



Towards biodiversity hotspots effective for conserving mammals with small geographic ranges



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ABSTRACT

The main goal of using global biodiversity hotspots for conservation purposes is to protect taxa with small geographic ranges because these are highly vulnerable to extinction. However, the extent to what different hotspots types are effective for meeting this goal remains controversial because hotspots have been previously defined as either the richest or most threatened and richest sites in terms of total, endemic or threatened species. In this regard, the use of species richness to set conservation priorities is widely discussed because strategies focused on this diversity measure tend to miss many of the taxa with small geographic ranges. Here we use data on global terrestrial mammal distributions to show that, hotspots of total species, endemism and threat defined in terms of species richness are effective in including 27%, 29% and 11% respectively, of the taxa with small geographic ranges. Whilst, the same hotspot types defined in terms of a simple diversity index, which is a function of species richness and range-size rarity, include 68%, 44% and 90% respectively, of these taxa. In addition, we demonstrate that index hotspot types are highly efficient because they conserve 79% of mammal species (21% more species than richness hotspot types), with 59% of species shared by three hotspot types (31% more than richness hotspot types). These results suggest that selection of different diversity measures to define hotspots may strongly affect the achievement of conservation goals.

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1. Introduction

The identification of biodiversity hotspots at multiple scales have become one of the most used strategies to prioritize areas for conservation worldwide (Myers et al., 2000; Mittermeier et al., 2004). From its genesis, the main goal of using global biodiversity hotspots for conservation purposes was to protect taxa with small geographic ranges because these are highly vulnerable to extinction (Myers, 2003). However, the extent to what hotspots are effective for meeting this goal remains controversial because hotspots were defined as either the richest or most threatened and richest sites in terms of total, endemic or threatened species (Ceballos and Ehrlich, 2006). In this regard, the use of species richness to set conservation priorities is widely discussed (Brooks et al., 2006) because taxa with large geographic ranges contribute more to the spatial patterning in species richness than taxa with small geographic ranges (Brooks et al., 2006). Under this evidence,

we expect that hotspots of total species, endemism and threat defined in terms of species richness be biased to protect a high proportion of taxa with large than small geographic ranges. To increase the protection of taxa with small geographic ranges, we propose that hotspots should be defined in terms of diversity measures that promote the representativeness of these taxa. In this work, we assess how the effectiveness to include mammals with small geographic ranges change in hotspots of total species, endemism and threat defined from measures of (a) species richness and (b) a diversity index which is function of species richness and range sizes rarity (Kier and Barthlott, 2001).

To increase the protection of taxa with small geographic ranges, we propose that hotspots should be defined in terms of diversity measures that promote the representativeness of these taxa while maximizing the total number of species to be conserved (Myers et al., 2000; Myers, 2003). We consider that a measure that can accomplish with this requirement is an index that is function of species richness and range sizes rarity (Kier and Barthlott, 2001). Conceptually, the calculation of this index will give higher weights to species with small ranges, and progressively lower weights to

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those species with larger ranges (i.e., this index is proportional to the inverse of species distributional range size) (Laffan and Crisp, 2003). For example, when the totality of a species' range falls into a mapping unit (such a biogeographic region, or a grid cell), its entire value (i.e., 1 range equivalent) is attributed to this area, but if a species is distributed in two mapping units, the half of its value (i.e., 0.5 range equivalent), are attributed to each mapping unit and so on (Kier et al., 2009). Then, the index is calculated by summing the fractions of the inverse of species range size by mapping unit. Although we are conscious that other diversity measures, such as dispersion fields (Graves and Rahbek, 2005), can be tested for its ability to identify hotspots that include a high number of small ranged taxa, this measure has lower correlation with species richness. Therefore, for this contribution, we prefer the diversity index presented herein because it better reflects both range size rarity and species richness (Kier and Barthlott, 2001). This decision is based on the spirit of biodiversity hotspots thesis which is to protect the greatest number of species with small range sizes per dollar invested (Myers et al., 2000; Myers, 2003).

In this work, we assess how the effectiveness to include mammals with small geographic ranges change in hotspots of total species, endemism and threat defined from measures of (a) species richness and (b) the diversity index.

2. Materials and methods

2.1. Data source and diversity measures

To estimate measures of mammal diversity, we utilized digital maps of the geographic ranges of 5285 terrestrial species (IUCN, 2013). Diversity measures were obtained by dividing the world (except Antarctica) into 18,571 equally-distanced cells of $1^\circ \times 1^\circ$, with geographic projection and coordinate system measured in decimal degrees of latitude/longitude. We used this scale because the use of range map data at finer scales increases the probability of false occupancies, whereas using coarser scales reduces such probability (Hurlbert and Jetz, 2007). We calculated species richness by counting the number of overlapping range maps that fall within each of 18,571 cells. Conversely, the diversity index was calculated as follows: first, counting the number of cells in which each species is distributed; second, calculating its inverse value (i.e., dividing one by the number of cells in which each species is distributed); and third, summing the inverse value of all species that fall within each of 18,571 cells (Kerr, 1997; Kier and Barthlott, 2001). Using this index, cells with equal species richness, but with a high proportion of taxa with small geographic ranges, will have higher scores than cells containing taxa with large geographic ranges (Kerr, 1997). Species richness and diversity index were calculated for three nested categories of mammal distributions: total species ($n = 5258$); endemic species ($n = 2236$), and threatened species ($n = 1096$). We considered as endemic those taxa with geographic ranges smaller than or equal to 25 cells (Ceballos and Ehrlich, 2006), and as threatened those taxa deemed susceptible to extinction by the IUCN (i.e., critically endangered [CR], endangered [EN], vulnerable [VU]; Ceballos and Ehrlich, 2006; IUCN, 2014). Hotspots were defined as 2.5% of cells with the highest scores (Ceballos and Ehrlich, 2006; Lennon et al., 2004) for each diversity measure in the three categories of mammal distributions. Thus, we identified six types of hotspots: three based on measures of species richness (RH), considering total (RHS), endemic (RHE) and threatened species (RHT); and three based on measures of diversity index (IH), considering total (IHS), endemic (IHE) and threatened species (IHT). For a precise evaluation about the effectiveness of these six hotspot types for conserving taxa with small but also with larger geographic ranges, we partitioned the data on

total, endemic, and threatened species into geographic range-size quartiles (Rahbek et al., 2007): from those with small ranges (1st quartile), to those with large ranges (4th quartile).

2.2. Mapping and hotspots

To build the grids at different scales and rasterize the range maps shapefiles of terrestrial mammal species, we used the freely available SAM software (Rangel et al., 2010). As in Orme et al. (2005), hotspot definitions were based on the percentage of terrestrial cells covered; thus, where quantile scores fell within a diversity class, we used the number of cells for that class. Particularly, with this methodology we found a higher number of grid cells as richness hotspot types (because species counts are a discrete variable) than as index hotspot types (where index scores are a continuous variable). In order to assess whether the effectiveness of IH for including more taxa with small geographic ranges, compared to RH, depends on the threshold and scale used in our study, we performed the same analyses at different thresholds (5%, 10%, 25%, 50% and 75%) and scales ($2^\circ \times 2^\circ$, $4^\circ \times 4^\circ$ and $8^\circ \times 8^\circ$). When we analysed the number of endemic species falling within both RHE and IHE at scales of $4^\circ \times 4^\circ$ (approximately 160,000 km²), we divided species range-sizes into two groups (based on the median value): taxa with small and with large geographic ranges. At scales of $8^\circ \times 8^\circ$, there was a only one range-size group, because geographic ranges of endemic species were smaller than grid cells sizes.

2.3. Statistical analyses

To recognize the ability of diversity measures to capture richness patterns of species with different geographic ranges, we used the SAM software (Rangel et al., 2010) to perform Spearman rank correlations (with Bonferroni correction) between diversity measures (richness and diversity indices) and richness patterns of total, endemic and threatened species belonging to range-size quartiles. In addition, we also performed Spearman rank correlations to assess spatial correspondence among richness patterns of total species, endemism and threat and among index patterns of total species, endemism and threat. Spatial structure of species composition between RH and IH was analysed with Mantel tests. To this end, we calculated a Jaccard similarity matrix based on the species composition found in each hotspot type, and a matrix of Euclidean geographic distances according to hotspot locations (we used latitude and longitude considering the centroid of grid cells). Based on these analyses, we were able to evaluate the similarity in composition of closely located cells. We performed Mantel tests with the package ade4 (Dray and Dufour, 2007) in R (R Core Team, 2012), correlation scores were based on Spearman rank, using 99,999 randomizations.

3. Results and discussion

Global geographic distributions of grid cells identified as being RH were similar to those described elsewhere (Ceballos and Ehrlich, 2006) (Fig. 1a–c); instead, in cells identified as being IH there were some overlapped with their respective RH and others were idiosyncratic, the latter recognized here as potential new hotspots (Fig. 1d–f). The percentages of spatial overlap between IH and RH were very variable: 23% between RHS and IHS, 62% between RHE and IHE, and 12% between RHT and IHT. Overlapping hotspots were roughly located, IHS, IHE and IHT in the north of South America, Central Africa and south east of Asia, IHS and IHE in the south of Central America, and IHE in the south of North America and Central South America. Instead, potential new

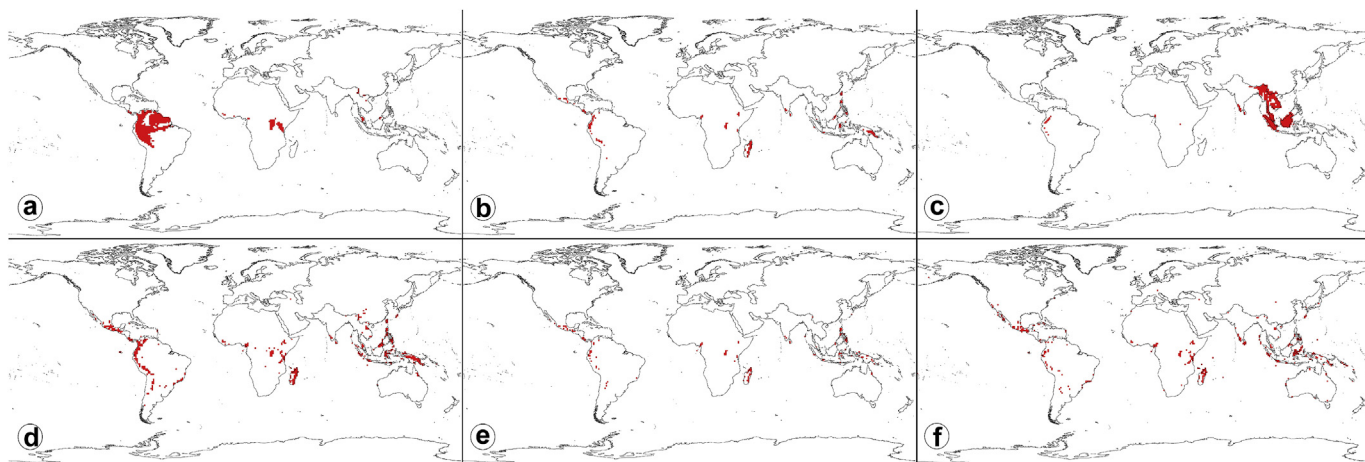


Fig. 1. Geographic distribution of richness and index hotspots (cells in red) for the three categories of mammal distributions. a, Richness hotspots of total species. b, Richness hotspots of endemicism. c, Richness hotspots of threat. d, Index hotspots of total species. e, Index hotspots of endemicism. f, Index hotspots of threat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hotspots were located, *IHS* in southern North America, Caribbean islands and central and southern South America, Madagascar, India, Sri Lanka, Indonesia, Papua and New Guinea, Solomon Islands, Australia, Japan, Taiwan, Vietnam, Thailand, Philippines, and the Caucasus; *IHE* in the central coast of Brazil, Sao Tome & Principe, China, Japan, Australia, and *IHT* in Alaska, central and southern North America, Central America and the Caribbean, central South America, continental and insular Africa, Austria, Armenia, Pakistan, Papua and New Guinea, Australia, Solomon Islands, Vanuatu, New Caledonia, Fiji, Japan.

When calculating the proportion of total, endemic and threatened species by range-size quartiles included within their respective *RH* or *IH*, we note that all *RH* are scarcely effective in protecting taxa with small geographic ranges (1st range-size quartile), but this effectiveness strongly increases stepwise towards species with larger geographic ranges (from 2nd to 4th range-size quartile; Fig. 2a–d). In contrast, all *IH* are more effective in protecting taxa with small geographic ranges than *RH*, being almost as effective as for species of other range-size quartiles. Taking into account the taxa belonging to the 1st range-size quartile, *RHS*, *RHE* and *RHT* are effective in including 27%, 29% and 11% of them respectively; while *IHS*, *IHE* and *IHT* respectively include 68%, 44% and 90% of these taxa. Furthermore, when we discriminated threatened species based on their conservation status (IUCN, 2014), we found that *RHT* were effective in including a greater proportion of vulnerable species, rather than endangered and critically endangered ones, with the latter being the least protected, whereas *IHT* included a high proportion of vulnerable, endangered, and critically endangered species, with the latter being the most protected.

Effectiveness for including taxa with small geographic ranges between *RH* and *IH* is related to the capacity of each diversity measure used in hotspot definitions to capture their richness patterns. Measures of species richness (considering total, endemic and threatened species) are less correlated with richness patterns of taxa belonging to the 1st range-size quartile, compared with richness patterns of species belonging to the remaining range-size quartiles (which increases from 2nd to 4th; Table 1, Appendix A). Instead, measures of the diversity index for the same categories of mammal distributions are highly correlated with richness patterns of taxa with small geographic ranges because these taxa contribute the most to this diversity measure. However, the index are also

highly correlated with richness patterns of taxa with higher geographic ranges because, although these species contribute less to the index, their distributions tend to be more spatially overlapped (Lennon et al., 2004), leading also to high diversity index scores. This evidence supports that, regardless of the type of measure of species richness used, taxa with large geographic ranges mainly determine the identification of *RH* that disfavour the inclusion of taxa with smaller geographic ranges due to lack of concordance among their richness patterns (Lennon et al., 2004; Brooks et al., 2006); whilst taxa belonging to the first three range-size quartiles, which comprise the bulk of terrestrial mammals, mainly determine the identification of potential new *IH* that favour the protection of a great proportion of species across all range-size quartiles.

Our findings also show that each *IH* is more efficient in including species in other categories of mammal distributions than its respective *RH* (Table 2). Differences in efficiencies are related to the spatial structure of hotspots which determines their ability to include a complementary set of species. For instance, *RHS*, *RHE* and *RHT* show geographically close hotspots with a higher level of species similarity (Mantel correlation coefficients 0.842, 0.320 and 0.533 respectively, $P < 0.001$), than *IHS*, *IHE*, and *IH* (Mantel correlation coefficients 0.523, 0.241, and 0.268 respectively, $P < 0.001$). These results have strong implications for the use of *IH* in conservation practices, because any diversity index can act as an effective surrogate for other indices. In fact, when we tested for the level of congruence within *IH* by measuring the number of mammal species found in cells that were common among hotspot types, we found that *IH* conserve 79% of mammal species (21% more species than *RH*), with a congruence of 59% among them (31% more than richness hotspot types; Fig. 2e–f). The high congruence in *IH* is caused by greater spatial correlations among diversity indices than among species richness measures (Appendix B). This is because taxa with small geographic ranges are often endemic or under threat; thus, they contribute to all three diversity indices, making *IH* more spatially overlapped. Instead, taxa with large geographic ranges are basically different among categories of mammal distributions; thus, they contribute differentially to the three species richness measures, making *RH* less spatially overlapped (Appendix C).

When we identified hotspots at different thresholds and scales, results showed that *IH* included more species with both small with

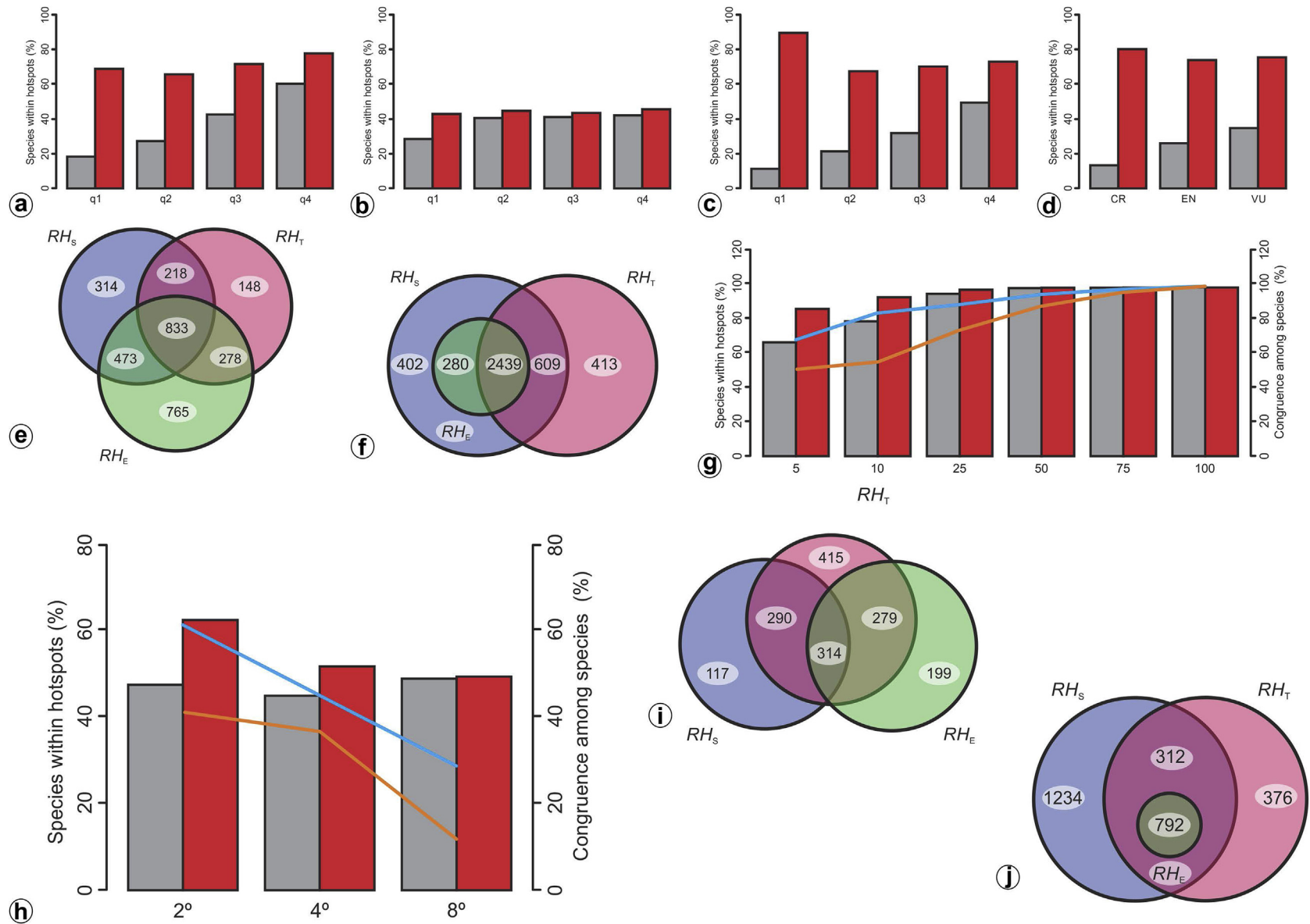


Fig. 2. Mammal species included within global hotspot types. a, Proportion of total species by range size quartile within richness (grey bars) and index (red bars) hotspots of total species. b, Proportion of endemic species by range size quartile in richness (grey bars) and index (red bars) hotspots of endemism. c, Proportion of threatened species by range size quartile in richness (grey bars) and index (red bars) hotspots of threat. d, Proportion of threatened species by conservation status in richness (grey bars) and index (red bars) hotspots of threat. e, Number of species ($n = 3029$) shared among richness hotspots of total species (RHS), richness hotspots of threat (RHT) and richness hotspots of endemism (RHE). f, Number of species ($n = 4143$) shared among index hotspots of total species (IHS), index hotspots of threat (IHT) and index hotspots of endemism (IHE). g, Proportion of total species within richness (grey bars) and index (red bars) hotspot types across different thresholds. h, Proportion of total species within richness (grey bars) and index (red bars) hotspot types across different scales. i, Number of species ($n = 1614$) shared among richness hotspots of total species (RHS), richness hotspots of threat (RHT) and richness hotspots of endemism (RHE) defined at scales of $8^\circ \times 8^\circ$. j, Number of species ($n = 2714$) shared among index hotspots of total species (IHS), index hotspots of threat (IHT) and index hotspots of endemism (IHE) at a spatial scale of $8^\circ \times 8^\circ$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Spearman rank correlations between the two diversity measures used to define hotspots (species richness and diversity index) and richness patterns of species belonging to each range-size quartile in all categories of mammal distributions.

Diversity measures	Hotspot types	Number of cells	Total species (%)	Endemic species (%)	Threatened species (%)
Species richness	Total species	473	1953 (37)	480 (21)	272 (25)
	Endemism	147	2371 (45)	860 (38)	430 (39)
	Threat	375	1586 (30)	422 (19)	306 (28)
Diversity index	Total species	464	3730 (71)	1489 (67)	763 (70)
	Endemism	135	2719 (52)	1000 (45)	533 (49)
	Threat	339	3689 (70)	1329 (59)	825 (75)

Table 2

Representation of mammals belonging to the three distribution categories within richness and index hotspot types.

Categories of mammal distributions	Range-size quartiles	Diversity measure	
		Species richness	Diversity index
Total species	1	0.152*	0.703*
	2	0.320*	0.760*
	3	0.662*	0.883*
	4	0.963*	0.676*
Endemic species	1	0.426*	0.625*
	2	0.576*	0.651*
	3	0.683*	0.683*
	4	0.837*	0.694*
Threatened species	1	0.228*	0.658*
	2	0.295*	0.594*
	3	0.375*	0.561*
	4	0.971*	0.751*

moderately small geographic ranges (1st and 2nd range-size quartiles), up to thresholds of 50% (Appendix D). Above that threshold, the number of species included became practically equal for *IH* and *RH*. At different scales, *IH* always protected more species with small geographic ranges than *RH*, except for *IHE* at scales of $8^\circ \times 8^\circ$ where the diversity index matches species richness since the inverse of range-size of endemic species equals 1 (Appendix E). Furthermore, when assessing for efficiency between *IH* and *RH* by comparing the total number of species conserved and the level of congruence across thresholds and scales, we found that *IH* always include a higher number of species with a greater level of congruence than *RH* (Fig. 2g-h). This evidence strongly supports that, irrespective of the threshold used to define hotspots and the scale of analysis, use of the diversity index to identify biodiversity hotspots should be preferred over use of species richness. Indeed, at scales of $8^\circ \times 8^\circ$ i.e., approximately 640,000 km², which is close to the average of global hotspot sizes recognized by Conservation International (Mittermeier et al., 2004), using endemic species richness to define hotspots would lead to loss of significant information for assessing conservation priorities, because the hotspot of endemism showed full congruence with *IHS* and *IHT* (Fig. 2i-j). Thus, by choosing any of these indices, we would be able to protect more species.

Similarly, as Grenyer et al. (2006), we have focused on the use of diversity measures to define biodiversity hotspots, but ignoring political and socio-economic factors commonly considered to set up conservation actions. Therefore, our findings should be interpreted with caution with respect to applied conservation policies. However, we have shown that selecting different diversity measures to define hotspots may strongly affect the achievement of conservation goals. We consider that effectiveness of hotspots for setting up conservation practices can be improved by identifying and overcoming their current limitations. Although we are aware that the use of the index proposed in this work demands

information about species' geographic ranges, we argue that there are several groups of organisms for which this information is currently available, and species protection efforts would profit from the ability of *IH* to include taxa with small geographic ranges compared with the traditional use of species richness. In fact, when comparing the spatial overlap between global biodiversity hotspots (Mittermeier et al., 2004) and *IH*, we notice that a great proportion of the latter are located in areas where biodiversity conservation is not a priority (Appendix F). To conclude, we hope this work contributes to revitalizing progress towards “silver bullet” conservation strategies.

Author contributions

Team leader R.C. conceived and designed the analyses for this study. All other authors discussed the methods and results, and made substantial contributions to the manuscript, revising and commenting on subsequent drafts.

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Appendix A. Global maps of diversity measures used to define hotspots and species richness patterns by range-size quartile across categories of mammal distributions.

Appendix B

Table 1
Spearman rank correlations among categories of mammal distributions according to diversity measures used to define hotspots.

Diversity measure	Categories of mammal distributions	Total species	Endemic species	Threatened species
Species richness	Total species	1	0.23*	0.71*
	Endemic species		1	0.29*
	Threatened species	1		1
Diversity Index	Total species	1	0.80*	0.86*
	Endemic species		1	0.61*
	Threatened species			1

*P < 0.001.

Appendix C

Table 2
Total number of cells identified as being richness or index hotspot types and percentages of spatial overlap among them.

Hotspot types	Number of cells identified as hotspots (%)	Number of cells shared among three hotspot types (%)	Number of cells shared between two hotspot types (%)	Number of cells idiosyncratic to one hotspot type (%)
Richness	903 (100)	9 (1)	74 (8)	820 (91)
Diversity index	558 (100)	103 (18)	174 (31)	281 (51)

Appendix D

Table 3
Number of species by range-size quartile included within richness and index hotspot types at different thresholds.

Hotspot type	Threshold	Range-size quartiles	RH	IH
Total species	5%	1	404	1150
		2	486	1005
		3	720	1131
		4	891	1158
		Total	2501	4444
	10%	1	564	1270
		2	589	1106
		3	793	1199
		4	943	1217
		Total	2889	4792
	25%	1	962	1355
		2	1058	1220
		3	1186	1278
		4	1277	1291
		Total	4483	5144
	50%	1	1168	1366
2		1187	1263	
3		1278	1308	
4		1303	1306	
	Total	4936	5243	
75%	1	1257	1366	
	2	1246	1265	
	3	1312	1313	
	4	1314	1314	
	Total	5129	5258	

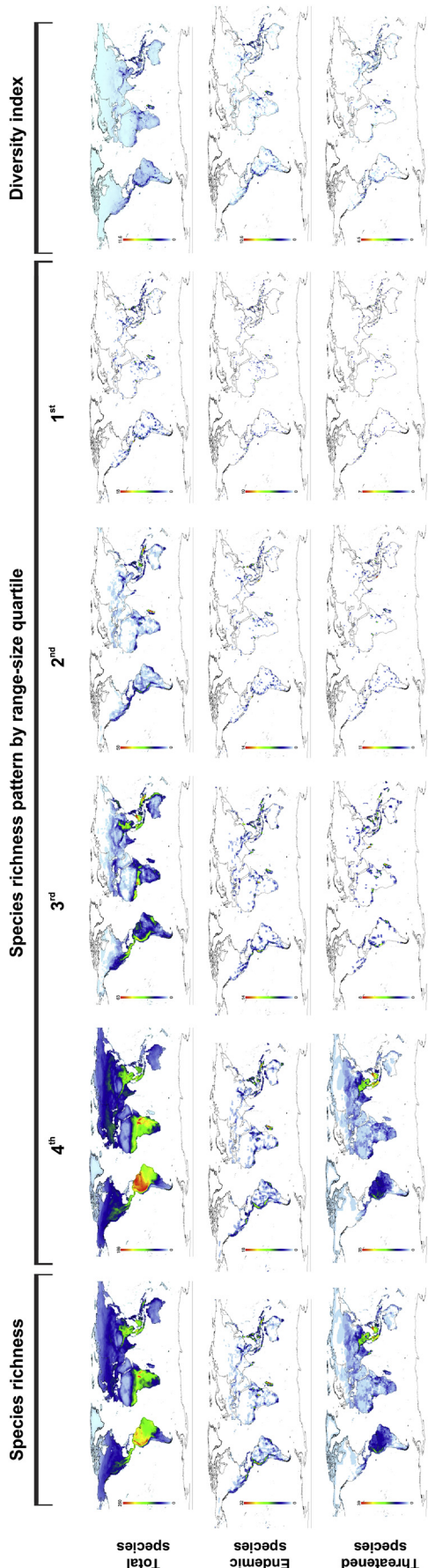


Table 3 (continued)

Hotspot type	Threshold	Range-size quartiles	RH	IH
Endemism	100%	1	1366	1366
		2	1265	1265
		3	1313	1313
		4	1314	1314
		Total	5258	5258
	5%	1	255	374
		2	305	341
		3	277	289
		4	278	297
		Total	1115	1301
	10%	1	344	497
		2	388	420
		3	363	375
		4	376	381
		Total	1471	1673
	25%	1	465	600
2		506	525	
3		472	466	
4		467	457	
	Total	1910	2048	
50%	1	554	600	
	2	559	583	
	3	518	510	
	4	515	501	
	Total	2146	2194	
75%	1	600	600	
	2	583	583	
	3	526	526	
	4	527	515	
	Total	2236	2224	
100%	1	600	600	
	2	583	583	
	3	526	526	
	4	527	527	
	Total	2236	2236	
Threat	5%	1	96	299
		2	132	235
		3	121	183
		4	188	223
		Total	537	940
	10%	1	139	299
		2	167	286
		3	151	208
		4	216	249
		Total	673	1042
	25%	1	230	299
		2	255	292
		3	212	232
		4	262	271
		Total	959	1094
	50%	1	282	299
2		276	292	
3		230	232	
4		273	273	
	Total	1061	1096	
75%	1	299	299	
	2	292	292	
	3	232	232	
	4	273	273	
	Total	1096	1096	
100%	1	299	299	
	2	292	292	
	3	232	232	
	4	273	273	
	Total	1096	1096	

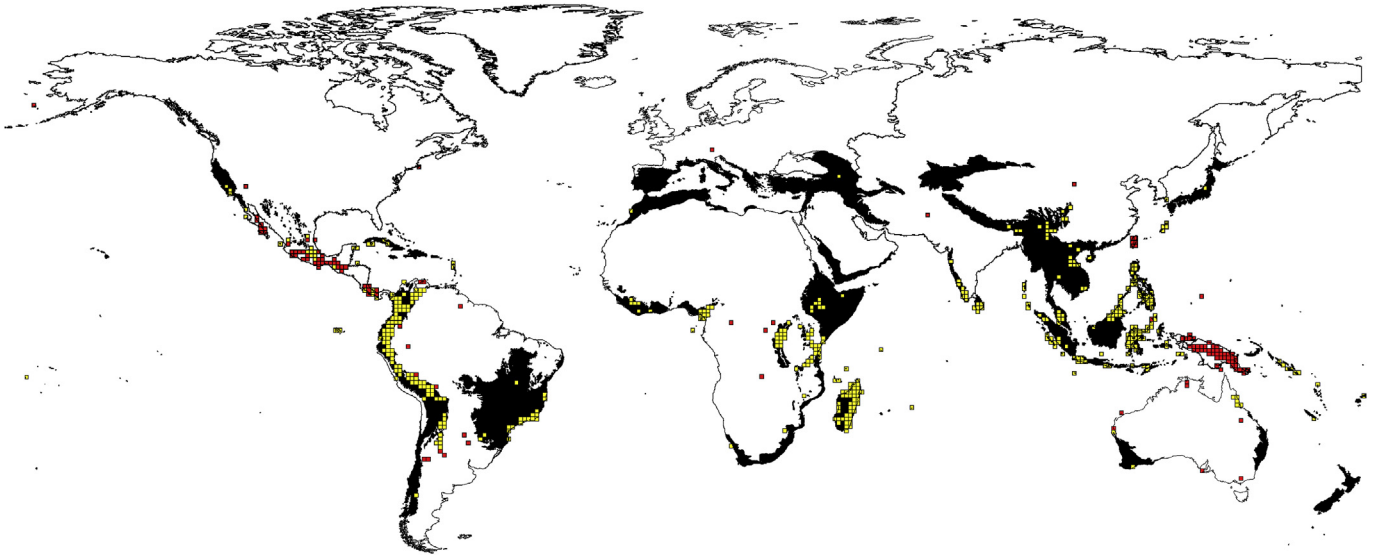
Appendix E

Table 4

Number of species by range-size quartile included within richness and index hotspot types at different spatial scales.

Hotspot type	Scales	Range-size quartiles	RH	IH
Total species	2° × 2°	1	331	834
		2	423	746
		3	624	805
		4	827	937
		Total	2205	3322
	4° × 4°	1	316	612
		2	423	702
		3	585	642
		4	855	887
		Total	2179	2843
	8° × 8°	1	372	579
		2	246	325
		3	268	338
		4	413	602
		Total	1299	1844
	Endemism	2° × 2°	1	130
2			216	241
3			153	165
4			108	106
		Total	607	687
4° × 4°		1	124	129
		2	152	113
		3	164	164
		4	276	242
		Total	616	646
8° × 8°		1	164	164
		2	164	164
		3	109	173
		4	153	184
		Total	418	746
Threat		2° × 2°	1	120
	2		36	64
	3		109	173
	4		153	184
		Total	418	746
	4° × 4°	1	62	174
		2	71	116
		3	110	132
		4	136	128
		Total	379	550
	8° × 8°	1	116	170
		2	60	94
		3	46	51
		4	92	78
		Total	314	393

Appendix F. Spatial overlap between current terrestrial global biodiversity hotspots (areas in black) and index hotspot types (cells in yellow indicate overlapping hotspots and cells in red indicate non-overlapping hotspots).



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