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ORIGINAL ARTICLE

Global patterns and environmental correlates of high-priority conservation areas for vertebrates

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ABSTRACT

Aim A major challenge for the emerging discipline of conservation biogeography is to identify conservation areas and understand the factors and processes that govern the spatial distribution of those areas. We aimed to identify high-priority conservation cells (HPCC) – 1° cells that efficiently represent species – for amphibians, birds and mammals at the global extent, to identify the environmental variables associated with conservation priority, and to evaluate how well the areas of highest species richness correspond to these high-priority areas.

Location A global analysis.

Methods Distribution maps for 21,697 vertebrates and complementarity-based approaches were used to map HPCCs for vertebrates. We used 41 potential predictor variables and varimax-rotated factor analysis (VrFA) to identify sets of relatively uncorrelated environmental factors, and then used random forest models to investigate the relationships between VrFA factors and vertebrate conservation priorities. Finally, we evaluated whether species richness and threatened-species richness were efficient surrogates to identify HPCCs for each vertebrate taxon.

Results For each of the three taxa, HPCCs were concentrated in the Neotropical, Afrotropical and Indo-Malay biogeographical realms. The spatial distribution of HPCCs was strongly correlated with environmental variables, especially energy-related variables. The cells with the highest species richness did not correspond to HPCCs for either birds or mammals.

Discussion We suggest that elucidating the patterns and drivers of conservation priority could become a major focus of conservation biogeography. The ability to identify high-priority conservation sites from the environmental conditions in those sites may improve how sites are prioritized for conservation, so that all or most species can be conserved in affordable areas.

Keywords

Complementarity, conservation biogeography, global biodiversity pattern, prioritization, random forests, species accumulation index, species representation, species richness, surrogacy, threatened species.

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INTRODUCTION

One of the most common ways of prioritizing sites for conservation is to identify sites that represent all or most species in a relatively small total area (Moilanen *et al.*, 2009). In this paper, we use the term 'high priority' to refer to sites that contribute to the efficient representation of species, ignoring other conservation priorities such as connectivity, compactness, intact disturbance regimes and trophic webs, and genetic vigour. Many biogeographical studies have identified sites that are individually rich in rare, endemic or total species (e.g. Orme *et al.*, 2005; Grenyer *et al.*, 2006) and the environmental factors associated with species richness (e.g. Currie & Paquin, 1987; Stein *et al.*, 2014). These maps have

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often been used as global maps of conservation priority areas. Such maps can help donors with global missions to allocate resources, and can help citizens advocate for particular actions in priority areas. Myers *et al.* (2000) produced the best known map, which identified 25 hotspots, each of which was selected because it had more than 1500 endemic plant species and less than 30% remaining natural land cover.

Until about 2006, many prioritizations relied on opinions of specialists regarding the number of endemic or threatened species in irregular polygons, such as ecoregions or political jurisdictions (Brooks *et al.*, 2006). Since then, some prioritizations have used global range maps of amphibians, birds and mammals to identify the equal-area grid cells that harbour the largest numbers of terrestrial vertebrates, endangered terrestrial vertebrates or range-restricted terrestrial vertebrates (e.g. Jenkins *et al.*, 2013), but species richness may be a poor indicator of global conservation priority, because richness does not reflect complementarity. When sites with high species richness contain overlapping assemblages of species, a collection of species-rich sites fails to represent species efficiently (Kirkpatrick, 1983). For this reason, for the last 20 years, conservation planners have used complementarity-based algorithms rather than species richness to prioritize sites within regions (Pressey *et al.*, 1993; Moilanen *et al.*, 2009). Using species inventories or range data for all sites in a planning area, these algorithms identify optimal or near-optimal sets of sites (Moilanen & Ball, 2009). Some of these algorithms assign each site a priority from 0 (least important) to 1 (most important). These priority values reflect the complementarity value of the site, i.e. how much it contributes to an assemblage of sites that collectively represents species in a small area (Pressey *et al.*, 1993; Moilanen *et al.*, 2009).

Our goals in this paper are (1) to provide complementarity-based global maps of high-priority conservation sites (in this case, 1° cells) for amphibians, birds and mammals, (2) to identify the environmental variables associated with conservation priority for these vertebrates, and (3) to evaluate how well the sites with the highest species richness correspond to these high-priority areas. To address these goals, we applied a complementarity-based approach to the global ranges of 6252 amphibians, 9598 birds and 5244 mammals to score each terrestrial 1° cell in the world in terms of conservation priority for each taxon. We used random forest models (Breiman, 2001) to identify the environmental drivers of conservation priority at the global extent. We then used the species accumulation index (SAI; Rodrigues & Brooks, 2007) to evaluate the efficiency of two surrogates (species richness and threatened-species richness) in prioritizing cells to collectively represent species.

MATERIALS AND METHODS

Data sources

We obtained shape-files depicting the known distributions of mammals and amphibians from IUCN Red List Spatial Data (IUCN, Gland, Switzerland; available at: http://www.iucnredlist.org/technical-documents/spatial-data) and of birds from BirdLife International (2012). We processed these range maps in GRASS 6.4.2 (GRASS Development Team, 2012) to generate presence/absence values for each 1° grid cell (n = 18,043). We analysed range maps of 6252 of the 6307 amphibians and 5244 of the 5318 mammals in the IUCN database, and 9598 of the 10,072 bird range maps in the joint BirdLife International–NatureServe database. We excluded species that occurred only on small oceanic islands, because we did not have environmental data specific to the land areas within the 1° cells where these species occurred. We did not analyse these range maps at a resolution finer than 1° cells, because that would have mischaracterized the spatial patterns of biodiversity (Hurlbert & Jetz, 2007).

We selected 41 potential predictor variables associated with patterns of species richness at the global extent. We obtained temperature and precipitation variables from Hijmans *et al.* (2005), PET [potential evapotranspiration, calculated using the Hargreaves (1994) equation] from Zomer *et al.* (2008), sunshine variables from Neteler (2005), normalized difference vegetation index (NDVI) from Tucker *et al.* (2004), elevation and slope from Global 30 Arc-Second Elevation data (GTOPO30; USGS, Washington, DC; available at: https://lta.cr.usgs.gov/GTOPO30), and topographic diversity (Benito *et al.*, 2013) from GTOPO30. We calculated the mean or range of each environmental variable across each 1° cell. Human footprint was obtained from the Global Human Footprint Dataset (WCS & CIESIN, 2005). We also calculated five soil variables representing depth to bedrock, bulk density, soil organic carbon content, soil pH and soil diversity, expressed as the number of different soil classes according to the US Department of Agriculture. Soil variables were obtained from SoilGrids1km – a system for automated soil mapping (ISRIC, 2013; Hengl *et al.*, 2014).

Measuring global conservation priority

We used the core-area form of the reserve-selection software ZONATION (Moilanen *et al.*, 2014), a complementarity-based method, to produce a hierarchical prioritization of cells for each taxon. ZONATION starts with all cells tentatively 'reserved' and iteratively removes the cells that are least needed to maintain the core areas of each species. The algorithm minimizes biological loss by minimizing proportional loss of geographical range (number of sites) for the worst-off species (those species with the smallest remaining range in the current tentative solution). This produces a hierarchy of sites in which the most important 5% is a subset of the most important 10%, and so on.

Identifying globally high-priority conservation cells (HPCC)

For each taxon, we identified the most important 15%, 20%, 25%, 30% and 35% of the cells. The lowest level reflects the

current extent of the world's protected areas (13% of land area; Bertzky *et al.*, 2012), with larger levels corresponding to various plausible levels of expansion of the network of protected areas.

Relationships between environmental variables and conservation priority

We used varimax-rotated factor analysis (VrFA) to reduce the dimensionality of the data, to discern major environmental gradients and, most importantly, to identify sets of relatively uncorrelated environmental variables. The highest factor loadings (with absolute values > 0.70) for the first factor corresponded to 16 energy predictors (see Appendix S1 in the Supporting Information), 10 related to temperature, one related to potential evapotranspiration (PET) and five variables related to hours of sunshine, of which mean annual temperature had the highest loading (highest correlation with the factor). The second factor corresponded to NDVI and topographic variables. The third and sixth factors corresponded to precipitation variables. The fourth factor corresponded to soil variables and the fifth factor reflected the interaction between mean hours of sunshine and topography (Appendix S1).

We used random forest models (Breiman, 2001; Liaw & Wiener, 2014) to investigate the relationships between environmental predictors (VrFA factors) and vertebrate conservation priority. Using random forests, bootstrap samples are drawn randomly from the original data: for each of 500 regression trees, the best split among a given number of predictors is chosen. In each bootstrap iteration, trees were constructed using about 66% of the data. The remaining data (about 33%) were used to provide an estimation of the error rate based on the training data [out-of-bag (OOB) error]. The OOB error was then used to estimate the relative importance of the predictors by observing how much the OOB error changes when the values for a particular predictor were permuted in the training set, while all other predictor values were left unchanged. Specifically, the predictor error on the OOB data was calculated for each tree and for each predictor variable. The importance score for each variable is the mean difference in OOB error before and after permutation. For each random forest model, we evaluated 500 trees, which was substantially beyond the point (about 200 trees) at which mean squared error dropped below 0.05.

For each taxon, we developed random forest models with the six VrFA factors (related to energy, water, vegetation, soil and topography) and human footprint representing independent variables, and conservation priority as the dependent variable. We included human footprint as an independent variable because, although it was not strongly correlated with any VrFA factors (loading < 0.393 on each factor), it could plausibly affect conservation priority. All analyses, including VrFA, were performed within GRASS and R, including the R packages PSYCH 1.5.1 (Revelle, 2015), SPGRASS6 (Bivand *et al.*, 2014) and RANDOMFOREST (Liaw & Wiener, 2002).

Correspondence of species-rich cells to high-priority conservation cells

For each taxon, we evaluated two within-taxon surrogates, namely species richness and threatened-species richness in each cell, in terms of their ability to identify cells that represented many species in relatively few cells. For each surrogate, cells were selected (added to the notional 'reserve') starting with the cell with the highest richness (total or threatened) and adding the cell with the next highest richness at each succeeding step. At each step, we calculated the number of species represented in at least one cell of the hypothetical reserve.

We used the species accumulation index, SAI (Rodrigues & Brooks, 2007), to evaluate the efficiency of species-richness surrogates in representing that taxon. SAI compares S, the number of species represented at least once in the set of sites selected using the surrogate, to an optimum value O (the largest number of species that can be represented in the same number of sites) and to R, the mean number of species represented at least once in the same number of randomly selected sites. We calculated O from the ZONATION run used to generate true conservation priority. To calculate R, we accumulated cells in random order, and at each step we calculated the number of species represented at least once in the randomly selected cells. We repeated the random selection procedure 1000 times, used the mean value as R, and calculated a 95% confidence interval for R. We used 'representation in at least one cell' as a convenient benchmark to evaluate species richness as a surrogate; the occurrence of a species in a single cell will often not be adequate for species conservation.

Formally, $\mathrm{SAI} = (S - R) / (O - R)$. SAI varies from $-\infty$ to 1; negative SAI indicates a worse than random result, 0 indicates random performance, and positive SAI is a measure of efficiency. For example, an SAI of 0.6 indicates that the surrogate was 60% as effective as the optimal solution in its ability to improve on a random selection of sites. SAI is sometimes calculated using the entire area under each S, O and R curve. We used an alternative procedure, calculating SAI at 15%, 20%, 25%, 30% and 35% of the landscape hypothetically reserved. We chose this procedure to reflect performance of each surrogate at levels as low as the current extent of the world's protected areas (13% of land area; Bertzky *et al.*, 2012), increasing to various plausible levels of expansion of the network of protected areas. We used the mean of these five SAI values as an overall estimate of performance of the surrogates.

We calculated Kendall rank correlation coefficients (τ) between conservation priority between pairs of taxa. We also calculated τ between conservation-priority scores and species richness (both for all species and for threatened species). Pearson correlation would have been inappropriate, because it assumes that values are normally distributed, whereas priority scores are uniformly distributed between 0 and 1. Kendall's τ is less sensitive to errors in the data and yields more

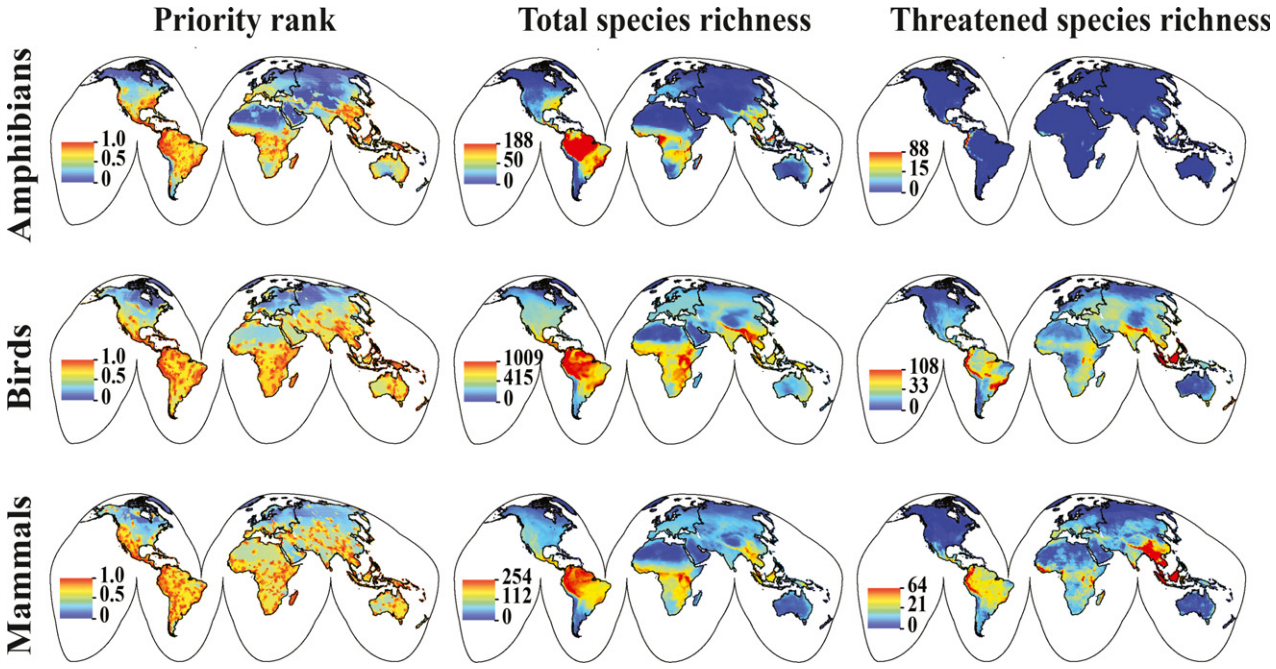

Figure 1 (left) Priority of 1° cells for representing all the world's amphibians, birds and mammals, as estimated in the core-area form of the reserve-selection software Zonation, scaled from 0 (least important, dark blue) to 1 (most important, red). (centre) Cells ranked in order of total species richness. (right) Cells ranked in order of richness of threatened species.

accurate *P*-values than Spearman's rank correlation coefficient, ρ; values of τ are usually smaller than values of ρ (Gibbons, 1993)

RESULTS

The tropical and subtropical forests of Neotropical, Afrotropical and Indo-Malay biogeographical realms had large concentrations of HPCCs for each of the three taxonomic groups, with secondary concentrations in mediterranean and montane environments (Figs 1 & 2). Cells with high species richness were also concentrated in tropical forest regions (Fig. 1). Many HPCCs had relatively few species, however, and many of the cells with the highest species richness were not HPCCs (Fig. 1). Similarly, conservation priority was only moderately correlated with species richness (Kendall's $\tau = +0.72$ for amphibians, +0.48 for birds and +0.46 for mammals) and threatened-species richness ($\tau = +0.48$ for amphibians, +0.47 for birds and +0.49 for mammals) (Table 1).

The conservation priority of 1° cells was highly predictable from environmental variables; models with seven environmental factors explained about 85%, 85% and 78% of the variance in conservation priority for amphibians, birds and mammals, respectively (Fig. 3). For each taxon, energy-related and water factors were the main drivers of conservation priority, followed by factors related to human footprint, topography and soil (Fig. 3, Appendix S1).

Within-taxon richness was a poor surrogate for HPCCs, as indicated by the species accumulation index. Selecting cells with the highest diversity of total species or threatened species performed well for amphibians (efficiencies of 58% and 70%, respectively), but performed poorly (worse than the same number of randomly selected cells) for birds and mammals (Table 2, Appendix S2).

DISCUSSION

We believe that Fig. 2 presents the first global maps of HPCC for amphibians, birds and mammals. Myers *et al.* (2000) identified hotspots based solely on a threshold value for endemic plant species richness combined with a measure of habitat loss. Grenyer *et al.* (2006) also identified global hotspots of total, rare and threatened species richness. Our map confirms the importance of these hotspots, but suggests that the conservation of vertebrates will also require areas outside these hotspots. Le Saout *et al.* (2013) ranked the world's major protected areas (13% of terrestrial land area). Our map augments their effort by providing information on the priority of 100% of the planet's terrestrial land area (not just protected areas), albeit at coarser resolution. A recent map of global conservation priorities (Jenkins *et al.*, 2013) prioritized areas on the basis of species richness, not complementarity values. Furthermore, that study analysed range maps at 10-km cell resolution, although analysing range maps at resolutions finer than 1° (about 111 km) can yield invalid inferences about biodiversity pattern (Hurlbert & Jetz, 2007).

Mapping priority cells at the global extent can minimize the inefficiencies that occur when priorities are mapped at

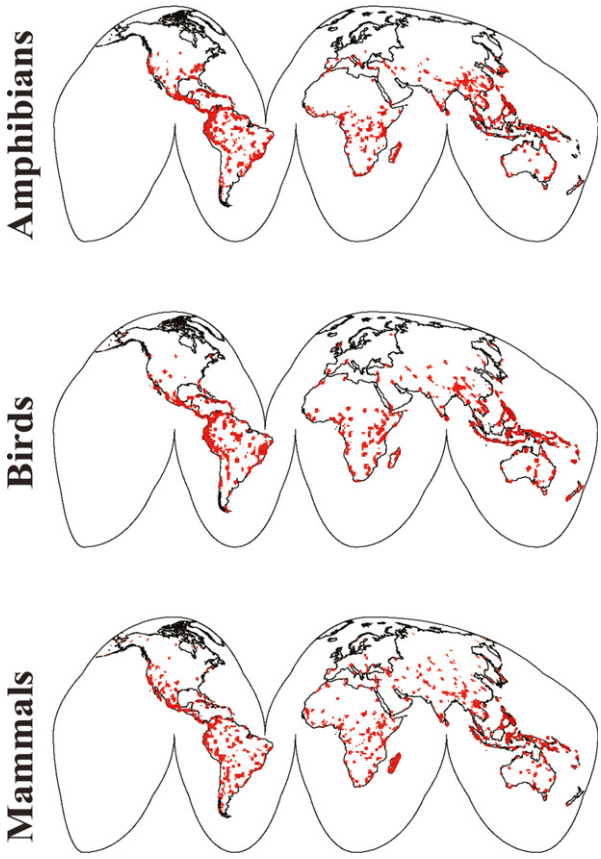

Figure 2 Spatial distribution of the 15% highest-priority conservation areas (1° cells) selected by the core-area form of the reserve-selection software Zonation to represent amphibians, birds and mammals. Zonation selects a complementary set of sites to represent all species.

smaller extents, such as nations or ecoregions. For example, Moilanen *et al.* (2013), using the datasets we used but restricted to the Western Hemisphere, found that national-scale analyses tended to prioritize sites near national boundaries and that hemisphere-scale analyses provided about 50% higher mean protection levels per species. The national-scale analyses prioritized sites that represented nationally rare species that were more common in other nations. Prioritizing across political boundaries can result in better species representation for a given conserved land area.

The conservation priority of 1° cell for amphibians, birds and mammals was highly related to environmental factors. Because species richness is affected both by environmental heterogeneity and by particular environmental conditions (Currie & Paquin, 1987; Currie, 1991; O'Brien, 1993, 1998; Kerr & Packer, 1997; O'Brien *et al.*, 2000; Francis & Currie, 2003; Hawkins *et al.*, 2003a,b; Field *et al.*, 2005; Buckley & Jetz, 2007; Davies *et al.*, 2007; Kreft & Jetz, 2007; Tittensor *et al.*, 2010; Fitterer *et al.*, 2013; Schindler *et al.*, 2013; Stein *et al.*, 2014), we were not surprised that variables relating to environmental heterogeneity and to particular environmental conditions were also correlated with conservation priority. If conservation priority was solely a by-product of the influence of the environment on species richness, then conservation priority would be more correlated with species richness than with environmental variables, whereas we observed the reverse. For example, Kendall's τ between conservation priority and species richness was 0.72 for amphibians, 0.48 for birds, and 0.46 for mammals. In contrast, environmental factors explained 85%, 85%, and 78% of variance in conservation for the three taxa, respectively. Because Kendall's τ is an analogue of r (not r^2), environmental factors explains more than twice as much of the variation in conservation priority than is explained by species richness. This suggests that particular environments not only provide the conditions that promote the speciation, diversification and co-existence of species, but also promote the coexistence of unique assemblages of species.

HPCCs had high mean temperature, high PET, many hours of sunshine, high amount of precipitation, high topographic diversity and high NDVI (Table 1). Because these variables were highly correlated with other potential predictors (see Appendix S3), we are reluctant to make strong inferences about causality from our one study. Future studies using additional taxa across diverse settings, extents and grain sizes, and analyses that carefully consider multicollinearity are needed to infer causality and elucidate the mechanisms whereby energy and other environment factors drive the priority of sites for species representation.

We suggest two non-exclusive reasons for the large number of HPCCs in the tropics. First, tropical environments are diverse and patchily distributed and therefore provide many patches to be colonized and occupied by species (McCoy *et al.*, 1986; Lomolino *et al.*, 2010). Similarly, the exceptionally high

Table 1 Kendall rank correlation coefficients (τ) between conservation priority values (from the core-area form of the reserve-selection software Zonation) for each pair of taxa, and between conservation priority and species richness, in a global analysis of terrestrial 1° cells. Kendall's tau is an analogue of Pearson's r (not Pearson's r^2). All values are significant at $P < 0.001$.

	Conservation priority for			Total number of			Number of threatened		
	Amphibians	Birds	Mammals	Amphibians	Birds	Mammals	Amphibians	Birds	Mammals
Conservation priority for amphibians	+1.00	+0.52	+0.53	+0.72	+0.62	+0.56	+0.48	+0.46	+0.47
Conservation priority for birds	+0.52	+1.00	+0.56	+0.43	+0.48	+0.41	+0.34	+0.47	+0.49
Conservation priority for mammals	+0.53	+0.56	+1.00	+0.43	+0.48	+0.46	+0.35	+0.47	+0.49

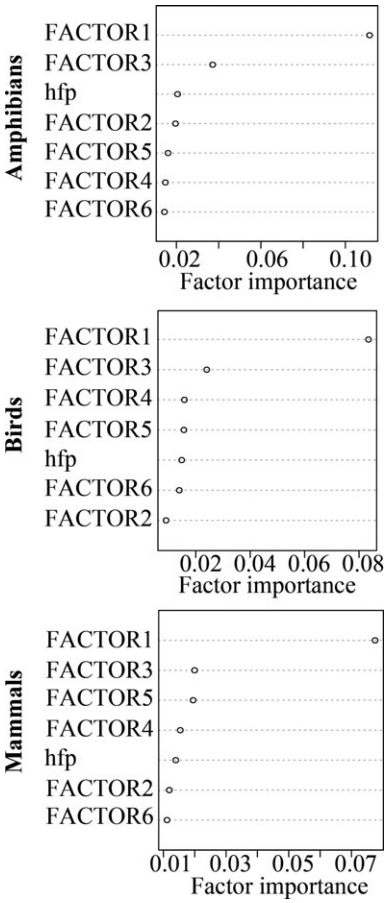

Figure 3 Importance of six PCA factors and human footprint (hfp) in random forest models for priority rank of 1° cells for amphibians, birds and mammals. Factor importance (*x*-axis) is how much the prediction error increases when that factor is randomly permuted. The percentage of variance explained (R^2) was 85.4%, 85.1% and 78.3% for amphibians, birds and mammals, respectively.

environmental heterogeneity and habitat diversity in the Andes is thought to be responsible for its high biodiversity, endemism and high rates of speciation (Larsen *et al.*, 2011), and might also explain the large number of HPCCs there. A second explanation for HPCC concentrations in the tropics is that the tropics harbour the oldest environments on Earth, and have thus accumulated species over a longer period than non-tropical environments (Pianka, 1966; Mittelbach *et al.*, 2007).

A recent meta-analysis demonstrated that environmental drivers had stronger effects on species richness as grain size increased and spatial extent decreased, and that the influence of climate variables (a subset of environmental drivers) showed the sharpest decrease as extent decreased (Stein *et al.*, 2014). We expect that the environmental drivers of conservation priority will also vary with spatial extent and grain, as well as between regions. Our models did not consider some potentially important predictors of conservation priority, because we could not devise meaningful measures for variables such as the topographic wetness index (widely used to quantify the influence of topography on hydrological processes; Sørensen *et al.*, 2006) or topographic landform in heterogeneous 1° polygons. Analyses at finer spatial resolution should consider them as potential drivers of conservation priority.

Species richness was a remarkably poor surrogate for conservation priority. Cells selected for the highest numbers of threatened or total species represented fewer birds and mammals than the same number of randomly selected cells. Orme *et al.* (2005) and Grenyer *et al.* (2006) similarly questioned the utility of richness as a tool for prioritizing land for conservation at the global extent.

Biogeography has focused primarily on identifying the patterns and drivers of individual species distributions and of species richness. Biogeographical inquiries have contributed to the development of evolutionary theory, ecology, habitat fragmentation and species distribution modelling, and are giving rise to an emerging discipline of conservation biogeography (Ladle & Whittaker, 2011). We suggest that elucidating the patterns and drivers of conservation priority could become a major focus of conservation biogeography. On the applied side, we note that limited resources require human investments in conservation lands to be prioritized. We hope that the ability to identify high-priority conservation sites from environmental conditions in those sites may improve the way in which sites are prioritized for conservation, so that all or most species can be conserved in affordable areas.

Table 2 Species accumulation index (SAI) at several potential conservation target levels. SAI indicates how much the surrogate improves on the number of species represented in the same number of randomly selected sites, compared with the largest number of species that could be represented in that number of sites. Target levels range from 15% (the approximate extent of the world's protected areas) to 35%, indicating various levels of expansion of the world's protected area network. Values in bold are significantly greater than the upper bound of the 95% confidence interval for species represented in randomly selected cells.

		Target					
Taxon	Surrogate	15%	20%	25%	30%	35%	Mean
Amphibians	Species richness	**0.46**	**0.52**	**0.58**	**0.62**	**0.69**	**0.58**
	Threatened-species richness	**0.66**	**0.70**	**0.72**	**0.70**	**0.75**	**0.70**
Birds	Species richness	−1.65	−2.16	−2.13	−2.51	−2.56	−2.20
	Threatened-species richness	−0.88	−0.66	−0.65	−0.42	−0.24	−0.57
Mammals	Species richness	−1.13	−1.19	−1.28	−1.29	−1.13	−1.20
	Threatened-species richness	−0.73	−0.61	−0.48	−0.38	−0.29	−0.50

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Loadings of environmental variables on six factors.
Appendix S2 Species accumulation plots indicating the number of species of amphibians, birds, and mammals represented in various percentages of cells.
Appendix S3 Maps of cell priority for each taxon.

BIOSKETCHES

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