ORIGINAL ARTICLE

Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural suitability

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ABSTRACT

Aim Twelve per cent of the Earth's terrestrial surface is covered by protected areas, but neither these areas nor the biodiversity they contain are evenly distributed spatially. To guide future establishment of protected areas, it is important to understand the factors that have shaped the spatial arrangement of the current protected area system. We used an information-theoretic approach to assess the ability of vertebrate biodiversity measures, resource consumption and agricultural potential to explain the global coverage pattern of protected areas.

Location Global.

Methods For each of 762 World Wildlife Fund terrestrial ecoregions of the world, we measured protected area coverage, resource consumption, terrestrial vertebrate species richness, number of endemic species, number of threatened species, net primary production, elevation and topographic heterogeneity. We combined these variables into 39 *a priori* models to describe protected area coverage at the global scale, and for six biogeographical realms. Using the Akaike information criterion and Akaike weights, we identified the relative importance and influence of each variable in describing protected area coverage.

Results Globally, the number of endemic species was the best variable describing protected area coverage, followed by the number of threatened species. Species richness and resource consumption were of moderate importance and agricultural potential had weak support for describing protected area coverage at a global scale. Yet, the relative importance of these factors varied among biogeographical realms. Measures of vertebrate biodiversity (species richness, endemism and threatened species) were among the most important variables in all realms, except the Indo-Malayan, but had a wide range of relative importance and influence. Resource consumption was inversely related to protected area coverage across all but one realm (the Palearctic), most strongly in the Nearctic realm. Agricultural potential, despite having little support in describing protected area coverage globally, was strongly and positively related to protection in the Palearctic and Neotropical realms, as well as in the Indo-Malayan realm. The Afrotropical, Indo-Malayan and Australasian realms showed no clear, strong relationships between protected area coverage and the independent variables.

Main conclusions Globally, the existing protected area network is more strongly related to biodiversity measures than to patterns of resource consumption or agricultural potential. However, the relative importance of these factors varies widely among the world's biogeographical realms.

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Understanding the biases of the current protected area system may help to correct for them as future protected areas are added to the global network.

INTRODUCTION

Humans now number more than 6 billion, and our population is expected to grow to 9 billion by 2050 (United Nations Population Division, 2005). Accompanying this population growth are dramatic increases in consumption of the Earth's resources (Imhoff *et al.*, 2004) and co-option of land to support this consumption (Hoekstra *et al.*, 2005). Rapid population growth and global consumption of natural resources have caused widespread loss of native land cover and ecosystem functioning, and together constitute one of the greatest threats to biodiversity (Balmford *et al.*, 2001; McKinney, 2001; Ceballos & Ehrlich, 2002; Baillie *et al.*, 2004). The conversion of native vegetation to agriculture is a primary driver of global habitat loss and this threat is unlikely to diminish (Wood *et al.*, 2000; Tilman *et al.*, 2001). Worldwide, more than 16,000 species have been documented to be at significant risk of extinction (Baillie *et al.*, 2004; IUCN, 2007), although the true number is probably much higher because the conservation status of most species is unknown (Pimm *et al.*, 1995).

Faced with these growing threats, a common and effective method of conserving biodiversity is the establishment of protected areas (Balmford *et al.*, 1995, 2002; Brandon *et al.*, 1998). The global network of protected areas now covers more than 12% of the world's land area (Chape *et al.*, 2005). However, because neither the pattern of protected areas nor patterns of species richness, endemism and endangerment are uniform around the world (Chape *et al.*, 2005; Hoekstra *et al.*, 2005; Ricketts *et al.*, 2005; Lamoreux *et al.*, 2006; Rodrigues *et al.*, 2006) it is important to understand where protected areas have been established and how they relate to patterns of biodiversity.

A number of studies have assessed the overlap between the existing network of protected areas and important targets for conservation (Balmford *et al.*, 2001; Scott *et al.*, 2001a; Rodrigues *et al.*, 2004b; Chape *et al.*, 2005; Hoekstra *et al.*, 2005). For example, Rodrigues *et al.* (2004b) examined the overlap of protected areas with vertebrate species' ranges to identify potential gaps in coverage, whereas Hoekstra *et al.* (2005) analysed the relationships between protected areas and habitat types. These studies have found considerable coverage of various biodiversity targets within existing protected areas, although numerous targets were overlooked or under-represented by the global system of protected areas. The frequency

with which existing protected areas are of exceptional value and serve to protect biodiversity (Bruner *et al.*, 2001) is somewhat surprising when many were not established to protect the biodiversity targets used to evaluate them. Indeed information on species ranges was probably not available when most protected areas were created.

The creation of protected areas is inherently a political process, and biodiversity conservation has rarely been the primary driver of the creation of protected areas. Previous studies have found that the establishment of protected areas coincided with wild and scenic areas far from human activity (Scott *et al.*, 2001a; Pressey *et al.*, 2002), and in low-productivity lands unsuitable for agriculture (Rebelo, 1997; Scott *et al.*, 2001b; Pressey *et al.*, 2002; Rouget *et al.*, 2003). Although a number of studies have evaluated these factors singly or for small regions, none have analysed them together to assess their importance globally.

Here, we analyse patterns of protected area coverage in relation to three classes of variables: biodiversity measures (species richness, endemism, threatened species), human resource consumption and agricultural potential (a combination of net primary productivity, median elevation and topographic heterogeneity). We used an information-theoretic approach to evaluate the relative importance and influence of each variable for describing the global distribution of protected areas. We evaluated 39 *a priori* models that included different combinations of variables to identify the relative importance and influence of each variable across all models. To reveal any regional variation masked by the global analysis, we repeated the analysis for each biogeographical realm.

DATA AND METHODS

Data

We used the World Wildlife Fund (WWF) terrestrial ecoregions as our unit of analysis (Olson *et al.*, 2001). Ecoregions are defined as 'relatively large units of land that contain a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of the natural communities prior to major land use change' (Olson *et al.*, 2001). Furthermore, we adopted the biogeographical realm classification from Olson *et al.* (2001) as the basis for our realm-level analyses. For each terrestrial ecoregion we collated

data for protected areas, biodiversity measures, human resource consumption and agricultural potential.

We calculated the total protected area coverage of each ecoregion using the 2004 World Database of Protected Areas (WDPA Consortium, 2004), and transformed these data as $\log_{10}$ (protection + 1) to improve normality (Fig. 1a). To arrive at our protected area estimates, we manipulated the WDPA data base in several ways. First, we excluded records that were identified as marine protected areas, were non-permanent sites or that lacked location information. Protected

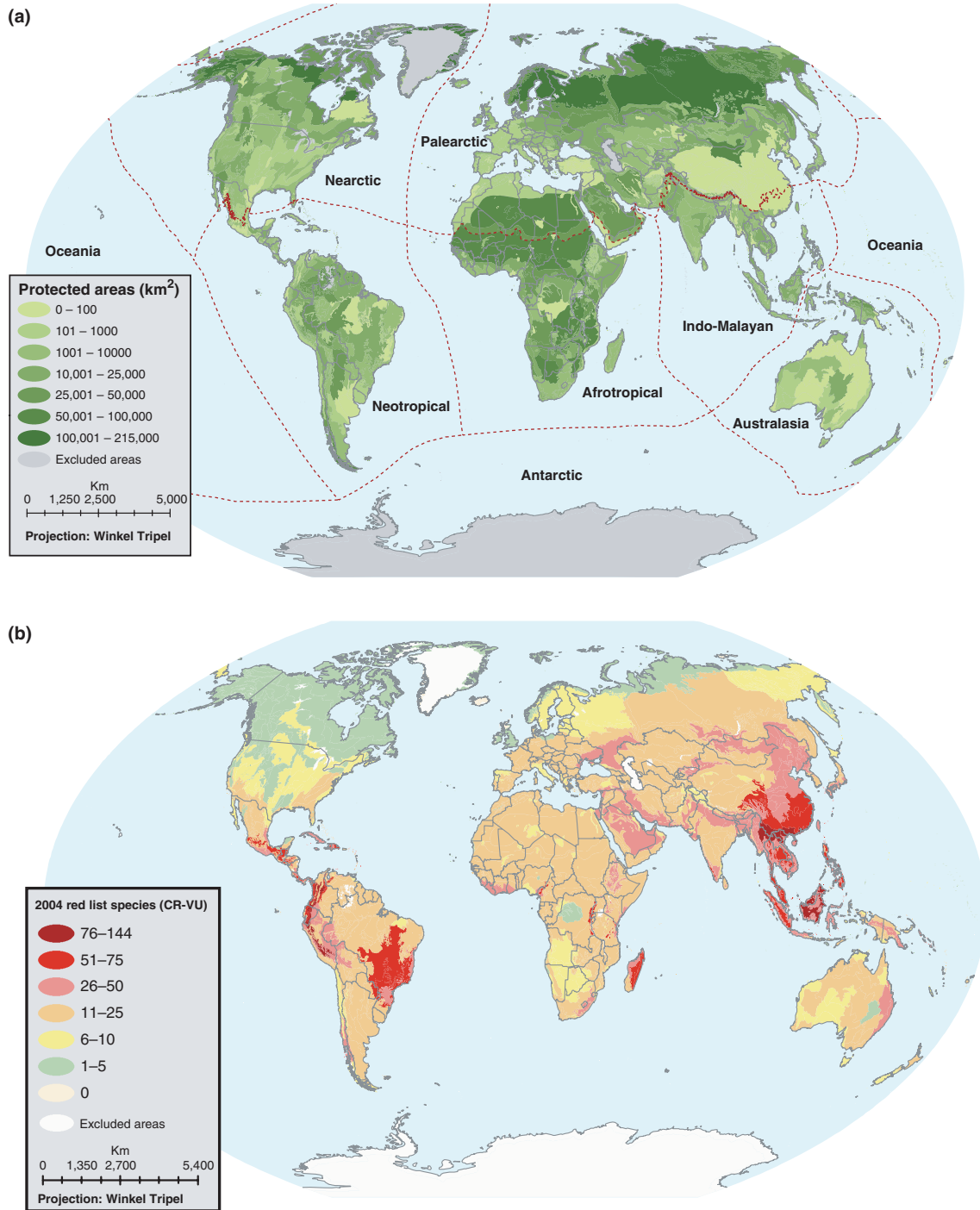**Figure 1** (a) Total protected area [World Conservation Union (IUCN) category I–IV] for World Wildlife Fund (WWF) terrestrial ecoregions. Biogeographical realms, as defined by Olson *et al.* (2001), are also delineated. (b) Number of 2004 Red List threatened species (IUCN categories: vulnerable, endangered, and critically endangered) for WWF terrestrial ecoregions. Maps use the Winkel-Tripel projection.

areas with only point location and area data were mapped as circles with the appropriate total area. The portions of the protected areas that extended into the marine realm were also clipped out. Lastly, overlapping protected areas were combined to prevent double-counting. The World Conservation Union (IUCN) recognizes six categories of protected areas, but we limited our analyses to categories I–IV, those which are managed primarily for biodiversity conservation (The World Conservation Union, 1994).

Our biodiversity measures of species richness, endemism and number of threatened species were based on two data sets. The species distributional data came from WWF's data base of vertebrates listed by ecoregion and containing all terrestrial amphibians ($n = 4797$), reptiles ($n = 7483$), birds ($n = 9470$) and mammals ($n = 4702$) (Lamoreux *et al.*, 2006). From these data, we calculated total species richness (i.e. the number of species in an ecoregion) and endemism (i.e. the number of species whose global distribution is confined to a single ecoregion). We estimated the number of threatened species for each ecoregion using the *2004 IUCN Red List of Threatened Species* (hereafter 'threatened species') (Baillie *et al.*, 2004). We considered a threatened species to be one identified as vulnerable, endangered, or critically endangered by IUCN. For each threatened species we identified the ecoregion(s) in which they occurred, and totalled them for each ecoregion (Fig. 1b). To improve normality for all three measures of biodiversity, we transformed the data as $\log_{10}$ (number of species + 1).

We measured resource consumption by people (hereafter 'resource consumption') as the amount of terrestrial net primary production (NPP) required to derive food and fibre products used by humans (Imhoff *et al.*, 2004). Imhoff *et al.* (2004) used Food and Agriculture Organization (FAO) data on food and fibre products (e.g. vegetal foods, meat, wood, paper) consumed. They calculated the per capita resource consumption of each country – measured in Pg carbon (C) (1 Pg C = 10^{15} g C) – and applied these values to a gridded human population data base with a 0.25° spatial resolution (Center for International Earth Science Information Network (CIESIN, 2000). From this map, we determined the total resource consumption (in Pg C) for each ecoregion (for a full description of methods see Imhoff *et al.*, 2004). To improve normality we transformed the data as $\log_{10}$ (resource consumption).

We used three parameters to measure agricultural potential: NPP, elevation and topographic heterogeneity. Total NPP for each ecoregion was derived from the Carnegie Ames Stanford Approach carbon model (Imhoff *et al.*, 2004). Elevation was calculated from a global topographic digital elevation model (DEM) with 1 km resolution (commonly referred to as GTOPO30). We used a GIS to excise all elevation grid cells for each ecoregion and then identified the median value. Topographic heterogeneity was also calculated as the standard deviation of elevation in the ecoregion to provide a measure of its 'roughness' (Kerr & Packer, 1999). To limit the number of models tested (see below) we included or excluded these three variables together.

Our analyses included 762 of the 825 WWF terrestrial ecoregions. Sixty-one ecoregions were eliminated because one or more of our data sets were too coarse relative to their size. The majority of these were small island ecoregions located in the Oceania realm. We also excluded the two ecoregions that compose the Antarctic realm. Taken together, ecoregions excluded from this study represent 1% of the Earth's total land area (not including areas of permanent ice).

Statistical analyses

We used an information-theoretic approach to assess the relative importance of each variable in describing protected area coverage (hereafter 'protected areas') (Burnham & Anderson, 2002). The information-theoretic approach is based on developing a set of *a priori* models and then selecting the best-fitting model from among the candidates. This method then allows for each variable used in the models to be assessed for its relative importance and influence (Burnham & Anderson, 2002; Rushton *et al.*, 2004). We developed a set of *a priori* models and identified the best model globally ($n = 762$ ecoregions) and for individual biogeographical realms: Palearctic ($n = 197$), Nearctic ($n = 118$), Neotropical ($n = 160$), Afrotropical ($n = 103$), Indo-Malayan ($n = 98$) and Australasia ($n = 78$) (Fig. 1a). Due to the large number of ecoregions that lacked resource consumption data we excluded the Oceania realm from the realm analysis.

Model development

We identified 39 *a priori* models, which followed the principle of parsimony and progressed from simple to complex (Burnham & Anderson, 2002) (Table 1). Our analysis included a model of each explanatory variable alone (five models); relevant two-variable models (seven models); three-variable models (four models); four-variable models (two models); and a single model that contained all five-variables. We repeated each of these models, but included an additional five geographical parameters. The geographical parameters included the ecoregion centroid's latitude, longitude, (latitude)^2, (longitude)^2 and (latitude × longitude). Finally, we included a model containing only the geographical parameters, to provide an appropriate 'core geographical model' against which to compare models containing biological and resource-use information. By including these coordinate variables, we aimed to control for broad spatial patterns that might be confounded with our variable of interest (Legendre & Legendre, 1998).

At the outset, we found that ecoregion area was correlated with several of our variables (e.g. species richness and threatened species). For this reason, in each of the 39 models tested we included ecoregion area to control for larger areas having greater numbers of species (Rosenzweig, 1995). Preliminary analyses also showed that many of our variables displayed significant spatial autocorrelation as measured by Moran's *I* across both global and realm scales – precluding the

Table 1 Model selection results using information-theoretic criteria to describe protected area coverage as a function of vertebrate biodiversity attributes for terrestrial ecoregions.

Model	K	Global AIC	ΔAIC	w_i	Nearctic AICc	ΔAICc	w_i	Palearctic AICc	ΔAICc	w_i	Neotropical AICc	ΔAICc	w_i	Afrotropical AICc	ΔAICc	w_i	Indo-Malayan AICc	ΔAICc	w_i	Australasia AICc	ΔAICc	w_i
R	3	2434.060	34.23	0.00	340.7465	22.78	0.00	625.746526	15.91	0.00	469.836526	17.41	0.00	312.3395	5.57	0.02	282.603526	3.20	0.03	283.6045	11.89	0.00
E	3	2419.880	20.05	0.00	338.1215	20.16	0.00	619.281526	9.44	0.00	456.751526	4.32	0.04	317.4505	10.68	0.00	282.190526	2.79	0.03	285.7375	14.02	0.00
T	3	2430.710	30.88	0.00	340.9145	22.95	0.00	626.542526	16.70	0.00	458.005526	5.58	0.02	314.7585	7.99	0.01	281.069526	1.67	0.06	283.8895	12.17	0.00
H	3	2428.680	28.85	0.00	328.6915	10.73	0.00	622.591526	12.75	0.00	473.921526	21.49	0.00	317.3955	10.63	0.00	282.450526	3.05	0.03	285.7115	14.00	0.00
A	5	2434.950	35.12	0.00	339.2677	21.30	0.00	623.656714	13.82	0.00	468.796714	16.37	0.00	319.1787	12.41	0.00	280.863714	1.46	0.06	288.8697	17.15	0.00
H + R	4	2430.200	30.37	0.00	317.963	0.00	0.58	624.584333	14.75	0.00	470.873065	18.45	0.00	314.4392	7.67	0.01	284.389108	4.99	0.01	284.2039	12.49	0.00
H + E	4	2412.060	12.23	0.00	326.788	8.82	0.01	615.193333	5.36	0.02	457.835065	5.41	0.02	319.3302	12.56	0.00	284.311108	4.91	0.01	287.9169	16.20	0.00
H + T	4	2422.990	23.16	0.00	325.78	7.82	0.01	624.483333	14.65	0.00	458.954065	6.53	0.01	316.9292	10.16	0.00	282.287108	2.89	0.03	286.1709	14.46	0.00
H + A	6	2431.530	31.70	0.00	335.0328	17.07	0.00	624.615	14.78	0.00	470.628	18.20	0.00	321.477	14.71	0.00	283.250	3.85	0.02	291.496	19.78	0.00
A + R	6	2436.340	36.51	0.00	337.2298	19.27	0.00	625.124	15.29	0.00	466.293	13.87	0.00	318.072	11.31	0.00	283.233	3.83	0.02	285.739	14.02	0.00
A + E	6	2422.130	22.30	0.00	338.5468	20.58	0.00	614.680	4.84	0.03	454.583	2.16	0.11	321.328	14.56	0.00	283.188	3.79	0.02	291.427	19.71	0.00
A + T	6	2431.310	31.48	0.00	340.9328	22.97	0.00	624.424	14.59	0.00	453.410	0.98	0.21	319.349	12.58	0.00	282.769	3.37	0.02	289.622	17.91	0.00
R + E + T	5	2422.730	22.90	0.00	341.9217	23.96	0.00	620.933714	11.10	0.00	457.145714	4.72	0.03	315.8857	9.12	0.00	285.013174	5.61	0.01	282.7077	10.99	0.00
H + A + R	7	2432.510	32.68	0.00	322.6342	4.67	0.06	625.813	15.97	0.00	468.358	15.93	0.00	320.323	13.56	0.00	285.554	6.15	0.01	288.142	16.43	0.00
H + A + E	7	2415.700	15.87	0.00	331.3862	13.42	0.00	614.488	4.65	0.03	456.441	4.01	0.05	323.560	16.79	0.00	285.508	6.11	0.01	293.873	22.16	0.00
H + A + T	7	2424.900	25.07	0.00	332.2452	14.28	0.00	625.341	15.50	0.00	455.463	3.04	0.07	321.391	14.62	0.00	285.020	5.62	0.01	292.039	20.32	0.00
H + R + E + T	6	2414.830	15.00	0.00	320.8338	2.87	0.14	619.211105	9.37	0.00	458.17102	5.74	0.02	318.217	11.45	0.00	285.445077	6.05	0.01	285.2471	13.53	0.00
A + R + E + T	8	2425.490	25.66	0.00	339.0801	21.12	0.00	618.908	9.07	0.00	452.427	0.00	0.34	322.199	15.43	0.00	286.816	7.42	0.00	287.291	15.58	0.00
H + A + R + E + T	9	2418.010	18.18	0.00	325.8327	7.87	0.01	618.853	9.01	0.00	454.415	1.99	0.12	324.328	17.56	0.00	288.220	8.82	0.00	289.817	18.10	0.00
G	7	2425.450	25.62	0.00	329.343	11.38	0.00	618.145	8.31	0.01	481.187	29.45	0.00	310.659	3.892	0.06	279.846	0.45	0.10	272.158	0.44	0.17
R + G	8	2425.410	25.58	0.00	324.5571	6.59	0.02	619.232957	9.39	0.00	479.130642	26.70	0.00	306.7669	0.00	0.40	282.215978	2.82	0.03	272.303	0.59	0.16
E + G	8	2401.180	1.35	0.16	327.6041	9.64	0.00	610.880957	1.04	0.21	463.802642	11.38	0.00	312.7089	5.94	0.02	282.167978	2.77	0.03	271.715	0.00	0.21
T + G	8	2412.040	12.21	0.00	330.5791	12.62	0.00	618.786957	8.95	0.00	467.346642	14.92	0.00	308.5279	1.76	0.17	281.685978	2.29	0.04	273.441	1.73	0.09
H + G	8	2426.700	26.87	0.00	330.5141	12.55	0.00	620.735101	10.90	0.00	483.610101	31.18	0.00	312.3941	5.63	0.00	281.494978	2.10	0.05	273.6811	1.97	0.08
A + G	10	2428.860	29.03	0.00	335.7891	17.83	0.00	620.310075	10.47	0.00	477.488075	25.06	0.00	316.7471	9.98	0.00	282.856736	3.46	0.02	275.0176	3.30	0.04
H + R + G	9	2426.400	26.57	0.00	321.4557	3.49	0.10	621.425567	11.59	0.00	480.322	27.90	0.00	309.0725	2.31	0.13	283.917455	4.52	0.01	274.4751	2.76	0.05
H + E + G	9	2401.330	1.50	0.15	329.1527	11.19	0.00	612.996567	3.16	0.07	464.546	12.12	0.00	314.8425	8.08	0.00	283.671455	4.27	0.02	274.1171	2.40	0.06
H + T + G	9	2411.350	11.52	0.00	330.6357	12.67	0.00	620.888567	11.05	0.00	468.452	16.03	0.00	310.9265	4.16	0.05	283.061455	3.66	0.02	275.9981	4.28	0.02
H + A + G	11	2429.540	29.71	0.00	336.5226	18.56	0.00	621.146	11.31	0.00	478.848	26.42	0.00	319.489	12.72	0.00	280.919	1.52	0.06	283.562	11.85	0.00
A + R + G	11	2428.010	28.18	0.00	330.3736	12.41	0.00	619.624	9.79	0.00	475.677	23.25	0.00	312.807	6.04	0.02	280.961	1.56	0.06	277.257	5.54	0.01
A + E + G	11	2405.700	5.87	0.02	333.4036	15.44	0.00	609.838	0.00	0.35	462.620	10.19	0.00	319.512	12.75	0.00	279.400	0.00	0.13	275.595	3.88	0.03
A + T + G	11	2415.140	15.31	0.00	337.0746	19.11	0.00	618.753	8.92	0.00	463.289	10.86	0.00	315.595	8.83	0.00	280.768	1.37	0.07	277.071	5.36	0.01
R + E + T + G	10	2400.740	0.91	0.21	324.8091	6.85	0.00	615.164796	5.33	0.02	465.58351	13.16	0.00	310.5143	3.75	0.06	285.427736	6.03	0.01	276.3066	4.59	0.02
H + A + R + G	12	2428.810	28.98	0.00	327.8654	9.90	0.00	621.628	11.79	0.00	477.714	25.29	0.00	315.350	8.58	0.00	283.516	4.12	0.01	278.895	7.18	0.01
H + A + E + G	12	2404.880	5.05	0.03	334.2684	16.31	0.00	611.791	1.95	0.13	464.266	11.84	0.00	321.984	15.22	0.00	282.001	2.60	0.04	277.496	5.78	0.01
H + A + T + G	12	2414.060	14.23	0.00	336.4404	18.48	0.00	620.443	10.60	0.00	465.334	12.91	0.00	318.158	11.39	0.00	283.358	3.96	0.02	278.928	7.21	0.01
H + R + E + T + G	11	2399.830	0.00	0.32	323.7006	5.74	0.03	617.363	7.53	0.03	466.373	13.95	0.00	312.790	6.02	0.02	286.192	6.79	0.00	278.307	6.59	0.01

Table 1 Continued

Model	K	Global AIC	ΔAIC	w_i	Nearctic AIC_c	ΔAIC_c	w_i	Palearctic AIC_c	ΔAIC_c	w_i	Neotropical AIC_c	ΔAIC_c	w_i	Afrotropical AIC_c	ΔAIC_c	w_i	Indo-Malayan AIC_c	ΔAIC_c	w_i	Australasia AIC_c	ΔAIC_c	w_i
A + R + E + T + G	13	2404.650	4.82	0.03	331.175	13.21	0.00	613.909	4.07	0.05	461.809	9.38	0.00	315.707	8.94	0.00	283.716	4.32	0.01	281.226	9.51	0.00
H + A + R + E + T + G	14	2402.680	2.85	0.08	331.0427	13.08	0.08	613.968	4.13	0.02	463.515	11.09	0.00	319.489	12.72	0.00	286.334	6.93	0.00	283.110	11.39	0.00

Each row represents a candidate model, and the letters identify the variables included in that model.

R, species richness; E, species endemism; T, 2004 Red List of threatened species; H, resource consumption by humans; A, agricultural potential parameters (net primary productivity; median elevation and elevation standard deviation); G, geographical parameters (ecoregion centroid x, y, x^2, y^2, xy). The number of variables (K) is given for each model; i, for the global and realm analyses.

$C_i - AIC_{min}$) and Akaike weight (w_i) is given for each model; i, for the global and realm analyses.

The w_i indicates the relative support for that model in describing protected area coverage.

The best model for the global and realm analyses is identified in bold. The models used in the analysis of importance of variables and coefficient multi-model averaging are highlighted in grey.

These models have a $\Delta AIC < 7$, and a $w_i > 0.005$.

use of ordinary least square (OLS) regression techniques to assess the importance of the model. To account for spatial autocorrelation we used GeoDa™ to develop a first-order queen-based contiguity spatial weight matrix for each ecoregion (Anselin, 2005). We then applied a spatially autoregressive error term to each spatial regression model. This technique removed spatial autocorrelation from our models, as measured by Moran's I (Lichstein *et al.*, 2002). Because they were included to control for 'nuisance variables', we report neither area nor Moran's I in the results.

Evaluating models and estimating parameter importance

We ran all spatial regression models in GeoDa™. We used the Akaike information criterion (AIC) and the second-order AIC_c as our basis for comparing the candidate models (Akaike, 1973; Burnham & Anderson, 2002). The AIC_c is used to correct for bias when the ratio of observations to variables is less than 40. We calculated the AIC for our global analysis and the AIC_c for the biogeographical analyses. The model with the minimum AIC or AIC_c (denoted AIC_{min}) was considered the 'best' model supported by the data, and all others were evaluated based on their difference from this minimum ($\Delta AIC = AIC_i - AIC_{min}$) (Burnham & Anderson, 2002; Hobbs & Hilborn, 2006). We limited future analyses to those models that had a ΔAIC of < 7, as ΔAIC values > 7 contain little empirical support as the best model (Burnham & Anderson, 2002).

Using the values of each candidate model's AIC or AIC_c, we calculated the Akaike weight (w_i) for each model. The Akaike weight provides an estimate of model uncertainty, and gives the relative likelihood that a given model is the best among candidate models. The standardized w_i ranges in values from 0 to 1, and can be interpreted as the probability that model i is the best model given the data and numerous repetitions of the model selection exercise (Burnham & Anderson, 2002; Welch & MacMahon, 2005; Hobbs & Hilborn, 2006).

The w_i also allows us to make inferences about individual variables across all models, in two ways. First, we developed a relative importance value for each variable by summing the w_i of every model in which it was included. The resulting values ranged from 0 to 1, with values closer to 1 indicating greater importance. Second, we calculated the average coefficient (i.e. the 'slope') for each variable, weighted by the w_i (Burnham & Anderson, 2002). Model averaging identifies the sign of the relationship as well as the relative explanatory power of a variable among realms.

RESULTS

Globally, the best model, with a w_i of 0.32, was that containing the resource consumption, richness, endemism, threatened species and geography (H + R + E + T + G) variables (Table 1). Summing w_i for each variable across the eight models with a $\Delta AIC < 7$ (Table 1), we found that endemism was the best global explanatory variable of protected areas,

Table 2 Overall importance of vertebrate biodiversity, resource consumption and agricultural potential variables in describing protected area coverage.

Model	Species richness	Species endemism	Threatened species	Resource consumption	Agricultural potential	NPP	Elevation	Elevation SD
Global	(−) 0.64	**1.00**	0.64	(−) 0.58	0.16		(−)	(−)
Nearctic	**0.95**	0.19	0.19	(−) 0.91	0.06		(−)	
Palearctic	0.11	**0.95**	0.11	0.29	0.63	(−)		(−)
Neotropical	(−) 0.51	0.73	0.82	(−) 0.29	**0.90**	(−)	(−)	
Afrotropical	**0.66**	0.10	0.30	(−) 0.23	0.03	(−)		(−)
Indo-Malayan	0.23	(−) 0.33	0.31	(−) 0.38	**0.60**	(−)		
Australasia	0.25	**0.34**	0.15	(−) 0.23	0.10		(−)	

The importance value equals the sum of the Akaike weights (w_i) across candidate models containing the given variable (see Table 1, those models highlighted in grey). The w_i ranges from 0 to 1, with values closer to 1 being more important in explaining protected area coverage.
Variables that are negatively related to protected area coverage are identified with '(−)'; all others are positively related. The agricultural potential variable is a combination of three specific parameters (see Data and Methods); therefore, the sign of the relationship of each parameter is provided.
The variable with the highest importance value for the global and realm analyses appears in bold.

followed by species richness, threatened species and resource consumption (Table 2). Agricultural potential had weak support for describing protected areas at the global scale.

When we analysed the model-averaged coefficient values for each variable in the global models (Table 3), we found that the coefficient for endemism was highly positive, strengthening the support for the importance of endemism in describing global protected areas. Threatened species also had a positive coefficient. In contrast, richness, despite having an equivalent importance to threatened species (Table 2), had a small negative coefficient (Table 3), indicating that species richness had a slightly inverse relationship to protected areas.

Realm-level analyses showed some similarities, but also notable differences among variables when compared with the global results. For example, in the Nearctic realm, species richness and resource consumption were the only strong explanatory variables of protected areas (Tables 2 and 3). They were more than five times as important as any of the other variables in describing protected areas. The richness coefficient

was strongly positive, more than three times the richness coefficient for the next highest realm (Afrotropical), signifying it as both an important and an influential variable. Likewise, the resource consumption coefficient was strongly negative (Table 3), indicating that resource consumption had an important and influential inverse relationship to protected areas in the Nearctic realm.

In the Palearctic realm, endemism had both a relatively high importance value (Table 2) and a strongly positive coefficient (Table 3), demonstrating that endemism was an important explanatory variable of protected areas in this realm. Agricultural potential was of relatively moderate importance (Table 2). When we analysed the coefficients for the three measures of agricultural potential, we found a strongly positive correlation with elevation and negative correlation with elevation standard deviation, indicating that protected areas were frequently found in montane ecoregions with relatively little fluctuation across elevational gradients (Table 3). Lastly, this was the only realm where protected areas were positively

Table 3 Model-averaged coefficient values for vertebrate biodiversity, resource consumption and agricultural potential parameters.

Model	Species richness	Species endemism	Threatened species	Resource consumption	Agricultural potential NPP	Elevation	Elevation SD
Global	−0.024	0.441	0.325	−0.063	0.008	−0.017	−0.021
Nearctic	**3.548**	0.083	0.038	**−0.525**	0.018	−0.009	0.033
Palearctic	0.015	**0.993**	0.032	0.008	−0.007	**0.412**	**−0.694**
Neotropical	−0.448	0.507	**0.401**	−0.049	**−0.190**	−0.394	0.361
Afrotropical	0.910	0.229	0.268	−0.008	−0.010	0.007	−0.001
Indo-Malayan	0.048	−0.076	0.216	−0.044	−0.082	0.030	0.376
Australasia	0.527	0.217	0.111	−0.011	0.062	−0.073	0.009

Parameter averages were derived by multiplying each coefficient value by the w_i for each model, i, the parameter occurs in, and then dividing by the sum of w_i across all candidate models (Burnham & Anderson, 2002). Model averaging identifies the relative strength of the variable in a given realm against that of other realms. Model-averaged coefficients were limited to those models with an $\Delta AIC < 7$ (see Table 1, models highlighted in grey). The realm with the highest coefficient value for each variable appears in bold.
Agricultural potential is composed of three parameters, and the coefficient for each parameter is given.

related to resource consumption, albeit weakly (Tables 2 and 3).

Agricultural potential was the most important variable in describing protected areas in the Neotropical realm (Table 2). Specifically, protected areas tended to be found in areas of low NPP and low elevation (Table 3). Threatened species and endemism were also important and influential descriptors of protected areas, with both variables having large positive coefficients – the coefficient for threatened species was the largest among realms. Species richness was of lesser importance, and was inversely correlated with protected areas. This is the only realm to display a negative association between species richness and protected areas.

Species richness was the most important variable in describing protected areas in the Afrotropical realm (Table 2). It was more than twice as important as the next most important variable, threatened species. The species richness coefficient was strongly positive, second only to that for the Neotropics (Table 3). All other variables had low importance values and small coefficient values (Tables 2 and 3), indicating little support in describing the Afrotropical protected area system.

In the Indo-Malayan realm there were no clear sets of models that outperformed the others (Table 1). Consequently, the importance value of most variables was relatively similar, although agricultural potential was the most important variable describing protected areas (Tables 2 and 3). NPP had a relatively strong negative coefficient and elevation standard deviation showed a relatively strong positive coefficient, indicating that protected areas tend to be found in ecoregions with complex topographies and containing lower levels of NPP. Furthermore, the Indo-Malayan realm was the only realm where protected areas were inversely related to endemism, albeit weakly (Table 3).

While endemism was the most important variable describing protected areas in the Australasian realm, its value was relatively low, and not much greater than the other variables (Table 2). This result was indicative of relatively little support for any one variable describing protected area coverage. Furthermore, with the exception of species richness, the variable coefficient values were also weak when compared with other realms (Table 3). Species richness, while the second most important explanatory variable, had a relatively strong positive coefficient, suggesting a relatively strong relationship to protected areas in the Australasian realm despite its low importance value.

DISCUSSION

Protected areas are a cornerstone of conservation strategies, but little is known about the factors that influence whether and where they are created. Understanding how current protected areas are located relative to biodiversity features is critical to the establishment of future protected areas. Using a retrospective analysis, we found that, globally, species endemism, species richness and to a lesser extent threatened species were better

explanatory variables of protection than resource consumption and measures of agricultural potential. These findings indicate that while their placement may not be optimal, the distribution of protected areas across the globe is broadly correlated with several measures of importance for biodiversity.

These results are somewhat unexpected, as the optimal placement of protected areas with respect to biodiversity conservation is often but one of several processes that determine the establishment of protected areas. In fact, several regional studies have indicated that the establishment of protected areas is more strongly influenced by the degree of human presence and availability of the land. These influences lead to the placement of protected areas both distant from human occupation (Scott *et al.*, 2001a; Pressey *et al.*, 2002) and in the least desirable agricultural areas (Rebelo, 1997; Scott *et al.*, 2001b; Pressey *et al.*, 2002; Rouget *et al.*, 2003). While our findings at first appear to be in opposition to those of these previous studies, underlying similarities emerge upon examining patterns within each biogeographical realm – and for each of our three biodiversity indicators – separately.

Endemism was found to be the most important variable in describing protected area distribution (Table 2). Globally, areas of high endemism are predominantly found in tropical montane, tropical and temperate deserts and island regions (Ceballos & Ehrlich, 2006; Lamoreux *et al.*, 2006). Likewise, a disproportionate number of protected areas have also been placed in many of these same areas, due to their inaccessibility or low suitability for human land use, and this is an important factor in our endemism results. Our findings are supported by a number of regional studies. For example, Hunter & Yonzon (1993) found that Nepali protected areas were preferentially located in areas both below 500 m and above 3500 m. The protected areas in lowland Nepal were established at a time when the human population was low due to the threat of malaria (e.g. they were established on lands that were considered not to be valuable for agriculture or other uses). Trisurat (2007) found that Thailand's montane regions higher than 400 m were well-represented in the protected area system, but that many lowland habitats were under-represented by protected areas. Pressey *et al.* (2002) found that gazetted reserves in New South Wales, Australia, were biased to steep or infertile parts of public lands.

The Indo-Malayan realm, a combination of continental and insular ecoregions, is the only realm where protected areas are inversely related to endemism (Table 2). Yet, analysing the distribution of endemic species, they are predominantly found in the lowland island ecoregions of Indonesia, Malaysia and the Philippines or the montane areas of Thailand, northern Indochina or India's Western Ghats. The area under protection was low in many of these areas (lowland Borneo and Thailand excepted), as much of the lowlands have already been converted or are under substantial pressure for conversion to agriculture (Clay, 2002; Dennis & Colfer, 2006). This inverse relationship between protection and endemism appears to be an exception to the global pattern. Overall, the tendency to place protected areas in remote, montane areas serves well to

conserve many unique species that occupy the varied elevational niches of these regions.

Vertebrate species richness was less important than endemism within all realms except the Afrotropical and Nearctic (Table 2). In the Afrotropical realm vertebrate richness reaches its highest levels in the tropical rain forests and tropical savanna-woodlands (Burgess *et al.*, 2004). Historically, many of Africa's early protected areas were created through the successful lobbying of big game hunters to conserve large mammal populations in hunting reserves (Jepson & Whittaker, 2002). Tanzania's Serengeti National Park, famous for its large mammal assemblages and migrations, was originally designated a hunting reserve, but like many other hunting reserves has subsequently been reclassified as a non-hunting area (Siegfried, 1989; Balmford *et al.*, 1992). More recently biodiversity priorities have driven the expansion of the protected area system in the tropical forests of the Congo Basin and other areas (Cowling *et al.*, 2003; Kamdem-Toham *et al.*, 2003; Burgess *et al.*, 2007). Consequently, unlike other realms, protected areas were preferentially located in the species rich lowland tropical forest and savanna ecoregions. Conversely, the protected area system has under-represented montane areas, rich in endemics, such as Tanzania's Eastern Arc Mountains or the Nigeria–Cameroon forested highlands (Bergl *et al.*, 2007; Burgess *et al.*, 2007).

Our third measure of biodiversity, threatened vertebrates – by definition those species most at risk of extinction – is an accepted conservation priority (Ricketts *et al.*, 2005; Rodrigues *et al.*, 2006). However, we found that only in the Neotropical realm were threatened species an important explanatory variable of protected areas (Table 2). Outside the Neotropics protected areas did a poor job in representing threatened species. Recently, Rodrigues *et al.* (2004a) found that the distributions of 89% of selected threatened vertebrate species may not overlap with protected areas. As most threatened species occur in the tropics, notably on mountains or islands (Baillie *et al.*, 2004), regions such as the Indonesian and Philippine archipelago, Madagascar and southern China will become important areas in which to focus future protection efforts toward conserving threatened species. However, expansion of protected areas may not be a viable option in many regions where there are human settlements or agricultural development (Luck, 2007).

Agricultural potential and resource consumption, while less important globally than biodiversity factors, were among the two most important variables describing protected area distribution in all but the Afrotropical and Australasian realms (Tables 2 and 3). Clearly the placement of protected areas reflects society's choices to retain productive lands for human use. The Nearctic realm had a strong inverse relationship between resource consumption and protected areas (Tables 2 and 3). This result supports a regional study of the United States by Scott *et al.* (2001a) who found that indeed protected areas were preferentially placed in higher elevations on less productive soils, which were those that were least populated and not already converted to agricultural uses. In the Palearctic realm, the inverse relationship between protected areas and

agricultural potential is probably related to the fact that agricultural activities have been in place for thousands of years, and consequently the protected areas were established in remaining lands, frequently in those areas with lower agricultural potential (Maiorano *et al.*, 2006). Other realms, notably the Neotropical and Indo-Malayan, have experienced substantial loss of natural habitat in many of their lowland ecoregions in recent decades, primarily due to agricultural development or livestock grazing (Clay, 2002; Dennis & Colfer, 2006). In these regions, protected areas have been frequently located in mountain ranges or distant from the current agricultural frontier.

In all realms except the Indo-Malayan and Australasian, the core geographical model was outperformed by at least five other models (Table 1). In these two realms, however, we found minimal differentiation among the best models, and the core geographical model proved to be the second best model (Table 1). Both Indo-Malaya and Australasia contain a mixture of continental and insular ecoregions. If drivers of protected area placement differ between continent and island areas, this mixture may have weakened our models in these two realms.

Our findings depend in part on the particular methods and assumptions we employ. The resolution of our data set is at the ecoregion scale, where ecosystems range in size from 39 to 4,629,416 km^2 with a median size of 72,359 km^2. We are unable to assess subecoregional effects, which will vary depending on ecoregion size. For example, even if an ecoregion has high levels of both threatened species and protection, those protected areas may be in different places within the ecoregion than the species requiring protection. Finer-scale studies have assessed this important question (Scott *et al.*, 2001a; Pressey *et al.*, 2002), but suitable data with which to conduct global analyses at the subecoregional scale were not available. Second, while our measure of the impact of humans on ecosystems did not include important forms of environmental impact, such as the use of fossil fuels and appropriation of NPP from freshwater or marine systems, it was correlated ($r = 0.997$) with another common measure of human terrestrial impact, the human footprint (Sanderson *et al.*, 2002), despite being based on different methods and input data sets. Lastly, this analysis includes data for only a small subset of known species; the inclusion of plant or insect data, for instance, would almost certainly alter the results and identify additional ecoregions whose threatened species lack protection.

Our results indicate that global patterns of habitat protection are more strongly related to vertebrate biodiversity patterns than to patterns of resource consumption or agricultural potential. However, the relative importance of these factors varies strongly among the world's biogeographical realms. In some, avoiding areas of high land-use competition appears to have had greater influence than biodiversity factors in the placement of protected areas. Understanding these biases can help to correct for them as future protected areas are added to the global network. Indeed, recent research suggests that in most unprotected priority areas for conservation – as

defined by a subset of terrestrial vertebrates – land is often available and conducive to conservation activities (Gorenflo & Brandon, 2006). Adding to this network, however, will require more than better information – establishing protected areas requires political will and, since many species move across political boundaries, international cooperation.

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