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Environmental diversity as a surrogate for species representation

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Abstract: *Because many species have not been described and most species ranges have not been mapped, conservation planners often use surrogates for conservation planning, but evidence for surrogate effectiveness is weak. Surrogates are well-mapped features such as soil types, landforms, occurrences of an easily observed taxon (discrete surrogates), and well-mapped environmental conditions (continuous surrogate). In the context of reserve selection, the idea is that a set of sites selected to span diversity in the surrogate will efficiently represent most species. Environmental diversity (ED) is a rarely used surrogate that selects sites to efficiently span multivariate ordination space. Because it selects across continuous environmental space, ED should perform better than discrete surrogates (which necessarily ignore within-bin and between-bin heterogeneity). Despite this theoretical advantage, ED appears to have performed poorly in previous tests of its ability to identify 50 × 50 km cells that represented vertebrates in Western Europe. Using an improved implementation of ED, we retested ED on Western European birds, mammals, reptiles, amphibians, and combined terrestrial vertebrates. We also tested ED on data sets for plants of Zimbabwe, birds of Spain, and birds of Arizona (United States). Sites selected using ED represented European mammals no better than randomly selected cells, but they represented species in the other 7 data sets with 20% to 84% effectiveness. This far exceeds the performance in previous tests of ED, and exceeds the performance of most discrete surrogates. We believe ED performed poorly in previous tests because those tests considered only a few candidate explanatory variables and used suboptimal forms of ED's selection algorithm. We suggest future work on ED focus on analyses at finer grain sizes more relevant to conservation decisions, explore the effect of selecting the explanatory variables most associated with species turnover, and investigate whether nonclimate abiotic variables can provide useful surrogates in an ED framework.*

Keywords: complementarity, conservation planning, environmental diversity, *minisum*, species accumulation index, surrogates

La Diversidad Ambiental como Sustituto para la Representación de Especies

Resumen: *Ya que muchas especies no han sido descritas y la mayoría de las extensiones de las especies conocidas no se han mapeado, los planeadores de la conservación usan frecuentemente sustitutos para la planeación de la conservación, pero la evidencia para la efectividad de los sustitutos es débil. Los sustitutos son características bien mapeadas como los tipos de suelo, las formaciones geológicas, las presencias de un taxón fácil de observar (sustitutos discretos), y las condiciones ambientales bien mapeadas (sustituto continuo). En el contexto de la selección de una reserva, la idea es que un conjunto de sitios, seleccionados para abarcar a la diversidad en el sustituto, represente eficientemente a la mayoría de las especies. La diversidad ambiental (DA) es un sustituto casi nunca usado, que selecciona sitios para abarcar efectivamente al espacio de ordenación multi-variado. Ya que selecciona a lo largo de un espacio ambiental continuo, la DA debería tener un mejor desempeño que los sustitutos discretos (los cuales ignoran inevitablemente la heterogeneidad entre-contenedores y dentro-de-contenedores). A pesar de esta ventaja teórica, la DA parece haber tenido un desempeño pobre en pruebas previas de su habilidad para identificar celdas de 50 × 50 Km, las cuales representaban a los vertebrados en el oeste de Europa. Al usar una implementación mejorada de la DA, la re-evaluamos en aves, mamíferos, reptiles anfibios y vertebrados terrestres combinados del oeste de Europa. También evaluamos a la DA en conjuntos de datos de plantas de Zimbabue, aves de España y aves de Arizona*

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(E.U.A.). Los sitios seleccionados al usar a la DA representaron a los mamíferos europeos no mejor que celdas elegidas al azar, pero representaron a las especies en los otros siete conjuntos de datos con el 20% y hasta el 84% de efectividad. Esto excedió por mucho el desempeño de la DA en pruebas anteriores, y excede también el desempeño de la mayoría de los sustitutos discretos. Creemos que la DA tuvo un desempeño pobre en las evaluaciones previas porque estas sólo consideraron a unas cuantas variables explicativas de candidatos y usaron formas sub-óptimas del algoritmo de selección de la DA. Sugerimos que el trabajo futuro sobre la DA se enfoque en análisis más finos con mayor relevancia para las decisiones de conservación, explore el efecto de seleccionar a las variables explicativas que más se asocian con el total de especies, y que investigue si las variables abióticas no-climáticas pueden proporcionar sustitutos útiles en un marco de trabajo de la DA o no.

Palabras Clave: complementareidad, diversidad ambiental, índice de acumulación de especies, *minisum*, planeación de la conservación, sustitutos

Introduction

Because many species have not been described and most species ranges have not been mapped, conservation planners have long used surrogates to select sites that will protect biodiversity. Surrogates are features that are well-mapped in the planning region, such as soil types, landforms, climate conditions, or occurrences of an easily observed taxon. The idea is that a set of p sites selected to span diversity in the surrogate will efficiently represent diversity of the species whose true distributions are not known.

Surrogates are usually conceptualized as a set of distinct types or bins (e.g., discrete physical settings such as land facets [Beier & Brost 2010] or individual species of a well-mapped indicator taxon), and the planner selects p sites in a way that represents each surrogate at a desired level (e.g., n occurrences of each land facet or indicator species). This type of surrogate has 3 limitations (Faith & Walker 1996*a*), first it ignores within-bin heterogeneity; selection of sites within a bin is left to chance. Second, it ignores between-bin heterogeneity. For example, assume that 5 discrete surrogates are not yet represented in a reserve network and that 4 of these occupy the same small region of environmental space (and relatively likely to share species) and the fifth is environmentally unique (and more likely to harbor unique species). Under selection for discrete surrogates, a site from one of the closely related bins is 4 times more likely to be selected than a site from the unique bin. Third, once enough sites are selected to represent the surrogates, the model provides no information on which additional sites could be selected to increase representation of target species.

We focused on a different type of surrogate that avoids these 3 problems. In this environmental diversity (ED) model, the surrogate is conceived as continuous (unbinned) environmental space quantified as an ordination (Faith & Walker 1996*a*, 1996*b*; Faith et al. 2004). Given a budget sufficient to conserve p sites, the selection algorithm (a particular form of minisum algorithm [see Methods]) selects sites to span the ordination space. Key assumptions of the model are that each species has a unimodal, symmetric distribution and that centroids of distributions could be anywhere in environmental space. If these assumptions are true, Faith and Walker (1996*a*) argue that sites selected to span environmental space will efficiently represent target species. This critical assumption could be false if species distributions were driven less by environmental conditions than by other factors, such as habitat degradation and loss due to human activities, species-specific dispersal limitations (e.g., after retreat of continental glaciers or formation of a land bridge between land masses), stochastic colonization events, interspecific interactions, or frequent disturbance. Despite violations of this critical assumption, if enough species have environmental niches that are approximately unimodal and symmetric and well distributed across environmental space, ED could be a useful surrogate for species.

ED appeared to perform poorly in the 3 studies that attempted to evaluate it. Ferrier and Watson (1997) used a minisum (minimum sum) selection algorithm to select sites that spanned environmental ordination space in northeastern New South Wales, Australia. For each of 10 high-level groups (e.g., trees, understory plants, insects, birds), those sites represented about as many species as randomly selected sites. Araújo et al. (2001) and Hortal et al. (2009) reported that 50 $\times$ 50 km cells selected to represent environmental variation (which they considered an implementation of ED) represented Western European amphibians, reptiles, birds, and mammals no better than randomly selected cells. Thus, although the ED approach is theoretically attractive, these studies did not support its reliability as a surrogate for identifying sites that would represent species. However, Faith (2013, 2011) argues that these 3 studies should have used a different p-median (i.e., minisum) algorithm (see Methods) and that Araújo et al. (2001) and Hortal et al. (2009) considered only a few potential explanatory variables (6 and 7 variables, respectively). Perhaps if these issues were remedied, ED would identify sites that efficiently represent species.

Our goal was to determine whether ED would identify sites that efficiently represent species when a large

Table 1. Eight data sets used to evaluate the environmental diversity approach.

Taxon and geographic area	*Extent of study area (km²)*	*No. of sites*	*Size of grid cell (km²)*	*No. of species*	*Type of data set*[a]
Birds, Arizona, United States[b]	295,234	1317	6	359	Inventory
Birds, Spain[c]	505,992	5301	100	294	Atlas
Plants, Zimbabwe[d]	390,757	360	625	1315	Atlas
Vertebrates, Western Europe	$\sim 3 \times 10^6$	2195[b]	2500	698	Atlas
Amphibians, Western Europe[e]	$\sim 3 \times 10^6$	2195	2500	49	Atlas
Reptiles, Western Europe[e]	$\sim 3 \times 10^6$	2195	2500	83	Atlas
Birds, Western Europe[f]	$\sim 3 \times 10^6$	2195	2500	424	Atlas
Mammals, Western Europe[g]	$\sim 3 \times 10^6$	2195	2500	142	Atlas

[a]*In atlas data sets, each site was a grid cell, survey efforts did not cover the entirety of every grid cell, and the sites collectively comprised the entire geographic area of interest. In the inventory data set, the sites were a systematic subsample of the geographic area of interest.*
[b]*Data from Corman and Wise-Gervais (2005).*
[c]*Data from INB (2007).*
[d]*Data from South African National Biodiversity Institute, PRECIS available from http://www.gbif.org/dataset/1881d048-04f9-4bc2-b7c8-931d1659a354 (accessed March 2014).*
[e]*Data from Gasc et al. (1997).*
[f]*Data from Hagemeijer and Blair (1997).*
[g]*Data from Mitchell-Jones et al. (1999).*
[b]*The 2 previous tests of ED in western Europe used the same 50-km grid cells and data sources (footnotes e, f, g) that we used. However, Araújo et al. (2001) used 2089 grid cells and Hortal et al. (2009) used 2289 grid cells. Thus, we evaluated data sets similar but not identical to the previous studies.*

number of candidate variables were considered and the ED approach was implemented in the manner suggested by Faith (2003, 2011). We evaluated ED with data for the same taxa, 50-km cell size, and general study area (Western Europe) evaluated by Araújo et al. (2001) and Hortal et al. (2009). We also used 3 additional data sets to evaluate ED (Table 1). For each data set, we considered a suite of 37 candidate environmental variables and applied the minisum selection algorithm described by Faith (2003, 2011). If ED failed our tests, the result would challenge ED's critical assumption (species have unimodal, symmetric distributions in environmental space). If ED performed well in our tests, the result would justify further work to improve the ED approach so that it can be used to prioritize sites for conservation. Our experiments are intended as theoretical tests of the effectiveness of ED as a surrogate; the sites selected in our analyses are not intended to represent conservation priorities.

Methods

We evaluated ED for 8 data sets (Table 1) covering a variety of cell sizes, taxa, and geographic regions. The work flow is illustrated in Fig. 1.

Environmental Data

We obtained values of 37 environmental variables (Supporting Information) that are widely available for all regions of the world. We obtained temperature variables from Hijmans et al. (2005), potential evapotranspiration and precipitation variables from Zomer et al. (2008), sunshine variables from Neteler (2005), land-cover diversity from GlobCover (2009), normalized difference vegetation index and net primary productivity from Tucker et al. (2004), and elevation and slope from U.S. Geological Survey (Global 30 Arc-Second Elevation [GTOPO30] https://lta.cr.usgs.gov/GTOPO30). We calculated topographic diversity (Benito et al. 2013) from elevation data. We calculated the mean or range of each environmental variable across each grid cell. We selected these variables because they were available for all study areas, each has been shown to be associated with species richness patterns at large spatial extents (Stein et al. 2014 and references therein), and each is plausibly related to species turnover across environmental space.

Identifying Environmental Gradients

For each data set, we used principal components analysis (PCA) to identify major environmental gradients and identify a set of environmental variables with low multicollinearity. Each PCA factor with an eigenvalue greater than 1 was considered significant. There were 5 significant PCA factors for the Zimbabwe study area, 7 for the Arizona study area, and 6 for Western Europe and Spain.

We then identified the single environmental variable that was most highly correlated with each significant factor. Because PCA factors are by definition orthogonal to each other, these environmental variables tend to have relatively low multicollinearity. Table 2 lists the environmental variables most highly correlated with each factor. The most important variable across study areas, seasonality of precipitation, was highly correlated with the first PCA factor in 1 study area, with the second PCA factor in 2 study areas, and with the fourth PCA factor in the other study area (Table 2).

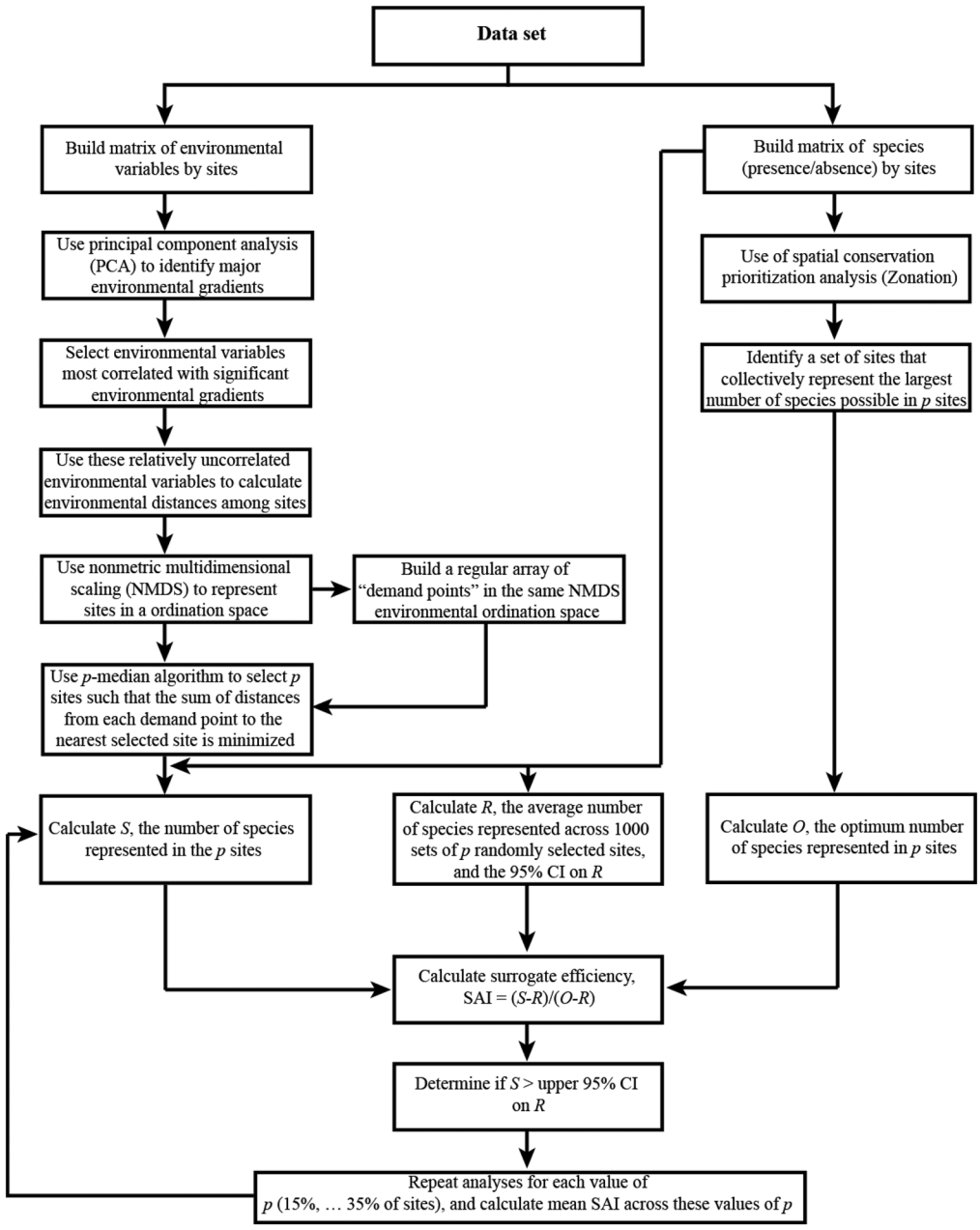

Figure 1. Steps in evaluating environmental diversity (ED) as a surrogate.

Defining Environmental Space

To apply our algorithm for selecting environmentally diverse sites (see "Selecting Environmentally Diverse Sites"), we needed to depict those sites in an environmental space with 2 dimensions, rather than in a space in which the number of dimensions equals the number of environmental variables. To define such a space, we first calculated environmental Euclidean distances among sites in the 5-, 6-, or 7-dimensional space defined by the relatively uncorrelated environmental variables identified in the previous step. Then, we used nonmetric multidimensional scaling (NMDS) (Minchin 1987) to create a 2-dimensional ordination space where inter-site distance reflects those Euclidean distances.

NMDS is an ordination technique that summarizes a multivariate distance matrix (with number of dimensions equal to the number of environmental variables) in 2 dimensions. The NMDS algorithm uses trial and error to place each grid cell in ordination space such that the rank order of distances between cells in ordination space matches the rank order of true distances (i.e., distances calculated using the important environmental variables identified in our PCA analysis). Ordinations were performed using R package vegan (Oksanen et al. 2013; R Core Team 2013). The stress values (badness of fit

Table 2. Variables with highest loading on each significant principal components analysis (PCA) factor for each of 4 geographic areas in which environmental diversity was evaluated.*

Variable	*Europe*	*Zimbabwe*	*Spain*	*Arizona*
Precipitation seasonality (coefficient of variation)	4	2	1	2
Mean temperature of coldest quarter		1		1
Precipitation of wettest quarter	1			
Hours of sunshine, interquartile range	2			
Precipitation of coldest quarter			2	
NDVI, average	3		4	4
Temperature seasonality		3		
Hours of sunshine, maximum			3	
Mean diurnal temperature range				3
NDVI, third quarter		4		
Elevation	5		6	
Slope		5		
NDVI, interquartile range			5	
NDVI, minimum				5
Mean temperature of wettest quarter	6			
Hours of sunshine, average				6
Hours of sunshine, range				7

** Number in each cell is the rank order of the eigenvalue of the PCA factor with which the variable is correlated. These variables were used to create 2-dimensional nonmetric multidimensional scaling ordinations of environmental space.*
NDVI, normalized difference vegetation index.

values) were 0.1696 for Europe, 0.1539 for Zimbabwe, 0.0260 for Spain, and 0.1565 for Arizona. Stress values <0.20 are generally considered reliable (Clarke 1993).

Selecting Environmentally Diverse Sites

With ED, a minisum algorithm (called *p*-median by Faith and Walker [1996*a*, 1996*b*]) is used to select environmentally diverse sites. Several types of minisum algorithms have been developed to solve problems related to distribution of services, such as efficient use of traveling salespersons or placement of utilities. For example, the algorithm can be used to select sites to install fire hydrants (facilities) by identifying the set of locations that minimizes the distance from each building (demand point) to the nearest hydrant. In the context of ED, the facilities are physical sites (grid cells) that could be selected for conservation. The facilities (sites) and the demand points are depicted not in geographic space, but in environmental niche space as quantified by the NMDS ordination (see Hortal et al.'s [2009] Fig. 1). The demand points are hypothetical locations in the same NMDS space that could be part of the environmental niche space of species. The minisum algorithm selects p sites that minimize the sum of distances (in environmental space) from each demand point to the nearest selected site. The p sites are selected not to represent discrete bins (conventional surrogates); rather, they are selected to span the underlying environmental space as quantified in the ordination.

Faith and Walker (1996*a*) argue that when demand points are a regular array of points on a grid in ordination space (a continuous arrangement of demand points) and each species has a unimodal, symmetric niche in ordination space, the minisum procedure will maximize the number of species represented in a given number of selected sites. In contrast to this continuous arrangement of demand points in environmental space, some implementations of minisum array physical sites (e.g., all of the 50-km cells in Western Europe) in environmental space and use these as discrete demand points. We used continuous demand points because Faith (2003) illustrate that algorithms with discrete demand points can select sites that do not increase environmental or species diversity. Ferrier and Watson (1997) and Araújo et al. (2001) used discrete minisum algorithms. Although Hortal et al. (2009) did create a continuous grid of demand points, instead of using the algorithm to select sites, they first selected demand points (and then selected the site closest to each selected demand point). This procedure is not equivalent to selecting sites than minimize the sum of environmental distances from each demand point to the nearest selected site (Faith 2011).

We divided each NMDS axis into equal intervals to create a 50×50 grid in 2-dimensional NMDS ordination space. We used the 2500 intersections of grid lines as demand points. (See Supporting Information for an explanation of why we used 2500 demand points.) We used the hybrid heuristic procedure in POPSTAR (Resende & Werneck 2003) with 32 random starts and hybridization among the top 10 solutions to identify a solution that best spanned environmental space. In previous tests with pathological data sets (data sets created with the sole purpose of being hard to solve), POPSTAR obtained solutions better than or within 0.1% of the best known solution (Resende & Werneck 2003). A POPSTAR run consisted of 32 random starts and hybridization at a particular value of p. We conducted 5 runs per data set, varying p to select 15%, 20%, 25%, 30%, and 35% of the total number

Table 3. Performance (species accumulation index[a]) of environmental diversity (ED) as a surrogate to prioritize sites to represent species for each of 8 data sets.

	Data set							
Percentage of sites prioritized	*Europe, reptiles*	*Europe, amphibians*	*Zimbabwe, plants*	*Europe, vertebrates*	*Arizona, birds*	*Europe, birds*	*Spain, birds*	*Europe, mammals*
15	1.00[b]	0.47[b]	0.62[b]	0.42[b]	0.45[b]	0.32[b]	0.25[b]	−0.63
20	1.00[b]	0.34	0.79[b]	0.42[b]	0.39[b]	0.41[b]	0.25[b]	−1.46[b]
25	0.18	0.62[b]	0.63[b]	0.23[b]	0.25[b]	0.42[b]	0.35[b]	−4.33[b]
30	1.00[b]	1.00[b]	0.79[b]	0.45[b]	0.26[b]	0.22	0.21[b]	−0.89
35	1.00[b]	1.00[b]	0.53[b]	0.48[b]	0.40[b]	0.31[b]	0.09	−1.94
Mean	0.84	0.69	0.67	0.40	0.35	0.34	0.26	−1.85

[a]*Species accumulation index (SAI) indicates how efficiently ED represents species relative to the same number of randomly selected sites. Columns are arranged from highest to lowest mean SAI. Positive values can be interpreted as efficiency values (1.0 is 100% efficient and is twice as good as 0.50), but negative values have only a qualitative interpretation (worse than random; −1 is not the mirror image of +1 and is not necessarily twice as bad as −0.5).*
[b]*Outside the 95% CI of the same number of randomly selected sites.*

of sites in each data set. Each run resulted in a set of sites that maximized ED by minimizing the distance from each demand point to the nearest selected site.

Evaluating Effectiveness of ED as a Surrogate

We used the species accumulation index (SAI) (Ferrier & Watson 1997; Rodrigues & Brooks 2007) to evaluate the effectiveness of the surrogate (selecting sites for maximum ED) in representing each taxon within a constrained number of sites (Supporting Information). An SAI compares S, the number of species represented in the set of sites selected using the surrogate, with an optimum value O (the largest number of species that can be represented in the same number of sites) and with R, the mean number of species represented in the same number of randomly selected sites. We calculated S by intersecting the p selected cells with the species data and counting the number of species represented. To calculate R, we randomly selected sets of p sites and calculated the number of species represented at least once in the randomly selected cells. We repeated the random selection procedure 1000 times, used the mean value as R, and calculated a 95% confidence interval on R.

We calculated O from the core area version of Zonation (Moilanen et al. 2014), a selection algorithm that starts with all sites tentatively reserved and progressively removes sites least needed to retain at least a small number of occurrences of each species. The algorithm minimizes the impact to the species with the smallest remaining number of cells in the tentative solution. Thus, if the worst-off species occurs in only 4 cells, Zonation would not remove any of those 4 cells from the solution until it would be impossible to remove a cell without causing 1 or more species to have fewer than 4 cells in the tentative solution. At that point, Zonation would remove the cell that causes the smallest number of species to be confined to 3 remaining cells. Although Zonation's algorithm cannot be guaranteed to find the true optimum (Moilanen & Ball 2009), Zonation represented 100% of species for each level of $p \geq 15\%$ of cells for all our data sets except plants of Zimbabwe, for which $> 94\%$ of species were represented at each level of p. Thus, any suboptimality had at most a trivial impact on the Zimbabwe data set and no impact on the other 7 data sets.

Formally, $\text{SAI} = (S - R)/(O - R)$. The SAI is scaled $-\infty$ to 1; negative SAI indicates a worse than random result, 0 indicates random performance, and positive SAI is a measure of effectiveness. For example, SAI of 0.6 indicates the surrogate was 60% as effective as the optimal solution in its ability to improve on random selection of sites. We calculated SAI at 15%, 20%, 25%, 30%, and 35% of the landscape hypothetically reserved and used the mean of these 5 SAI values as an overall estimate of surrogate performance. Because effectiveness is always assessed in terms of the maximum number of species represented in a specified number of sites, SAI measures both effectiveness and efficiency.

Results

ED represented European mammals slightly less effectively than randomly selected 50-km cells. Most species of mammals were represented in cells selected randomly, by ED, or by Zonation (Table 3 & Fig. 2).

For the other 7 data sets, sites selected for maximum ED represented more species than occurred in randomly selected sites (Table 3 & Fig. 2). Across all 8 data sets, median efficiency (SAI value) was 38% (interquartile range 30–68%). Across the 8 data sets, performance of ED (SAI values) did not vary with number of species (range 49–1315), number of sites (360–2195), or size of sites (6–625 km^2).

Figure 2 shows the number of species represented in a given number of sites selected to maximize ED, directly selected to maximize species representation (optimum or Zonation solution), and randomly selected sites. These

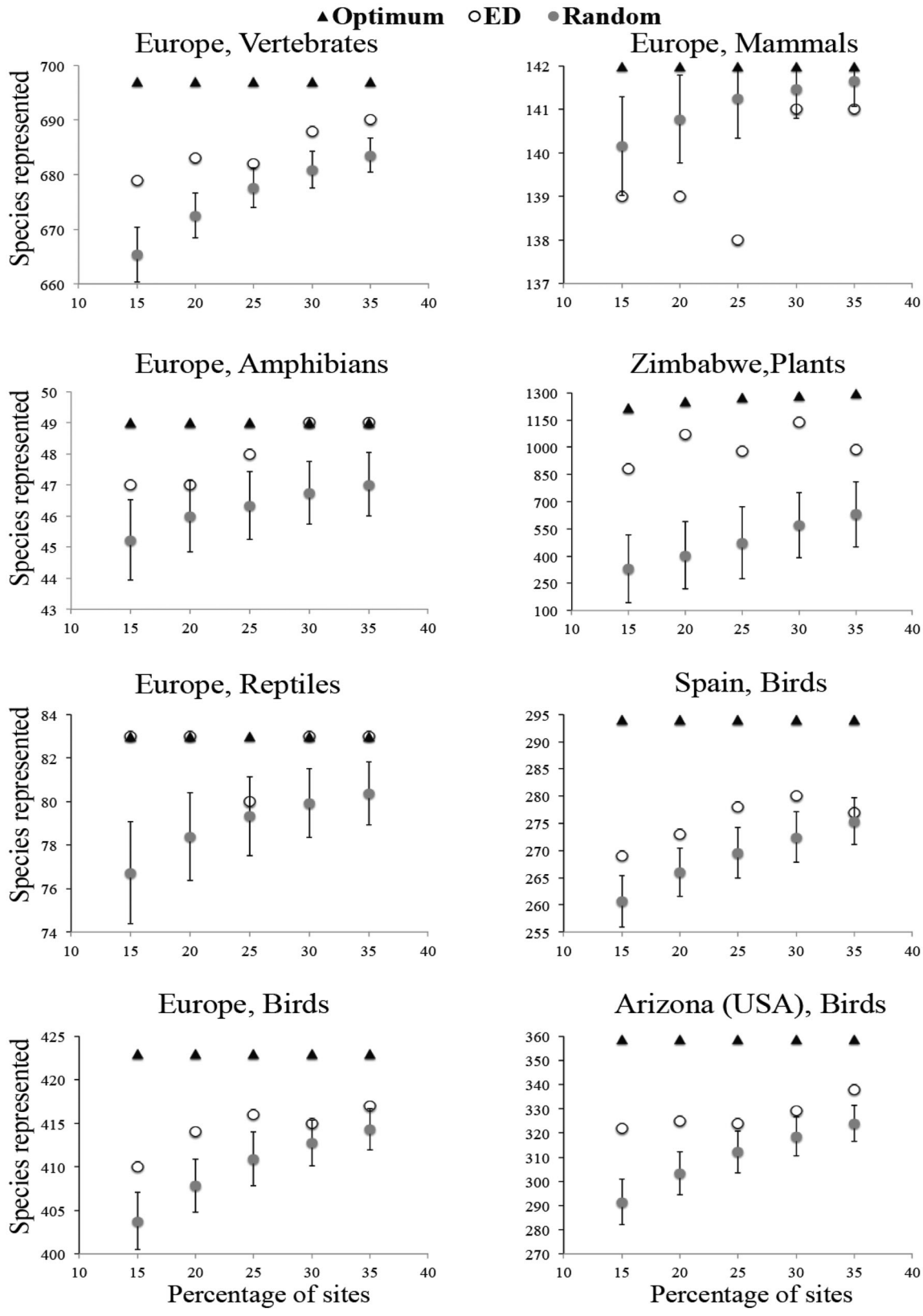

Figure 2. Number of species represented at least once in sites selected to maximize environmental diversity (ED) compared with the largest possible number of species represented at least once in the same number of sites (optimum) (estimated by Zonation [Moilanen et al. 2014]) and with the number of species represented at least once in the same number of randomly selected sites (random) (vertical bars, mean and 95% CI).

numbers convey information that is not evident in the summary SAI value. For instance, Fig. 2 shows that the SAI value of 0.42 for European vertebrates at $p = 15\%$ of the landscape reflects the fact that ED represented 679 of 698 species, whereas randomly selected sites represented an average of 665 of the 698 vertebrate species.

Discussion

For 7 of the 8 data sets we tested, sites selected to maximize ED represented species much more efficiently than random selection of sites. In contrast to previous analyses by Araújo et al. (2001) and Hortal et al. (2009), ED performed strikingly well for Western European reptiles, amphibians, birds, and all vertebrate taxa combined.

Why did ED perform so much better in our evaluations than in previous tests for the same taxa in Western Europe? We believe the main reasons are that we considered 37 candidate variables (instead of 6 or 7 variables), used PCA to thin these candidates to a smaller group of relatively uncorrelated variables, applied ED's minisum algorithm to a continuous grid of demand points in ordination space, and used a highly effective metaheuristic *p*-median (i.e., minisum) algorithm (Resende & Werneck 2003). Using a large suite of potential explanatory variables is advantageous because it allows one to identify the major environmental gradients in the data set; PCA can then help select a small number of orthogonal (relatively uncorrelated) axes that accurately reflect the environmental space of the study area. In contrast, the same number of preselected variables might not define major environmental gradients, and unless a procedure like PCA is used, multicollinearity among the preselected variables could yield a distorted environmental space. We also believe that POPSTAR software improved ED performance. POPSTAR searches solution space by using 32 random starts. Then it hybridizes the 10 best solutions to further improve them. Mladenović et al. (2007) reported that POPSTAR's hybrid metaheuristic algorithm outperformed other algorithms for solving minisum problems, correctly finding solutions for all 40 data sets for which exact solutions are known. In contrast, Hortal et al. (2009) used a greedy algorithm, which is more likely to obtain suboptimal results. Because our procedures (Fig. 1) were easy to implement and had no additional costs aside from the time required to acquire and process freely available data, future tests of ED should incorporate our procedures, or improve on them. Other differences between our analyses and those of Araújo et al. (2001) and Hortal et al. (2009) (e.g., Table 1, footnote h) may also have contributed to different results.

We suggest 2 ways to improve our implementation of the ED approach. First, our list of candidate variables (Supporting Information) should be expanded to include variables related to soil properties (we considered none) and more topographic variables than the 4 we considered (elevation, mean slope, aspect diversity, topographic diversity). For example, topographic wetness (Sorensen et al. 2006) can be calculated from freely available data, and it is plausible that diversity in this variable contributes to species representation. Second, using biotic information to select environmental variables associated with species turnover should improve performance of ED. Use of such biotically informed variables improved performance of discrete (binned) surrogates by at least 0.15 on the SAI scale (Ferrier & Watson 1997; Sutcliffe et al. 2015). Procedures such as gradient forests (Ellis et al. 2012) and generalized dissimilarity modeling (Ferrier et al. 2007) can not only be used to identify important drivers of species turnover, but they can also be used to model curvilinear (generalized dissimilarity modeling) or even nonmonotonic (gradient forests) relationships between environmental variables and compositional turnover. Although considering additional variables has no additional cost, using biotic information could be expensive, because it would require data on species composition in a subset of the cells in the planning area.

Our results provide a strong reason to pursue ED as a tool for prioritizing sites for conservation. Because species distributions are least available for regions with the highest biodiversity, greatest biodiversity loss, and most poorly developed protected area networks (Pimm 2000), a cost-effective surrogate like ED could be most useful precisely in those areas of the world that need it most. However, our study does not prove that ED is ready for use in conservation planning. For example, we did determine whether ED performs well for the small cell sizes that are most relevant for conservation planning. Although ED performed well for our finest-resolution data set (birds of Arizona), additional tests at similar and smaller cell sizes are needed before ED can be widely used for conservation planning. Future work should also evaluate ED performance for representation goals >1 occurrence per species and goals that vary among species. Finally, species representation is only 1 goal of conservation planning. Use of ED eventually must be integrated with goals for compactness, connectivity, and ecological and evolutionary processes (Margules & Pressey 2000). Another important advance would be to develop real-time interactive tools that would support flexible, incremental decisions, rather than a static list of sites with maximum ED. For example, suppose a manager commissions a study to identify 10 sites that would best expand the ED of an existing reserve network. During implementation, 2 of the 10 sites become unavailable for conservation and 2 unprioritized sites are donated to the reserve network. The manager needs the capacity to rearrange priorities without having to commission a new study.

ED represented mammals in Europe no better than random selection of sites. We speculate there are 2 reasons

why ED was a poor surrogate for European mammals. First, European mammals may not fully occupy their fundamental environmental niches because mammals do not persist in small, but otherwise suitable, habitat fragments in highly modified European landscapes. Second, our implementation of ED may not have been sufficient; perhaps additional variables or biotically informed variables (as discussed above) or other changes would improve ED performance for European mammals.

The performance of ED in our 8 tests (median SAI of 0.38, interquartile range 0.30–0.68) compares favorably to other surrogates as summarized in a major review by Rodrigues and Brooks (2007). For example, 90 tests of cross-taxon surrogates had median SAI of 0.35 and interquartile range 0.09–0.53, and 343 tests of abiotic surrogates had median SAI of 0.08 and interquartile range −0.07–+0.20 (Rodrigues & Brooks 2007). Not only is median performance of ED higher, but the interquartile range is much narrower, meaning there is less risk of a solution that is no better than random. We believe this superior performance of ED is due to the fact that the surrogate selects priority sites for their ability to span continuous (unbinned) environmental space. In contrast, conventional binned surrogates necessarily ignore within-bin and between-bin heterogeneity (Faith & Walker 1996*a*), and should be expected not to perform as well.

Our findings are relevant to efforts to conserve biodiversity in the face of climate change. Because nonclimate abiotic factors interact with climate (past, present, or future) to generate and maintain biodiversity, Hunter et al. (1988) suggest that conserving sites that are diverse with respect to combinations of these abiotic factors should conserve most species as climate changes. Conserving nature's stage (CNS) has been proposed as coarse filter conservation strategy that avoids the need for complex, highly uncertain models of future greenhouse gas emissions, future climate responses, species envelopes, and species dispersal (Beier et al. 2015). We urge additional, rigorous evaluations of ED based on only nonclimate abiotic factors. A finding that areas selected for diversity of nonclimate abiotic conditions efficiently represent species under 1 climate (today's climate) would justify further development of the CNS strategy.

Because species distributions are so poorly known in most planning areas, conservation planners sorely need reliable surrogates. Although much work remains to be done to evaluate ED as a surrogate in conservation planning, our results provide a strong motivation to engage in that work.

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Supporting Information

Optimization of the number of demand points, a generic illustration of species accumulation plots, and a list of variables used as independent variables (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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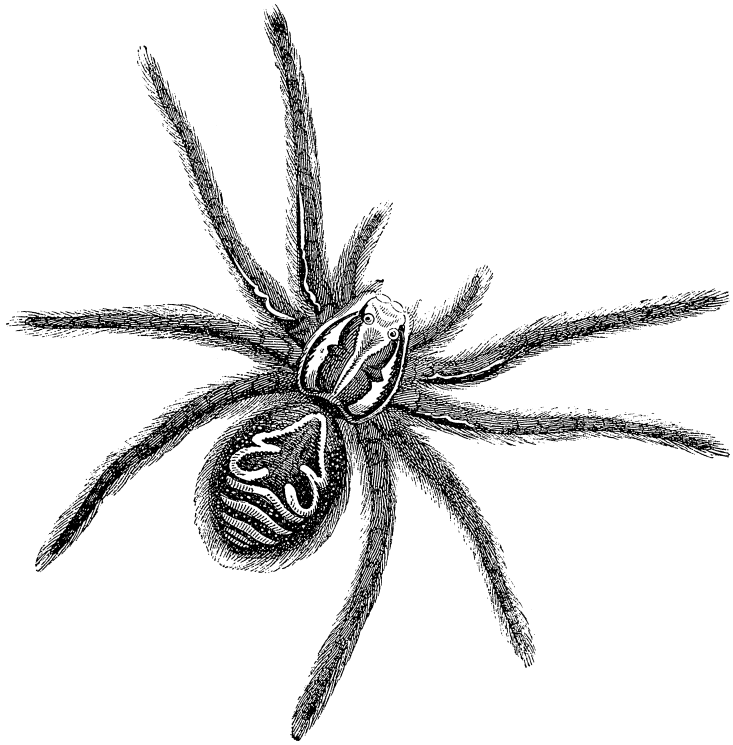
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