DOI: 10.1111/ddi.12571

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions A Journal of Conservation Biogeography

Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity

Victoria Veach[1] | Enrico Di Minin[2,3] | Federico M. Pouzols[1] | Atte Moilanen[1]

[1]Finnish Centre of Excellence in Metapopulation Biology, Department of Biosciences, University of Helsinki, Helsinki, Finland

[2]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

[3]School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

Correspondence
Victoria Veach, Finnish Centre of Excellence in Metapopulation Biology, Department of Biosciences, University of Helsinki, Helsinki, Finland.
Email: victoria.veach@helsinki.fi

Funding information
ERC-StG, Grant/Award Number: 260393; Academy of Finland, Grant/Award Number: 250444

Editor: Joern Fischer

Abstract

Aim: To quantify and compare species coverage in priority areas for conservation identified using species richness as opposed to approaches that use individual species range maps.

Location: Global.

Methods: We compare the coverage of species when global priority areas for conservation are identified based on (1) twelve species richness maps of all and small-range amphibians, birds and mammals and all and small-range threatened (i.e., vulnerable, endangered and critically endangered) species; (2) weighted range size rarity, a richness measure corrected for range size; and (3) a complementarity-based analysis including species range maps for 21,075 terrestrial vertebrate species listed by the International Union for the Conservation of Nature. We also assessed whether any combination of small-range and/or threatened species richness could be a suitable surrogate for a complementarity-based analysis by assessing species coverage in priority areas located using (1) richness of small-range species only; (2) richness of all threatened species only; and (3) richness of small-range and threatened species.

Results: Our results show clear differences in the spatial pattern of priority areas for conservation among the prioritizations based on species richness, weighted range size rarity and species range maps, with the species richness-based priority areas being highly aggregated in the tropics and the species range map priority areas being more evenly spread among the global terrestrial area. We also find that identifying priority areas for conservation using species richness produces a lower coverage of species than priority areas based on complementarity methods and identified using species range maps, where just one species was left without any protection.

Main Conclusions: As methods and software currently exist for processing large numbers of individual species distribution maps in spatial prioritization, the use of species richness appears to be an unnecessary simplification of biodiversity pattern.

KEYWORDS
complementarity, range size rarity, spatial conservation prioritization, species coverage, species richness, Zonation software

1 | INTRODUCTION

Protected areas are the primary mechanism to protect species from extinction (Margules & Pressey, 2000). Global terrestrial protected area coverage has gradually increased from around 10% in the mid-1990s to 15.4% in 2014 (Juffe-Bignoli et al., 2014) with a target of 17% terrestrial area protection by 2020 (Convention on Biological Diversity 2010). Despite the increase in terrestrial land placed under formal protection, biodiversity continues to be lost at an alarmingly rapid rate with estimates suggesting that current extinction rates are approximately 1,000 times higher than background rates (Pimm et al., 2014) and trends in biodiversity indicators continue to decline as they have for at least the past four decades (Butchart et al., 2010; Secretariat of the Convention on Biological Diversity 2014). Additionally, the current protected area network fails to represent all biodiversity that needs protection (Butchart et al., 2015). The current protected area network, in fact, protects less than 10% of the ranges for 60% of rare amphibians, 50% of rare birds and 44% of rare mammals (Cantú-Salazar, Orme, Rasmussen, Blackburn, & Gaston, 2013) and entirely omits 27% of threatened amphibians, 20% of threatened birds and 14% of threatened mammals (Pimm et al., 2014).

Understanding broad scale biodiversity patterns and identifying priority areas for conservation is an important focus of conservation science (Margules & Pressey, 2000). Understanding where the most important areas for biodiversity are located globally can help allocate limited conservation resources more effectively (Moilanen, Wilson, & Possingham, 2009). Much of the work to understand broad scale biodiversity patterns has used species richness of all, small-range and threatened species to map ‘hot spots’ of species richness (Brooks et al., 2004; Ceballos & Ehrlich, 2006; Grenyer et al., 2006; Jenkins, Pimm, & Joppa, 2013; Jenkins, Van Houtan, Pimm, & Sexton, 2015; Orme et al., 2005; Pimm et al., 2014). Some of these studies have gone on to suggest that small-range species richness is a suitable surrogate to identify priority areas for conservation (Ceballos & Ehrlich, 2006; Orme et al., 2005), and one has identified global conservation priority areas based on small-range vertebrate species richness (Jenkins et al., 2013). However, prioritization approaches based on richness do not always lead to the highest coverage of species in reserve networks (Albuquerque & Beier, 2015; Justus & Sarkar, 2002; Margules, Pressy, & Williams, 2002; Williams et al. 2006a, 2006b). Despite this, species richness, particularly richness of small-range species, continues to be used as a measure of conservation value in identifying global biodiversity hotspots (Ceballos & Ehrlich, 2006; Grenyer et al., 2006; Jenkins et al., 2013; Orme et al., 2005; Pimm et al., 2014) and priority areas for conservation (Jenkins et al., 2013; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). At the global scale, we currently lack evidence showing the differences in species coverage when priority areas are identified using species richness rather than individual species range maps.

In this study, we quantify and compare the coverage of species ranges from six different spatial conservation prioritization analyses to understand whether alternative analysis structures are suitable for well-informed conservation planning. The analyses considered are based on: (1) species richness, the total number of different species present; (2) weighted range size rarity, a richness measure corrected for individual species’ weights and global range size; and (3) complementarity using individual species range maps. We included priority areas based on weighted range size rarity to assess whether it could be a practical alternative to both species richness and a complementarity-based analysis. Prioritizing the landscape based on species richness offers a fast approach with low data and computing requirements. Knowing that species richness patterns are driven by wide-ranging, common species (Brooks et al., 2006; Eken et al., 2004) and that richness-based priority areas fail to maximize species coverage (Albuquerque & Beier, 2015; Justus & Sarkar, 2002; Margules et al., 2002; Williams et al. 2006a, 2006b), this may still be an attractive option when decisions need to be made quickly with limited information and resources. Basing priority areas on range maps for several thousand individual species in a complementarity-based analysis is extremely data intensive and the necessary computing requirements can easily be a limiting factor. Like species richness, a prioritization based on weighted range size rarity requires modest computing power, but unlike species richness, it should better highlight areas where there is a relatively high density of threatened and/or small-range species.

Previous studies have promoted the use of rare and/or threatened species richness as a surrogate for biodiversity (see e.g., Jenkins et al., 2013; Myers et al., 2000; Orme et al. 2005). We implement additional analyses based on species richness subsets including (1) small-range species richness; (2) threatened species richness; and (3) richness of species that are both small-range and threatened. These were conducted to evaluate this claim by assessing species coverage in priority areas based solely on the use of rare and/or threatened species richness. We assessed the difference in coverage achievable for all species, small-range species and threatened species in the 17% highest priority areas, representing a theoretical protection of 17% of terrestrial land area as proposed by the Convention on Biological Diversity in Aichi Target 11 (Convention on Biological Diversity 2010).

2 | METHODS

2.1 | Data

We based our analysis on a set of 21,075 species range maps included in the IUCN Red List of terrestrial vertebrates (IUCN 2014). Range maps for mammals and amphibians were downloaded from the IUCN Red List (IUCN 2014), while range maps for birds were downloaded from BirdLife International’s Data Zone page (BirdlLife International and NatureServe 2013). From the IUCN species database, we selected terrestrial species only, leaving out 79 entirely marine mammal species. At the time of this study, a significant fraction of reptiles remains unassessed and range distribution data are not available (IUCN 2014). Hence, they were not included in the analysis. Distribution data for species were available as GIS polygons, covering known or inferred areas where species occur (IUCN 2014). These distribution polygons are in practice positioned somewhere between the extent of occurrence and the true area of occupancy of the species. All range maps were converted to latitude/longitude coordinate system and rasterized to global high resolution grids (latitude/longitude coordinate system, harmonized to resolution 0.01667 degrees equalling 1.7 km at the Equator) using ARCGIS 10.1 (ESRI 2012) for use in the spatial prioritization analysis (see below).

The original polygon maps contained five discreet categories indicating the likelihood of the species occurring in that location (Brooks et al., 2016; IUCN 2014). In the rasterizing process, we translated these to four categories with a continuous scale from 1 to 0 and assigned pixel values according to the certainty of species presence with less reliable occurrence categories translated into lower values. The data transformation for our raster data is as follows: extant → 1.0, probably extant → 0.5, possibly extant → 0.5, possibly extinct → 0.1 and extinct → 0.0 (Pouzols et al., 2014).

2.2 | Species richness and weighted range size rarity

We produced 12 species richness layers in total: all amphibians, birds and mammals; small-range amphibians, birds and mammals; all critically endangered, endangered and vulnerable species; and small-range critically endangered, endangered and vulnerable species. Species richness was calculated from the rasterized IUCN Red List species range maps (IUCN 2014) by summing the values of each raster grid cell in the IUCN range maps corresponding to each richness layer (i.e., to produce a richness layer for small-range amphibians, we summed the IUCN range maps for small-range amphibians). We defined small-range species as those with a range <50,000 km^2 (Rodrigues et al., 2004; Stattersfield, Crosby, Long, & Wege, 1988). Prior to calculating species richness, we reclassified the pixel values of each raster (described above) from either 0.5 to 1.0 or 0.1 to 0.0 using the Reclassify function in ARCGIS 10.1 (ESRI 2012) to base the species richness calculation on presence/absence data rather than probability of occurrence.

The weighted range size rarity (Williams, Gibbons et al., 1996) map included in this study was created automatically from the Zonation spatial prioritization analysis (Moilanen et al., 2014) based on 21,075 species range maps. Weighted range size rarity for each cell, *i*, is defined as

$$wrsr_i = \sum_j w_j q_{ij},$$

where w_j is the weight assigned to species *j* in the prioritization and q_{ij} is the fraction of species *j*'s range falling within cell *i* (Moilanen et al., 2014). This measure lowers the contribution of wide ranging species to overall species richness and highlights the areas that have a relatively high proportion of narrow-range species.

2.3 | Spatial conservation prioritization

We used the ZONATION software for spatial conservation prioritization to identify priority areas for conservation action. ZONATION implements analytical methods for broad-scale high-resolution spatial prioritization and works by creating a hierarchical ranking which starts from the full landscape and generates a priority ranking by iteratively ranking and removing the grid cells in the order which cause the least loss in aggregate conservation value (Lethomäki & Moilanen, 2013; Moilanen et al., 2005, 2011, 2014; Pouzols et al., 2014).

During the prioritization process, the landscape-level coverage of each feature (i.e., species) declines by a small fraction after the ranking and subsequent removal of each grid cell in which the feature occurs. This loss is tracked and is used to balance the relative importance of the remaining occurrences of features (Moilanen et al., 2005, 2011, 2014). This balancing operation allows ZONATION to retain all or almost all features throughout the prioritization. There are several options for how ZONATION aggregates marginal loss of conservation value. Here we used the additive benefit function (ABF) variant of analysis (Moilanen, 2007), which bases ranking on minimization of expected extinction rates summed across species (Moilanen et al., 2011, 2014). As the ABF has an additive (sum) structure, it tends to emphasize locations where many species (both common and rare) occur (Moilanen et al., 2011, 2014).

2.4 | Analysis variants

We conducted six separate spatial conservation planning assessments (Table 1). In all assessments, the content of the data was restricted to non-Antarctic terrestrial areas using a binary land/water mask (downloaded from and processed by WorldGrids (http://www.worldgrids.org) and to the areas falling outside of medium intensive and intensive cropland, urban and peri-urban areas for the year 2000 (Van Asselen & Verburg, 2013). The analysis area in the small-range species richness, threatened species richness and small-range and threatened species richness prioritizations were further restricted to the combined extent of the species richness layers included in that assessment using a hierarchical analysis mask (i.e., the analysis area in the prioritization based on small-range species richness was restricted to the combined extent of richness layers for small range amphibians, birds and mammals). In contrast to a binary analysis area mask, a hierarchic mask can contain several different values where grid cells with a low value will be ranked and removed first and grid cells with a higher value will be ranked and removed last (i.e., forced into the top fraction of the priority areas) regardless of relative conservation value (Moilanen et al., 2014). Using the hierarchic mask ensured that the overall analysis area was the same in all analysis variants even though the combined extent of the small-range and/or threatened species richness layers was less than the total terrestrial surface. In the analyses based on small-range and/or threatened species richness, areas covered by the richness layers were given a higher value in the hierarchic mask while other terrestrial areas not covered by the richness layers were given a lower value.

We used a condition transformation (Leathwick, Moilanen, Ferrier, & Julian, 2010; Moilanen et al., 2014) in all analyses to adjust the species richness layers and range maps to reflect land-use effects for the year 2040. The condition layer was based on the land-use model for the year 2040 created by Van Asselen and Verburg (2013) as in Pouzols et al. (2014). Each land-use was assigned a value between

TABLE 1 Data, weights and analysis area extent included in each of the six analysis variants

Analysis	Data used	Feature weights	Extent of analysis area
Species richness	12 species richness layers: all amphibians, birds and mammals; small-range amphibians, birds and mammals; all critically endangered, endangered and vulnerable species; and small range critically endangered, endangered and vulnerable species	All layers equally weighted with weight 1.	Global, total terrestrial surface
Small range species richness	Species richness of small range amphibians, birds and mammals	All layers equally weighted with weight 1.	Global, analysis area restricted to the combined extent of these layers (7.44% of total area)
Threatened species richness	Species richness of all critically endangered, endangered and vulnerable species	All layers equally weighted with weight 1.	Global, analysis area restricted to the combined extent of these layers (86.84% of total area)
Small range + threatened species richness	Species richness of small range amphibians, birds and mammals and all critically endangered, endangered and vulnerable species	All layers equally weighted with weight 1.	Global, analysis area restricted to the combined extent of these layers (87.17% of total area)
Species range maps	21,671 IUCN species range maps	Critically endangered = 8; Endangered = 6; Vulnerable = 4; Near Threatened = 2; Least Concern = 1; Data Deficient = 4 (Pouzols et al., 2014)	Global, total terrestrial surface
Weighted range size rarity	Weighted range size rarity	Map produced automatically from analysis 5	Global, total terrestrial surface

0 and 1 to reflect its naturalness, with 0 representing areas that are severely degraded and/or altered from the natural habitat and 1 representing pristine conditions. Applying this land-use model as a condition transformation helped to reduce commission and omission errors in the species range maps by indicating the areas that are mostly unsuitable for red-listed species due to habitat loss or degradation, and thus ranking and removing those areas early in the prioritization. The land-use values in the condition layer were previously defined by Pouzols et al. (2014).

We conducted our assessment of species coverage at the 17% target for terrestrial land protection set under Aichi target 11 (CBD 2010). The analysis area for priorities based on species richness, species range maps and weighted range size rarity are identical and cover the entire terrestrial surface minus the extent of agriculture and urban areas, and so in these analyses, the top 17% priority areas correspond to 17% of the total analysis area. The analysis area for priorities based on small-range species richness, threatened species richness and small-range and threatened species richness is 7.44%, 86.84% and 87.17%, respectively, of the total analysis area. In the small-range species richness analysis, species coverage was assessed in the full extent of the small-range species richness layers as they covered only a fraction of the area proposed for terrestrial land protection in Aichi target 11. In the threatened species richness and small-range and threatened species richness analyses, we assessed species coverage at the fraction of the extent covered by the richness layers that is equal to 17% of the full global analysis area. For the analysis based on threatened species richness, this equals 19.57% of the extent of the analysis area. For the analysis based on small-range and threatened species richness, this equals 19.50% of the analysis area.

The original species richness and weighted range size rarity analyses do not contain any species-specific information, and, thus we are not able to determine species coverage in the priority areas based on these datasets. To solve this issue, we conducted a solution loading analysis in ZONATION. With a solution loading analysis, it is possible to evaluate the performance of alternative data in a priority ranking developed under different analysis settings and/or data. In this study, we loaded the output rank maps from the species richness-based and weighted range size rarity-based prioritizations each in a new analysis containing all 21,075 species range maps. These analyses proceed by ranking and removing the grid cells in the same order as they were ranked and removed in the loaded output rank map. The output of these two new analyses allows us to evaluate the species coverage of all 21,075 species in priority areas based on either species richness or weighted range size rarity. To obtain full information about species-specific coverage within the priority areas in the small-range species richness, threatened species richness and small-range and threatened species richness analyses, we included all 21,075 species range maps in the analysis with a weight 0.0. In ZONATION, a zero-weighted feature will not influence the priority ranking, but the coverage of the feature's range will be tracked throughout the analysis, thereby allowing evaluation of surrogacy effects (Di Minin & Moilanen, 2014). Post-processing of the data was carried out in the statistical software R v. 3.0.2 (R Core Team 2013) using the packages GGPLOT (Wickham, 2009) and RASTERVIS (Lamigueiro & Hijmans, 2014).

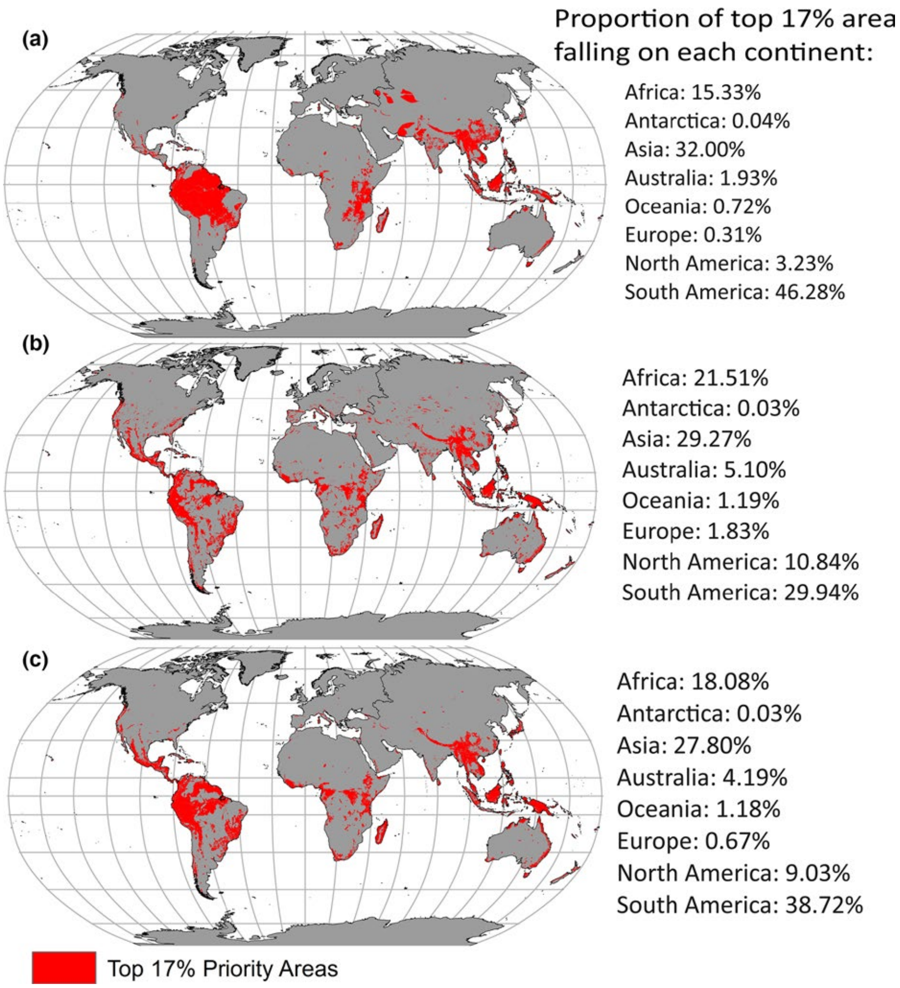

FIGURE 1 Spatial pattern of 17% highest priority areas for conservation based on (a) species richness, (b) individual species range maps and (c) weighted range size rarity. The numbers to the right of each map show the proportion of the top 17% priority areas that fall on each continent

3 | RESULTS

Prioritizations made using twelve species richness layers, weighted range size rarity and a full complementarity analysis based on 21,075 individual species range maps all resulted in different spatial patterns for global conservation priority. High priority areas were most aggregated in the species richness-based analysis and least aggregated in the species range map-based analysis (Figure 1). In the species richness-based prioritization, 15.33%, 32% and 46.28% of the 17% highest priority areas were confined to Africa, Asia and South America, respectively (Figure 1a). Priority areas highlighted by the individual species range map-based prioritization; however, identified important areas outside the tropics as well (Figure 1b). For example, of the 17% highest priority areas based on individual range maps, 10.84% and 5.10% occurred in North America and Australia, respectively, as opposed to only 3.23% and 1.93% that occurred on those continents in the priority areas based on species richness (Figure 1a and b). Priority areas highlighted by the weighted range size rarity layer showed a pattern that is intermediate between the analyses based on species richness and individual species range maps: the priority areas showed high aggregation in the tropics, but some high priority areas were also located outside the tropics in North America, Southern Europe, Australia and New Zealand (Figure 1c).

In all prioritizations, the maximum mean species coverage at the start of the analysis was 80% (Figures 2 and 3). This is a result of the adjustment to the species ranges that occurred after applying the landscape condition layer based on the land-use model for the year 2040 (Van Asselen & Verburg, 2013). Future land-use conditions resulted in an expected 20%–32% reduction in the species ranges potentially available for protection at the beginning of the prioritization (i.e., between 20% and 32% of species' ranges are expected to be lost due to unfavourable land-use change). At the 17% target for terrestrial land protection, prioritizations based on species richness measures systematically performed poorer for small-range species (Figure 2b), threatened species (Figure 2c) and small-range threatened species (Figure 2d) than prioritizations based on individual species range maps or weighted range size rarity (Figure 2, Tables 2 and 3). Mean species coverage in the priority areas based on individual species range maps and weighted range size rarity were similar across taxonomic groups

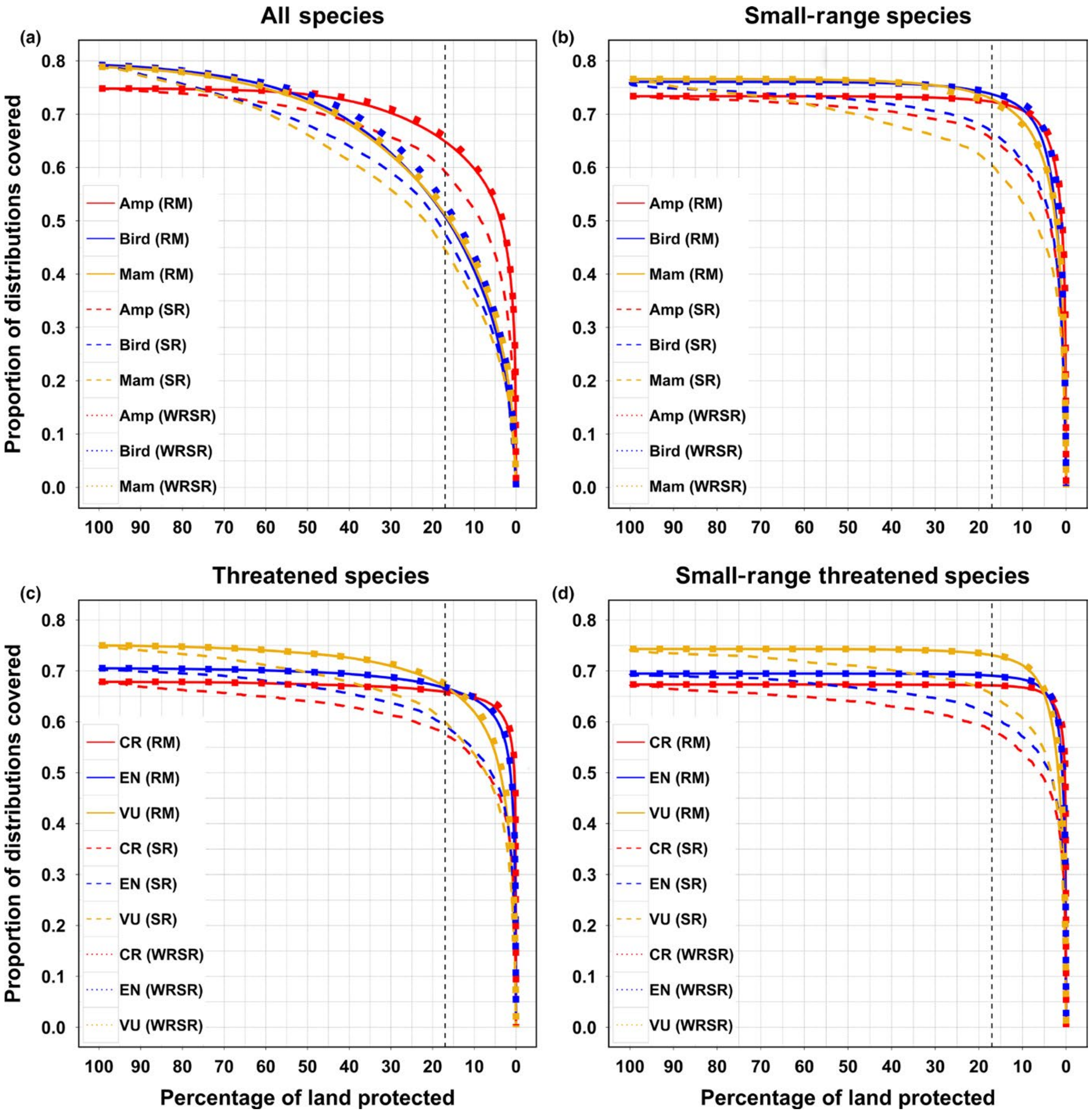

FIGURE 2 Performance curves of the ZONATION analyses based on species richness (SR), species range maps (RM) and weighted range size rarity (WRSR), which describe the mean coverage of species range maps as a function of land area under conservation. Solid lines show the mean species coverage for the spatial conservation prioritization based on RM. Dashed lines show the mean species coverage for the prioritization based on SR. Dotted lines show the mean species coverage in the WRSR layer. Note that the solid and dotted lines appear on top of one another in all panels. They are, however, two separate lines. Panels a and b show the mean coverage of all (a) and small range (b) amphibians (red lines), birds (blue lines) and mammals (yellow lines). Panels c and d show the mean coverage of all (c) and small range (d) critically endangered (red lines), endangered (blue lines) and vulnerable (yellow lines) species. The vertical dotted line shows the 17% target for terrestrial land protection

and IUCN threatened status categories at the Aichi 17% target for terrestrial land protection (Figure 2, Table 2).

A comparison of prioritizations based on three alternative species richness datasets showed that species richness of both small-range and threatened species generally performed better as a proxy for spatial conservation prioritization than richness of either small-range species or threatened species alone (Figure 3, Table 2). In the 17% highest priority areas, those based on both small-range and threatened species richness had an overall mean species coverage of 49.8% compared to 39.5% and 33.4% in priority areas based on small-range

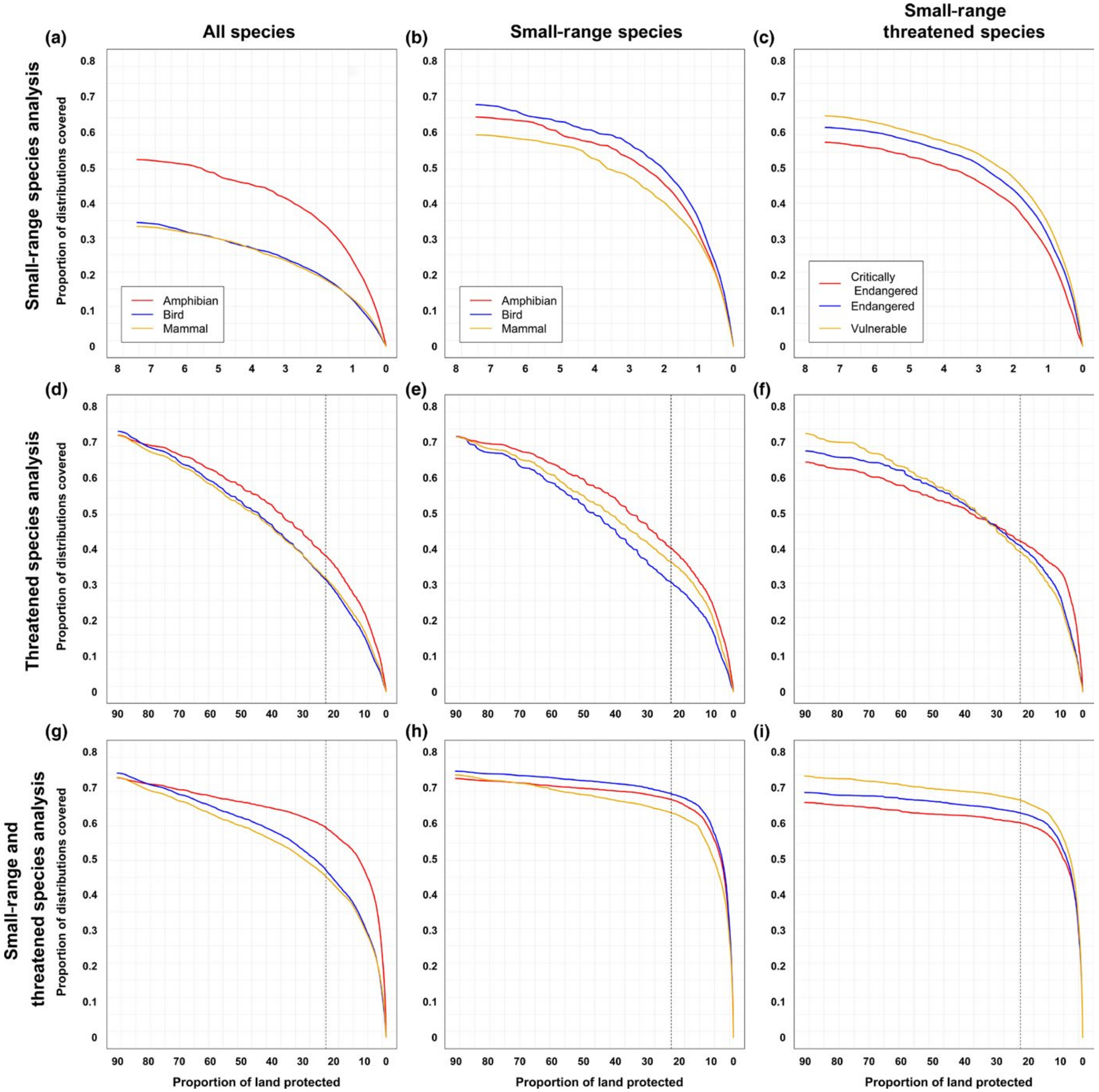

FIGURE 3 Performance curves of the ZONATION analyses based on small range species richness only (panels a–c), threatened species richness only (panels d–f) and small range and threatened species richness (panels g–i). The left column shows mean species coverage for all amphibians (red lines), birds (blue lines) and mammals (yellow lines). The middle column shows mean coverage for small range amphibians, birds and mammals. The right column shows mean coverage for small range critically endangered (red lines), endangered (blue lines) and vulnerable (yellow lines) species. The vertical dotted line in the graphs in the bottom two rows correspond to the area equal to the Aichi 17% target for terrestrial land protection

or threatened species richness only, respectively (Table 2). This pattern holds when examining the mean species coverage of each individual taxonomic and IUCN conservation category in the top 17% priority areas. Across each taxonomic and conservation category, priority areas based on both small-range and threatened species richness had the highest mean species coverage of the three species richness subsets while priority areas based on threatened species richness only had the lowest mean species coverage (Figure 3, Table 2). In priority areas based on small-range species richness only, the mean species coverage was similar to that in priority areas based on both small-range and threatened species richness, with most taxonomic and threatened categories having a relatively small difference in mean species coverage (Table 2). Priority areas based on threatened species richness only, however, had a very large difference in mean species coverage across all individual taxonomic and IUCN threat categories compared to those based on both small-range and threatened species richness

TABLE 2 Average species coverage in each group at the Aichi 17% land cover target for terrestrial protected areas

	Total number of species	Species richness (%)	Small range species richness (%)[a]	Threatened species richness (%)	Small range and threatened species richness (%)	Species range maps (%)	Weighted range size rarity (%)
All species	21,075	49.6	39.5	33.4	49.8	54.9	56.1
All amphibian	6,117	58.7	52.3	38.1	58.7	64.8	65.5
All bird	9,724	46.9	34.7	31.3	46.8	50.7	52.6
All mammal	5,234	44.0	33.6	31.8	45.0	51.0	51.6
Small range amphibian	4,336	65.1	64.2	40.2	66.6	72.3	72.3
Small range bird	2,378	66.4	67.7	30.7	68.2	73.7	73.9
Small range mammal	1,760	60.1	59.2	36.4	62.9	72.8	72.0
All CR	784	57.2	55.2	42.0	59.4	65.9	65.8
All EN	1,524	59.0	56.8	41.3	61.1	66.6	66.7
All VU	1,792	59.6	54.3	39.5	61.1	66.8	67.2
Small range CR	741	58.0	57.1	42.1	60.1	67.1	67.2
Small range EN	1,350	60.9	61.3	40.9	62.8	69.0	68.9
Small range VU	1,303	65.1	64.5	39.1	66.4	73.1	73.1

[a] Total area covered by small-range species layers, 7.44% of terrestrial land.

TABLE 3 The number of species (per cent of total) in each group left without protection at the Aichi 17% land cover target for terrestrial protected areas

	Total number of species	Species richness	Small range species richness[a]	Threatened species richness	Small range and threatened species richness	Species range maps	Weighted range size rarity
All species	21,075	749 (3.55%)	819 (3.89%)	3272 (15.53%)	473 (2.24%)	1 (0.005%)	165 (0.78%)
All amphibian	6,117	316 (5.17%)	294 (4.81%)	1352 (22.10%)	212 (3.47%)	1 (0.02%)	24 (0.39%)
All bird	9,724	94 (0.97%)	117 (1.20%)	914 (9.40%)	58 (0.60%)	0	19 (0.19%)
All mammal	5,234	339 (6.48%)	408 (7.80%)	1006 (19.22%)	203 (3.88%)	0	122 (2.33%)
Small range amphibian	4,336	241 (5.56%)	223 (5.14%)	1080 (24.91%)	173 (3.99%)	1 (0.02%)	7 (0.16%)
Small range bird	2,378	32 (1.35%)	37 (1.55%)	542 (22.79%)	25 (1.05%)	0	2 (0.08%)
Small range mammal	1,760	139 (7.90%)	136 (7.73%)	510 (28.98%)	102 (5.80%)	0	25 (1.42%)
All CR	784	60 (7.65%)	52 (6.63%)	182 (23.21%)	38 (4.85%)	0	2 (0.25%)
All EN	1,524	61 (4.00%)	63 (4.13%)	260 (17.06%)	38 (2.49%)	0	7 (0.46%)
All VU	1,792	54 (3.01%)	65 (3.63%)	313 (17.47%)	48 (2.68%)	0	8 (0.45%)
Small range CR	741	58 (7.83%)	49 (6.61%)	180 (24.29%)	37 (4.99%)	0	0
Small range EN	1,350	54 (4.00%)	54 (4.00%)	247 (18.30%)	34 (2.52%)	0	2 (0.15%)
Small range VU	1,303	84 (6.45%)	43 (3.30%)	270 (20.72%)	36 (2.76%)	0	0

[a] Total area covered by small range species layers, 7.44% of terrestrial land.

(Figure 3, Table 2). The mean species coverage in areas identified using threatened species richness only was between 15% and 38% lower than in areas identified using both small-range and threatened species richness (Table 2).

The mean species coverage in the 17% highest priority areas based on small-range and threatened species richness is similar to that in the areas based on total species richness, and may thus serve as a suitable surrogate for this measure (Figures 2 and 3, Table 2). However, small-range and threatened species richness is unlikely to be a suitable surrogate for individual species range maps or weighted range size rarity, as these measures were able to retain an overall higher mean species coverage in the top priority areas (Figures 2 and 3, Table 2).

Differences between methods persist also when considering the number of species left without any protection in the top 17% of the terrestrial landscape. Of the four analyses based on species richness, the proportion of species left without any coverage at the 17% target for terrestrial land protection was lowest in the small-range and threatened species richness analysis (Table 3). Nevertheless, the number of species left without protection in this analysis was much higher than in the prioritizations based on either weighted range size rarity or individual species range maps. While the mean species coverage was similar in the analyses based on individual species range maps or weighted range size rarity (Figure 2, Table 2), individual species range maps performed much better in terms of the absolute number of species protected. The priority areas based on individual species range maps left just one species without any coverage at the 17% target whereas the priority areas based on weighted range size rarity left a total of 165 species without coverage in the same fraction of the landscape (Table 3).

4 | DISCUSSION

As conservation resources are inadequate, it is vital to use the most appropriate data and tools to maximize species protection. Our results suggest that basing global priority areas for conservation on species richness layers will lead to lower mean coverage of species compared to when complementarity methods are used to identify priority areas. While the quality of the information on the distribution of species at the global level still needs to be improved (Di Minin & Toivonen, 2015; Meyer, Kreft, Guralnick, & Jetz, 2015), identifying priority areas using species range maps (Brooks et al., 2015) or newly developed species distribution models (Jetz, McPherson, & Guralnick, 2012) in spatial conservation prioritization will maximize coverage of species distributions. Sophisticated methods to identify priority areas for conservation actions based on individual species range or distribution models are already available for this purpose (e.g., Zonation—Moilanen et al., 2005, 2014; Marxan—Ball, Possingham, & Watts, 2009).

Regional and global scale studies have shown that complementarity-based methods are better able to represent more species in a smaller area (Kati et al., 2004; Reyers, Van Jaarsveld, & Krïger, 2000; Virolainen et al., 2000; Williams, Gibbons et al., 1996). Still, recent literature concerning global conservation priority areas suggests that small-range and/or threatened species richness could be used to locate priority areas for conservation (Ceballos & Ehrlich, 2006; Jenkins et al., 2013). In fact, recent work by Jenkins et al. (2013) suggests that conservation priority areas based on small-range vertebrate richness are able to also protect large proportions of all terrestrial amphibians, birds and mammals and that focusing conservation efforts on richness of small-range species can help prevent extinctions. In contrast, we show here that species richness, including small-range species richness and threatened species richness, is not an effective surrogate for other biodiversity. Global priority areas identified with species richness layers, in fact, had much lower average species range coverage compared to priority areas identified based on complementarity methods and individual species range maps.

There are, of course, significant trade-offs in data quality and availability that need to be considered when determining which criterion to use to identify conservation priority areas (Di Minin & Toivonen, 2015). The three approaches (species richness, species range maps, weighted range size rarity) explored in this study each have different data requirements which may influence the decision to use one approach over another. The species richness hotspot method is convenient as species richness is relatively easy to measure (Fleishman, Noss, & Noon, 2006), spatial data are not needed across the full area to calculate species richness locally, and broad-scale analyses can be performed with relatively little computing power or sophistication. However, species richness reduces the highly multidimensional entity of biodiversity into a single dimensional measure and removes all species-specific information (Fleishman et al., 2006). Furthermore, species richness patterns are highly influenced by the distributions of common, wide-ranging species (Brooks et al., 2006; Eken et al., 2004); thus, a conservation priority area network based on species richness might over-represent common, wide-ranging species and under-represent rare, small-range species while overall failing to maximize biodiversity coverage.

Weighted range size rarity, which we also assessed here, could be one relatively quick and easy alternative to using species richness to identify priority areas for conservation. Conceptually, weighted range size rarity is a richness like measure where the contribution of each species has been adjusted to reflect the species weight and the global range (or population) size prior to summing across all individual species (Williams, Prance, Humphries, & Edwards, 1996). Our results show that priority areas based on the weighted range size rarity map achieve average species coverage that is similar to that of priority areas based on individual species range maps. Nevertheless, the analysis based on weighted range size rarity fails to cover all species, because range-size rarity still is a one-dimensional simplification of biodiversity, albeit a more informative one than species richness. Consequently, priority areas based on individual species range maps still perform best.

As with previous global conservation planning assessments, a number of caveats need to be highlighted in this study. Species range maps such as the ones used in this analysis are susceptible to commission errors (when a species is mistakenly thought to be present) and omission errors (when a species is mistakenly thought to be absent), which may have affected our estimates of species coverage (Rondinini, Wilson, Boitani, Grantham, & Possingham, 2006). However, applying a high-quality land-use and land-use change model to improve the individual species range maps should certainly help reduce both commission and omission errors because selected areas are less likely to be those where species are absent owing to anthropogenic habitat loss. At the same time, availability of broad-scale high-resolution species distribution models is increasing (Jetz et al., 2012), and our present assessment could be improved in the future when this information becomes freely available.

The species richness layers used in this study were derived from the individual species range maps, implying that these richness layers are of relatively high quality. Nevertheless, we find that using species richness layers in spatial conservation prioritization will potentially lead to decreased coverage for many species. This reinforces that individual species range maps, such as the ones available from the IUCN, or other more refined species distribution models are a more preferable basis for spatial conservation prioritization. Finally, we used fine-resolution rasterized versions of the IUCN species range maps as a small cell size best approximates the shapes of the original polygons. We expect that using a coarser resolution would produce similar prioritization results, as has been found previously (see e.g., Pouzols et al., 2014).

This work evaluated the potential effectiveness of priority areas by examining how well they cover species range maps: this is a basic function of conservation areas as species cannot be protected where they do not occur. Nevertheless, coverage is just one of several ways that can be used to judge the effectiveness of a protected area. In order to deem a protected area successful, other factors may need to be considered, including ecosystem function and community structure (Barnes et al., 2014), ecosystem services (Kukkala & Moilanen, 2016), animal populations and habitat condition, and the effect of habitat loss and degradation in the broader landscape outside the protected area (Leverington, Costa, Pavese, Lisle, & Hockings, 2010). How effective a protected area is can also be evaluated with metrics related to the social benefit, such as protection of cultural values, socioeconomic impacts and effectiveness of the management in protected areas (Eklund & Cabeza, 2016; Leverington et al., 2010). Finding the best areas to protect biodiversity is a challenging task, especially when resources are limited and the human population continues to place expanding pressures on the landscape. Planning for new protected areas, as well as evaluating existing areas, should also take these additional factors into consideration.

5 | CONCLUSIONS

Our results confirm that identifying priority areas for conservation action using species range maps increases average species coverage as compared to priority areas identified using any form of species richness. The results show that priority areas based on species richness are more aggregated and protect fewer species than those identified using individual species range maps. Priority areas based on weighted range size rarity have a mean species coverage that is similar to the analyses based on individual species range maps. Potentially, this makes the weighted range size rarity layer map an important improvement over the species richness methods used in this study. However, priority areas based on the weighted range size rarity layer still leave some species without protection, showing that prioritization methods based on individual species range maps are able to cover the largest number of species. We do not claim that the priority areas produced from the IUCN range maps in this study should be the focus of future conservation efforts, as factors such as threats and costs should inform priorities as well. We simply show how using species richness to define conservation priority areas can negatively impact species coverage compared to when priority areas are based on single species range maps. Presently available methods and software for processing large numbers of fine-resolution species distribution maps in spatial prioritization greatly complement and improve upon approaches using species richness alone.

ACKNOWLEDGEMENTS

We thank Tuuli Toivonen for assistance in data preparation and CSC-IT Center for Science, Ltd of the Ministry of Education, Science and Culture of Finland for high-performance computing services. We also thank Henna Fabritius for helpful and insightful comments on earlier versions of this manuscript. We were supported by the ERC-StG grant 260393 to A.M., F.M.P, and E.D.M. (project GEDA). V.V. and A.M. thank the Academy of Finland Centre of Excellence programme 2012–2017, grant 250444. E.D.M. thanks the Academy of Finland 2016–2019, Grant 296524, for support.

AUTHOR CONTRIBUTIONS

VV, EDM, and AM conceived the ideas; FMP prepared data for the analysis; VV conducted the analysis; VV, EDM, and AM interpreted the results; and VV wrote the manuscript with input from EDM and AM.

REFERENCES

Albuquerque, F., & Beier, P. (2015). Global patterns and environmental correlates of high-priority conservation areas for vertebrates. *Journal of Biogeography*, *42*, 1397–1405.

Ball, I. R., Possingham, H. P., & Watts, M. (2009). Marxan and relatives: Software for spatial conservation prioritisation. Chapter 14. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritisation: Quantitative methods and computational tools* (pp. 185–195). Oxford, UK: Oxford University Press.

Barnes, A. D., Jochum, M., Mumme, S., Haneda, N. F., Farajallah, A., Widarto, T. H., & Brose, U. (2014). Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications*, *5*, 5351.

BirdLife International and NatureServe (2013). *Bird species distribution maps of the world*. Version 3.0. Retrieved from http://www.birdlife.org/datazone/info/spcdownload

Brooks, T. M., Akçakaya, H. R., Burgess, N. D., Butchart, S. H. M., Hilton-Taylor, C., Hoffmann, M., … Young, B. E. (2016). Analysing biodiversity and conservation knowledge products to support regional environmental assessments. *Scientific Data*, *3*, 160007.

Brooks, T. M., Bakarr, M. I., Boucher, T., Da Fonseca, G. A. B., Hilton-Taylor, C., Hoekstra, J. M., … Stuart, S. N. (2004). Coverage provided by the global protected area system: Is it enough? *BioScience*, *54*(12), 1081–1091.

Brooks, T. M., Butchart, S. H. M., Cox, N. A., Heath, M., Hilton-Taylor, C., Hoffmann, M., … Smart, J. (2015). Harnessing biodiversity and conservation knowledge products to track the Aichi Targets and Sustainable Development Goals. *Biodiversity*, *16*(2–3), 157–174.

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., … Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58–61.

Butchart, S. H. M., Clarke, M., Smith, R. J., Sykes, R. E., Scharlemann, J. P. W., Harfoot, M., … Burgess, N. D. (2015). Shortfalls and solutions for meeting national and global conservation area targets. *Conservation Letters*, *8*(5), 329–337.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., … Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, *328*, 1164–1168.

Cantú-Salazar, L., Orme, C. D. L., Rasmussen, P. C., Blackburn, T. M., & Gaston, K. J. (2013). The performance of the global protected area system in capturing vertebrate geographic ranges. *Biodiversity and Conservation*, *22*(4), 1033–1047.

Ceballos, G., & Ehrlich, P. R. (2006). Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(51), 19374–19379.

Convention on Biological Diversity (2010). *Report of the tenth meeting of the Conference of the Parties to the Convention on Biological Diversity*. Montreal, Canada. pp. 1–353.

Di Minin, E., & Moilanen, A. (2014). Improving the surrogacy effectiveness of charismatic megafauna with well-surveyed taxonomic groups and habitat types. *Journal of Applied Ecology*, *51*, 281–288.

Di Minin, E., & Toivonen, T. (2015). Global protected area expansion: Creating more than paper parks. *BioScience*, *65*, 637–638.

Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Fishpool, L. D. C., Foster, M., … Tordoff, A. (2004). Key biodiversity areas as site conservation targets. *BioScience*, *54*(12), 1110–1118.

Eklund, J., & Cabeza, M. (2016). Quality of governance and effectiveness of protected areas: Crucial concepts for conservation planning. *Annals of the New York Academy of Sciences*. https://doi.org/10.1111/nyas.13284

ESRI (2012). *ArcGIS desktop: Release 10.1*. Redlands, CA: Environmental Systems Research Institute.

Fleishman, E., Noss, R. F., & Noon, B. R. (2006). Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators*, *6*, 543–553.

Grenyer, R., Orme, C. D. L., Jackson, S. F., Thomas, G. H., Davies, R. G., Davies, T. J., … Owens, I. P. F. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature*, *444*(7115), 93–96.

IUCN (2014). *The IUCN red list of threatened species*. Version 2014.2. Retrieved from http://www.iucnredlist.org

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(28), E2602–E2610.

Jenkins, C. N., Van Houtan, K. S., Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(16), 5081–5086.

Jetz, W., McPherson, J. M., & Guralnick, R. P. (2012). Integrating biodiversity distribution knowledge: Toward a global map of life. *Trends in Ecology & Evolution*, *27*, 151–159.

Juffe-Bignoli, D., Burgess, N. D., Bingham, H., Belle, E. M. S., de Lima, M. G., Deguignet, M., … Kingston, N. (2014). *Protected planet report 2014*. Cambridge, UK: UNEP-WCMC.

Justus, J., & Sarkar, S. (2002). The principle of complementarity in the design of reserve networks to conserve biodiversity: A preliminary history. *Journal of Bioscience*, *27*(4 suppl 2), 421–435.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., & Lebrun, P. (2004). Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biological Conservation*, *120*(4), 471–480.

Kukkala, A. S., & Moilanen, A. (2016). Ecosystem services and connectivity in spatial conservation prioritization. *Landscape Ecology*, *32*, 5–14. https://doi.org/10.1007/s10980-016-0446-y

Lamigueiro, O. P., & Hijmans, R. (2014). rasterVis. R package version 0.31. Retrived from https://doi.org/10.5281/zenodo.12394.

Leathwick, J. R., Moilanen, A., Ferrier, S., & Julian, K. (2010). Complementarity-based conservation prioritization using a community classification, and its application to riverine ecosystems. *Biological Conservation*, *143*, 984–991.

Lethomäki, J., & Moilanen, A. (2013). Methods and framework for spatial conservation prioritization using Zonation. *Environmental Modelling and Software*, *47*, 128–137.

Leverington, F., Costa, K. L., Pavese, H., Lisle, A., & Hockings, M. (2010). A global analysis of protected area management effectiveness. *Environmental Management*, *46*, 685–698.

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405*(6783), 243–253.

Margules, C. R., Pressy, R. L., & Williams, P. H. (2002). Representing biodiversity: Data and procedures for identifying priority areas for conservation. *Journal of Bioscience*, *27*(Suppl. 2), 309–326.

Meyer, C., Kreft, H., Guralnick, R., & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nature Communications*, *6*(8221), 1–8.

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. *Biological Conservation*, *134*(4), 571–579.

Moilanen, A., Anderson, B. J., Eigenbrod, F., Heinemeyer, A., Roy, D. B., Gillings, S., … Thomas, C. D. (2011). Balancing alternative land uses in conservation prioritization. *Ecological Applications*, *21*(5), 1419–1426.

Moilanen, A., Franco, A. M. A., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. (2005). Prioritizing multiple-use landscapes for conservation: Methods for large multi-species planning problems. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1575), 1885–1891.

Moilanen, A., Pouzols, F. M., Meller, L., Veach, V., Arponen, A., Leppänen, J., & Kujala, H. (2014). *Zonation spatial conservation planning methods and software v.4*. Retrieved from http://cbig.it.helsinki.fi/software/zonation.

Moilanen, A., Wilson, K. A., & Possingham, H. P. (2009). *Spatial conservation prioritization*. Oxford: Oxford University Press.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858.

Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., … Owens, I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, *436*(7053), 1016–1019.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., … Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752.

Pouzols, F. M., Toivonen, T., Di Minin, E., Kukkala, A. S., Kullberg, P., Kuusterä, J., … Moilanen, A. (2014). Global protected area expansion is compromised by projected land-use and parochialism. *Nature*, *516*, 383–386.

R Core Team (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reyers, B., Van Jaarsveld, A. S., & Krïger, M. (2000). Complementarity as a biodiversity indicator strategy. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 505–513.

Rodrigues, A. S. L., Andelmann, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., … Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*, 640–643.

Rondinini, C., Wilson, K. A., Boitani, L., Grantham, H., & Possingham, H. P. (2006). Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, *9*, 1136–1145.

Secretariat of the Convention on Biological Diversity. (2014). Global Biodiversity Outlook 4. Montreal, CA. 155 pages.

Stattersfield, A. J., Crosby, M. J., Long, A. J., & Wege, D. C. (1988). *Endemic bird areas of the world. Priorities for biodiversity conservation*. BirdLife Conservation Series 7. Cambridge: BirdLife International.

Van Asselen, S., & Verburg, P. H. (2013). Land cover change or land-use intensification: Simulating land system change with a global-scale land change model. *Global Change Biology*, *19*, 3648–3667.

Virolainen, K. M., Ahlroth, P., Hyvärinen, E., Korkeamäki, E., Mattila, J., Päivinen, J., … Suhonen, J. (2000). Hot spots, indicator taxa, complementarity and optimal networks of taiga. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 1143–1147.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., & Pressey, R. (1996a). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology*, *10*(1), 155–174.

Williams, P. H., Prance, G. T., Humphries, C. J., & Edwards, K. S. (1996b). Promise and problems in applying quantitative complementarity areas for representing the diversity of some Neotropical plants (families Dichapetalaceae, Lecythidaceae, Caryocaraceae, Chrysobalanaceae, and Proteaceae. *Biological Journal of the Linnean Society*, *58*, 125–157.

BIOSKETCH

Victoria Veach is a PhD Student Researcher in the Metapopulation Research Centre (University of Helsinki). Her current interests include spatial conservation planning and addressing questions related to balancing the needs of biodiversity with the needs of the human population.

How to cite this article: Veach V, Di Minin E, Pouzols FM, Moilanen A. Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. *Diversity Distrib*. 2017;23:715–726. https://doi.org/10.1111/ddi.12571