
m_7	13	9	5	2	5	4	0			
m_8	18	10	4	5	2	9	1	0		
m_9	20	16	10	5	8	5	1	2	0	
m_{10}	32	20	10	13	4	17	5	2	4	0

And then we convert it into a square matrix.

	m_1	m_2	m_3	m_4	m_5	m_6	m_7	m_8	m_9	m_{10}
m_1	0	4	10	5	20	9	13	18	20	32
m_2	4	0	2	5	8	13	9	10	16	20
m_3	10	2	0	5	2	13	5	4	10	10
m_4	5	5	5	0	9	2	2	5	5	13
m_5	20	8	2	9	0	17	5	2	8	4
m_6	9	13	13	2	17	0	4	9	5	17
m_7	13	9	5	2	5	4	0	1	1	5
m_8	18	10	4	5	2	9	1	0	2	2
m_9	20	16	10	5	8	5	1	2	0	4
m_{10}	32	20	10	13	4	17	5	2	4	0

A.1. Stage 1: first selection

Step 1: Calculate the p -median scores for each candidate area m_i . To do this, we calculate the distance of each unselected demand point to the set of formerly chosen sites (S), and then we create a matrix of the $d_{m,s}$ distances that all m_d unselected demand points would have to the set of selected sites if each candidate demand point m_i is included in the set of selected areas ($S + m_i$).

- Step 1a: Calculate the distances $d_{d,s}$ to the previously selected sites.

For each unselected demand point m_d the distances to all S_s sites included in the selected set are calculated, and the minimum of these distances is selected, since this is the distance to the nearest site S_s in the selected set.

$$\text{For all } m_d : d_{d,s} = \text{MIN}(\text{dist}(m_d, S_1), \dots, \text{dist}(m_d, S_s))$$

Obviously, if there are no selected sites in the first selection this step is not necessary.

- Step 1b: Calculate the matrix of distances $d_{m,s}$ between the unselected sites and the hypothetical sets of selected sites that will appear if each of the candidate sites would be incorporated to the selected set.

The distance of each unselected demand point m_d when the candidate demand point m_i is included in the selected set of areas is calculated as the minimum of $d_{d,s}$ and the distance between m_d and m_i , assuming that the distance $d_{m,s}$ between the site m_d and the new set of sites ($S + m_i$) is different from $d_{d,s}$ only when the site m_i is placed nearer to m_d than any of the S_s previously selected sites.

For each cell d, i in the matrix : $d_{m,s}$
 $= \text{MIN}[d_{d,s}, \text{dist}(m_d, m_i)]$

In the first step, the matrix of $d_{m,s}$ is equal to the original matrix of distances.

- Step 1c: Calculate the p -median score for each candidate demand point.

The p -median score for each candidate point m_i is simply the sum of all its $d_{m,s}$ distances to the rest of unselected points m_d .

For each demand point m_i (column I in the matrix)

$$: p - \text{median}_i = \text{SUM}(\text{cell}_{1,i} : \text{cell}_{d,i})$$

For example, for the demand point m_1 , $p\text{-median}_1 = 4 + 10 + 5 + 20 + 9 + 13 + 18 + 20 + 32 = 131$.

	p -Median
m_1	131
m_2	87
m_3	61
m_4	51
m_5	75
m_6	89
m_7	45
m_8	53
m_9	71
m_{10}	107

Step 2: Select one site from the p -median scores.

Once the $p\text{-median}_i$ scores for all m_i candidate sites are calculated, the criteria for selecting a site is to minimize such sum of distances. To do this, one site is randomly chosen from all the sites included in the confidence interval

defined by the minimum p -median score and their standard deviation.

For all p -median_{*i*}, select those included in the interval [MIN p -median_{*i*}, (MIN p -median_{*i*}) + (SD MIN p -median_{*i*})].

In this case, the minimum p -median score is 45 (site m_7), and the standard deviation of all p -median scores is 27.1. Therefore, the five sites with p -median scores between 45 and 72.1 are selected (m_3, m_4, m_7, m_8 and m_9).

From these cells, select one at random.

In this case, m_8 is selected during a random selection (note that the size of the interval can be reduced for highly dispersed data, or even be reduced to include only the candidate sites with the minimum p -median score. However, given the sub-optimality of the greedy algorithms and the possible uncertainty in the original environmental data, including a confidence interval is always desirable).

A.2. Stage 2: second selection

Once a given candidate site has been selected (in this case, m_8) the algorithm goes back to the step 1.

- Step 1a: In this case, these are the distances from all remaining m_d cells to m_8 .

	$d_{d,s}$
m_1	18
m_2	10
m_3	4
m_4	5
m_5	2
m_6	9
m_7	1
m_8	n.a.
m_9	2
m_{10}	2

n.a.: not applicable.

- Step 1b: Here, the matrix of distances is re-calculated taking into account the distance to the previously selected site m_8 .

	m_1	m_2	m_3	m_4	m_5	m_6	m_7	m_8	m_9	m_{10}
m_1	0	4	10	5	18	9	13	n.a.	18	18
m_2	4	0	2	5	8	10	9	n.a.	10	10
m_3	4	2	0	4	2	4	4	n.a.	4	4
m_4	5	5	5	0	5	2	2	n.a.	5	5
m_5	2	2	2	2	0	2	2	n.a.	2	2
m_6	9	9	9	2	9	0	4	n.a.	5	9
m_7	1	1	1	1	1	1	0	n.a.	1	1
m_8	0	0	0	0	0	0	0	n.a.	0	0
m_9	2	2	2	2	2	2	1	n.a.	0	2
m_{10}	2	2	2	2	2	2	2	n.a.	2	0

n.a.: not applicable.

- Step 1c: The p -median scores for all m_i candidate points are calculated (in this case all but the previously selected m_8).

	p -Median
m_1	29
m_2	27
m_3	33
m_4	23
m_5	47
m_6	32
m_7	37
m_8	n.a.
m_9	47
m_{10}	51

n.a.: not applicable.

- Step 2: Now, the minimum p -median score is 23 (site m_4), and the standard deviation of all p -median scores is 9.9, so the four sites with p -median scores between 23 and 32.9 are pre-selected (m_1, m_2, m_4 and m_6). From these, m_4 is randomly chosen.

A.3. Stage 3: third selection

- Step 1a: in this case, these are the minimum of the distances from all remaining m_d cells to either m_4 or m_8 .

	$d_{d,s}$
m_1	5
m_2	5
m_3	4
m_4	n.a.
m_5	2
m_6	2
m_7	1
m_8	n.a.
m_9	2
m_{10}	2

n.a.: not applicable.

- Step 1b:

	m_1	m_2	m_3	m_4	m_5	m_6	m_7	m_8	m_9	m_{10}
m_1	0	4	5	n.a.	5	5	5	n.a.	5	5
m_2	4	0	2	n.a.	5	5	5	n.a.	5	5
m_3	4	2	0	n.a.	2	4	4	n.a.	4	4
m_4	0	0	0	n.a.	0	0	0	n.a.	0	0
m_5	2	2	2	n.a.	0	2	2	n.a.	2	2
m_6	2	2	2	n.a.	2	0	2	n.a.	2	2
m_7	1	1	1	n.a.	1	1	0	n.a.	1	1
m_8	0	0	0	n.a.	0	0	0	n.a.	0	0
m_9	2	2	2	n.a.	2	2	1	n.a.	0	2
m_{10}	2	2	2	n.a.	2	2	2	n.a.	2	0

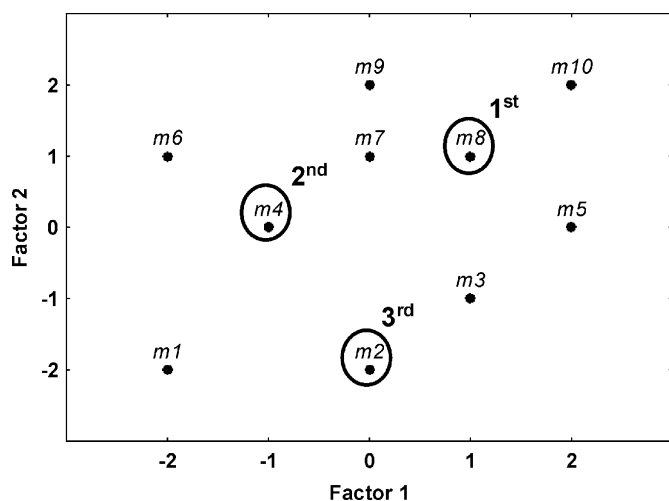
n.a.: not applicable.

• Step 1c:

	p-Median
m_1	17
m_2	15
m_3	16
m_4	n.a.
m_5	19
m_6	21
m_7	21
m_8	n.a.
m_9	21
m_{10}	21

n.a.: not applicable.

Step 2: The minimum p -median score is 15 (site m_2), and the standard deviation is 2.5; three sites lay within 15 and 17.5 (m_1 , m_2 and m_3). From these, m_2 is randomly chosen.



The algorithm continues until all required selections have been made.

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