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Evaluating the performance of rarity as a surrogate in site prioritization for biodiversity conservation

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ABSTRACT

To solve the minimum-set coverage problem in conservation planning (representing the greatest number of species in the least number of sites), several metrics can be used to prioritize sites based on their conservation importance. Traditionally, species richness has been the most widely used approach, but previous studies suggest that it is one of the least effective. Alternative metrics such as complementarity algorithms have produced better results, for which they have been used in recent conservation studies. In this study, we assessed the performance of a new potential surrogate: rarity indices. Specifically, we tested rarity-weighted richness (RWR), index of summed rarity (ISR) and index of relative rarity (IRR), to determine if they are effective surrogates of biodiversity when solving the minimum-set coverage problem. We tested the rarity indices in 14 datasets spanning varying extents and grains, and found that rarity consistently outperformed species richness, even when accounting for the differences in rarity index performance. In some cases, rarity outperformed the complementarity solution, suggesting that it is a promising alternative surrogate that can be easily tested in situations where conservation action resources are limited. Rarity indices have been seldom assessed for their surrogacy effectiveness, and to the best of our knowledge, we are the first to test IRR and ISR in this context. Our results justify the need for future studies to elucidate the importance and applicability of rarity indices in conservation planning.

1. Introduction

Because much of the spatial information on the distribution of biodiversity is yet to be formally described and inventoried, the importance of surrogates of biodiversity is becoming widely recognized (e.g. Rodrigues and Brooks, 2007; Grantham et al., 2010, Beier et al., 2015 and references therein). Surrogates are often conceptualized as features such as vegetation maps, geodiversity, or well-known taxa such as birds. The idea is that sites selected to represent the surrogate will also efficiently represent other species which true distributions are not known (Rodrigues and Brooks, 2007).

The efficiency of surrogates, however, has been questioned (e.g. Rodrigues and Brooks, 2007, Beier et al., 2015). Because there is no consensus about the reliability of surrogates for conservation planning, testing its efficiency is critical to understand if surrogates are useful for representing other taxa or species, and whether different types of surrogates yield better results than others (Rodrigues and Brooks, 2007). For example, Albuquerque and Beier (2015a) evaluated how well the sites with the highest species richness represented the diversity of amphibians, birds and mammals at a global scale. They

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observed that species richness was a poor surrogate of vertebrate diversity. Species richness is widely used as a descriptor of a site's biodiversity and has been broadly used for addressing the underlying causes of biodiversity loss at the global scale (Ladle and Whittaker, 2011; Sala and Knowlton, 2006; Ramírez et al., 2017).

Although a useful metric in some contexts, species richness not always indicates the importance of a site for the goal of species representation. The problem is that sites with high species richness often contain overlapping assemblages of species, such that sets of species-rich sites almost always fail to represent species in a small number of sites (Kirkpatrick, 1983, Csuti et al., 1997, Albuquerque and Beier, 2015a,b, and references therein). Accordingly, for about 30 years, biogeographers and conservation planners have used another descriptor – site complementarity – as a measure of conservation values of sites, which ensures that sites selected for inclusion in a reserve network complement those already selected. Complementarity scores can be estimated by integer programming (Haight and Snyder, 2009), and by heuristic reserve-selection algorithms such as Marxan (Ardron et al., 2010), C-Plan (Pressey et al., 2009), or Zonation, a spatial conservation method used for spatial conservation planning and conservation practice (Moilanen et al., 2014).

Another potential surrogate of biodiversity is rarity, a metric that has been used to implement management actions to conserve imperiled species (Williams et al., 1996; Stein et al., 2000; Soberón and Ceballos, 2011; Villalobos et al., 2013; Guerin and Lowe, 2015). Rarity is often related to geographic range, habitat specificity, and local abundance (Rabinowitz, 1981). Normally, a species is considered rare if its geographical range or abundance drops below a given cut-off point. Gaston (1994) recommends using the first quartile of the distribution frequency of species occurrence as a cut-off to define the species considered rare (i.e. species with the lowest occurrence). Nevertheless, quantifying rarity of a site (hereafter rarity) is not a straightforward process. For example, Williams et al. (1996) assessed rarity of a species by the inverse of the number of sites where it is present, and the rarity-weighted richness (RWR) of a site as the sum of rarity scores for all species present at that site (see Williams et al., 1996 for further details). RWR uses rarity scores to select sites with high concentrations of small-ranged species (Stein et al., 2000). More recently, Leroy et al. (2012, 2013) proposed new metrics to calculate rarity with the index of summed rarity (ISR) and the index of relative rarity (IRR), for a set of sites. ISR calculates rarity based on the sum of weights of species, while IRR assigns values to sites based on rarity cut-off points and the proportion of rare species (Leroy et al., 2012, 2013). As species occurrences drop below the rarity cut-off, the weight of rare species should increase exponentially (Leroy et al., 2012). IRR provides an improved understanding of patterns of rarity in sites (Leroy et al., 2013).

Previous analyses by Albuquerque and Beier (2015c) reported that RWR performed strikingly well for vertebrates and plants in tropical and temperate environments. Integer programming is not widely used for solving these problems, because the number of possible combinations increases to astronomical numbers, and computing time can become prohibitively long (Moilanen et al., 2009). On the other hand, RWR, ISR, and IRR do not require specialized geographical software, programming experience, or analytic skill. Calculations can be completed in open source software such as R (R Core Team, 2017), or in a spreadsheet. Therefore, rarity indices may represent a simple and reliable alternative to integer programming and heuristic algorithms for minimum-set coverage problem (i.e. how well rarity represents the greatest number of species in the smallest number of sites), and the maximum-set coverage problem (i.e. how well rarity represents species in a determined number of sites) in conservation planning (Albuquerque and Beier, 2015c). If applicable to biodiversity, a low-cost surrogate like rarity could be most useful precisely in those areas of the world that need it most (i.e. areas with high biodiversity and limited resources for conservation, such as tropical countries).

Here, we investigated if rarity is an effective surrogate of biodiversity. Our objectives were to: (1) test if rarity can be used as a surrogate for biodiversity when solving the minimum-set coverage problem (representing the greatest number of species in the least number of sites); and (2) investigate whether the approach used to define rarity (e.g. RWR, ISR, and IRR) affects its ability to select sites that efficiently represent biodiversity. Successful performance of rarity as an efficient surrogate of biodiversity in our tests would justify future studies that also use rarity to prioritize sites for conservation. Additionally, understanding which surrogates are more effective in conservation planning would improve our use of the available information and provide better guidance for future data acquisition.

2. Materials and methods

2.1. Data

We used 14 biodiversity datasets that span a broad range of taxa (plants and animals), spatial extents, and grain (Table 1). In the "inventory" datasets, we considered sites as a systematic subsample of the geographic area of interest. In the "atlas" datasets, we calculated presences and absences for each grid cell that collectively comprised the entire geographic area of interest. Range maps were processed in grass 6.4.2 (GRASS Development Team, 2012) to generate presence/absence values for each 1° grid cell (ca 110 km). We considered grid cells (atlas) and inventory sites as the entire planning area (hereafter sites); although in some cases, species data was not available for the whole study region (e.g. birds of Arizona).

2.2. Estimating rarity of sites

For each dataset, we used the rarity-weighted-richness (RWR) index algorithm (Williams et al., 1996), the index of relative rarity (IRR) and the index of summed rarity (ISR) (Leroy et al., 2012, 2013) to calculate the rarity of a site and to produce a hierarchical spatial selection prioritization of sites for each taxon.

Table 1
Biodiversity data sets used to evaluate the performance of rarity and species richness metrics for species representation in conservation planning.

Id	Data set (citation)	# Species	Extent
1	Birds (BirdLife International, 2012)	9367	Global[A]
2	Amphibians (IUCN Red List Spatial Data)	6250	Global[A]
3	Mammals (IUCN Red List Spatial Data)	5243	Global[A]
4	Birds of Mexico (Sigüenza and Rivera, 2017)	1113	Regional[I]
5	Birds of Arizona (Corman and Wise-Gervais, 2005)	359	Regional[A]
6	Birds of Florida (FBBA, 2007)	211	Regional[A]
7	Birds of Ireland (National Biodiversity Data Centre, 2017)	280	Regional[A]
8	Birds of Spain (INB, 2007)	294	Regional[A]
9	Terrestrial species of Spain (Villares, 2018)	1733	Regional[A]
10	Mammals of Ireland (National Biodiversity Data Centre, 2014)	43	Regional[A]
11	Butterflies of Denmark (Calabuig, 2016)	89	Regional[A]
12	Forest species of Spain (Vallejo Bombín, 2018)	245	Regional[I]
13	Flora vascular of Portugal (Carapeto and Porto, 2016)	2467	Regional[A]
14	Plants, Sierra Nevada (Pérez Luque, 2018)	258	Local[I]

A = atlas. I = inventory.

To calculate RWR, we scored species as the inverse of the number of sites where they were present. We gave the maximum score for species that occurred only in one site (1.0) and we summed the individual scores of all species occurring in each cell (Stein et al., 2000). We calculated RWR as follows:

$$RWR = \sum_{i=1}^{n} \frac{1}{c_i}$$

where c_i represents the number of sites in which species *i* occurs and *n* represents the number of species occurring in a site.

To calculate the IRR and ISR, we first used the first quartile of species occurrences (the 25 percent species with the lowest occurrence) as the rarity cutoff point (Gaston, 1994; Leroy et al., 2013). We then used the *rWeights* function in R to calculate the rarity weight with two weighted functions: *W* and inv*Q* (Leroy et al., 2012). In the former, weights of species with occurrence lower than the cut-off are expected to increase exponentially, while weights of species with occurrence higher than the rarity cut-off are close to zero (Leroy et al., 2013). *W* is defined as:

$$\exp\left(-\left(\frac{Q_i - Q_{min}}{r_j \times Q_{max} - Q_{min}} \times 0.97 + 1.05\right)^2\right)$$

where Q_i represents the occurrence of species *i*, Q_{min} and Q_{max} represent the minimum and the maximum occurrences, and *r* is the chosen rarity cut-off point.

The inv*Q* is expressed by the inverse of the occurrence and it was calculated as:

$$\frac{1}{Q_i}$$

We used the sum of the rarity weights of species, as produced by *W* and inv*Q*, to calculate ISR, and the rarity weight (also as produced by *W* and inv*Q)* and species richness to calculate IRR. We calculated the ISR and IRR as follows:

$ISR = (\sum w_i); IRR = \frac{\frac{\sum w_i}{S} - W_{min}}{W_{max} - W_{min}}$ Where W_i represents the weight of the i_{th} species, S represents species richness, and W_{min} and W_{max} the minimum and maximum weights, respectively.

2.3. Evaluating rarity surrogate performance

We evaluated rarity, as estimated by RWR, IRR and ISR, in terms of their ability to represent biodiversity. For each dataset, we selected sites (added to the notional “reserve”) starting with the site with the highest rarity value and adding the site with the next highest rarity at each succeeding step. At each step, the number of species represented in at least one site of the hypothetical reserve was calculated.

We used the Species Accumulation Index, SAI (Rodrigues and Brooks, 2007) to evaluate the efficiency of rarity and richness in representing each taxon. SAI was calculated as follows:

$$SAI = (S\text{-}R)/(O\text{-}R)$$

Where S is the number of species represented in the set of sites selected using each rarity metric. O represents an optimum value O (the largest number of species that can be represented in the same number of sites), which was calculated using Zonation (Moilanen et al., 2014) from the run used to generate priority ranks. R is the mean number of species represented in 100 randomly selected sites. We used the species accumulation curves approach (SAC) to calculate the number of species represented at least once in the randomly selected sites (R), and calculated a 95% confidence interval.

SAI is scaled $-\infty$ to 1; a negative SAI score indicates a worse than random result, values near 0 indicate random performance, and positive SAI measures efficiency; e.g., SAI of 0.9 indicates that rarity was 90% as effective as the optimal solution in its ability to improve on random selection of sites. We calculated SAI across 201 potential conservation targets. These represent the percentage of the landscape hypothetically reserved. For example, a target of 10%, for a system of 1000 sites, represents the number of species represented by 100 sites. Targets ranged from 10% to 30% at 1% intervals (i.e. 10%, 11%, 12% …. 30%). We used the mean of these 201 SAI values as an overall estimate of surrogate performance.

3. Results

In all dataset cases and targets (percentages of sites prioritized), rarity and Zonation (complementarity) solutions represented more species than the same number of randomly selected sites (Fig. 1). In two datasets (birds, global and mammals, global), species richness was outperformed by the random solutions, and in all cases rarity outperformed species richness (Fig. 1).

On average across 11 datasets, rarity solutions were as effective as complementarity (as expressed by Zonation) in improving on random selection of sites (Fig. 2), and rarity was more effective than Zonation in the remaining three datasets (closer to the true optimum; terrestrial species, Spain; butterflies, Denmark; and plants, Sierra Nevada) (Fig. 2). In 3,209 (20%) instances (each instance referring to a SAI calculation considering the different random values for each target), rarity indices outperformed Zonation. Different indices performed at different levels of efficiency (i.e. representing more species than would be represented by random site selection). RWR provided the best results (in 731 instances), followed by ISR *invQ* (731 instances), IRR *invQ* (685 instances), ISR *W* (604 instances), and IRR *W* (459 instances). Collectively, rarity and Zonation solutions represented the same number of species in 7,035 instances (50%).

4. Discussion

While the performance of RWR as a surrogate of biodiversity has been assessed in previous studies (e.g. Albuquerque and Beier, 2015c; Csuti et al., 1997), to the best of our knowledge, this is the first assessment of the performance of IRR and ISR as surrogates of biodiversity in solving the minimum-set coverage problem. Our results indicate that the rarity indices tested here are indeed good surrogates of biodiversity for that purpose. Results also show that rarity is ideally suited to represent sites that contain all or most of the species. Like heuristic algorithms, rarity indices attempt to find maximum efficiency of representation, in terms of the number of selected sites. RWR is identical to *invQ* (Leroy et al., 2012); both consider the sum of the inverse of the frequency of species within a site. These results are strengthened by the overall performance across the different extents and grains of the datasets.

However, not all indices performed equally across the different datasets. When comparing indices performance for atlas versus inventory datasets (see Table 1), the overall trends of the dataset types do not seem to indicate they have an effect on the performance of the indices (Figs. 1 and 2). In the case of comparisons based on extent, the results indicate that generally in local and regional analyses, indices perform better and with more consistency than in global analyses. For taxa comparisons, results suggest that rarity is a highly effective surrogate for most of the datasets tested, with slight overall variation in indices performance in the case of the amphibians, mammals, and plants datasets, and moderate variation in the flora, Portugal dataset (Figs. 1 and 2). Rarity indices worked well even when different taxonomic species where considered (Terrestrial species, Spain). Indices performance indicate that rarity is also an effective surrogate for biodiversity (Figs. 1 and 2). The differences here described indicate that there is not a silver bullet, and that rarity indices must all be tested in each situation to determine the best index to use for each case scenario.

In contrast, species richness inefficiently represented the greatest number of species across the datasets (with the most relevant exception being the butterflies, Denmark dataset; Figs. 1 and 2). Species richness also outperformed IRR_Q in the flora, Portugal dataset, but was outperformed by the rest of the rarity indices tested (Figs. 1 and 2). These results suggest that generally, species richness is a poor surrogate for species representation when solving the minimum-set coverage problem, as suggested by previous studies (e.g. Albuquerque and Beier, 2015c; Veach et al., 2017). The species richness approach for prioritizing sites for conservation purposes often fails in representing the greatest number of species in a limited number of sites (Kirkpatrick, 1983). This occurs because of its greedy nature; it assigns higher conservation values to sites with the highest number of species, regardless of the species composition of those selected sites. Therefore, sites that have the highest number of species will be given priority even if all sites selected are comprised of the same species. This approach assumes the same conservation values for all species and leaves sites with rare species at the end of the line when those species are the only ones found in a particular site (Veach et al., 2017). It is for this reason that we recommend against using species richness as the metric to prioritize sites conservation values when solving the minimum-set coverage problem in conservation planning.

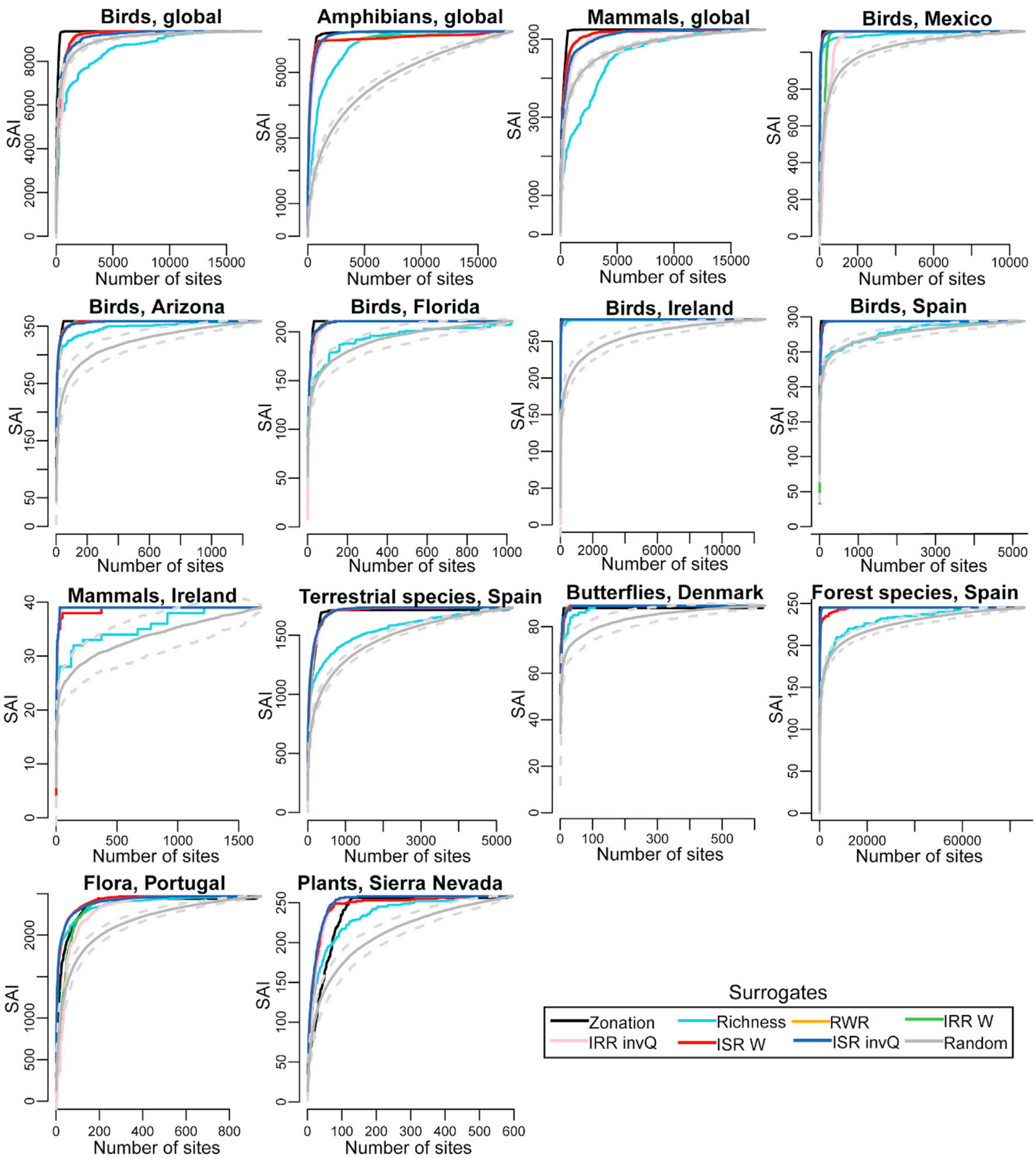

Fig. 1. Species accumulation curves for surrogates of biodiversity, represented by species richness, complementarity (Zonation), rarity and random solutions. Rarity indices are rarity weighted richness (RWR), the index of relative rarity (IRR) and index of summed rarity (ISR) as defined by two rarity weights: *W* and inv*Q*.

Because the occurrence of rare species in a site gives it a higher value than other sites with no rare species (Ratcliffe, 1977), rarity seems to be a more effective surrogate for species representation in this context. Rarity algorithms are completely intuitive approaches that do not rate species equally in conservation value. They also ensure that rare species are represented first (Justus and Sarkar, 2002). Another advantage of rarity indices is the time needed to guarantee an efficient solution. In all datasets, R produced rarity solutions in a few seconds (real time decision). Depending on how fast an answer is needed, the computation time may become an impediment to the conservation planning process (Pressey et al., 1996).

Perhaps the main advantage of using rarity indices is ensuring that areas chosen for including in high-quality sites for prioritization complement those already selected (Justus and Sarkar, 2002). As reported by this study, rarity indices selected similar sets of sites and found the same sized solutions as complementarity for most datasets and targets. Complementarity

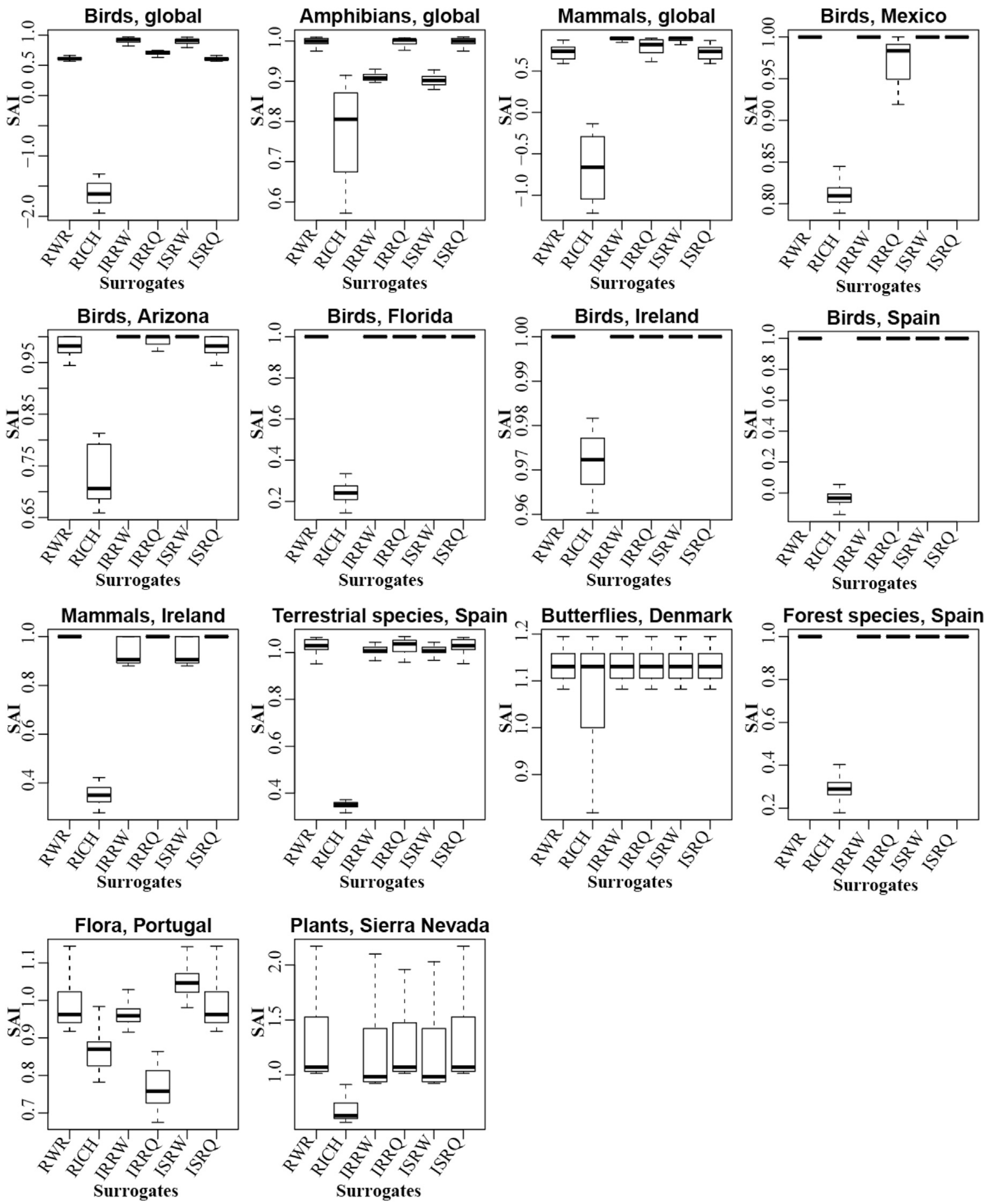

Fig. 2. Boxplot illustrating the species accumulation index (SAI) used to evaluate the efficiency of rarity and richness in representing each taxon. Rarity indices are rarity weighted richness (RWR), the index of relative rarity (IRR) and index of summed rarity (ISR) as defined by two rarity weights: *W* and inv*Q*.

algorithms prioritize sites for conservation by first favoring sites with higher species richness, but subsequently adding sites to a hypothetical reserve, which contain new species that have not yet been represented in the already selected sites (Pressey et al., 1996 Moilanen et al., 2009). Complementarity adds these subsequent sites regardless of the number of species present in them (see e.g. Moilanen et al., 2014). In a similar fashion, rarity prioritizes sites not based on the number of species, but instead on the weight given to each species based on its current condition (i.e. rare or endemic, and is more vulnerable to extinction than other more common species). This way, species with limited distributions are given priority over those that are more widespread (see Leroy et al., 2012, 2013).

Our results are in a theoretical framework and as they are, they might not be directly applicable to conservation planning. For these findings to be applicable to conservation action, more information such as species-specific and place-specific needs must be incorporated, such as maximizing the adjacency of selected sites, minimizing the cost of achieving a reservation goal or avoiding sites in poor conditions (Pressey et al., 1996). Nonetheless, we believe that our results are promising and that future work can benefit from our findings. As we face the biggest biodiversity loss crisis to date (Ceballos et al., 2015), it is important to test alternative approaches to maximize the effectiveness of conservation efforts. Studies like this help fulfill this purpose by providing new and improved ways to facilitate conservation initiatives, especially in places that have the most limited resources.

Rarity is a powerful tool for solving the problems requiring at least one occurrence of each species. In our study, we demonstrated how rarity indices, specifically RWR, IRR, and ISR, could be used as potential surrogates of biodiversity when solving the minimum-set coverage problem in conservation planning. More specifically, results suggest that while there may be some variation in the performance of the different indices depending on the type of dataset, overall performance of these rarity indices are effective at the local, regional, and global scale in terrestrial systems such as those here tested, and consistently outperform species richness as the metric for site prioritization. In some cases, rarity results even outperformed those produced by the complementarity approach (Zonation), making it a promising alternative for situations where conservation actions are most needed but resources are scarce. To the best of our knowledge, we are the first to assess the performance of ISR and IRR as surrogates of biodiversity in this context.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00639.

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