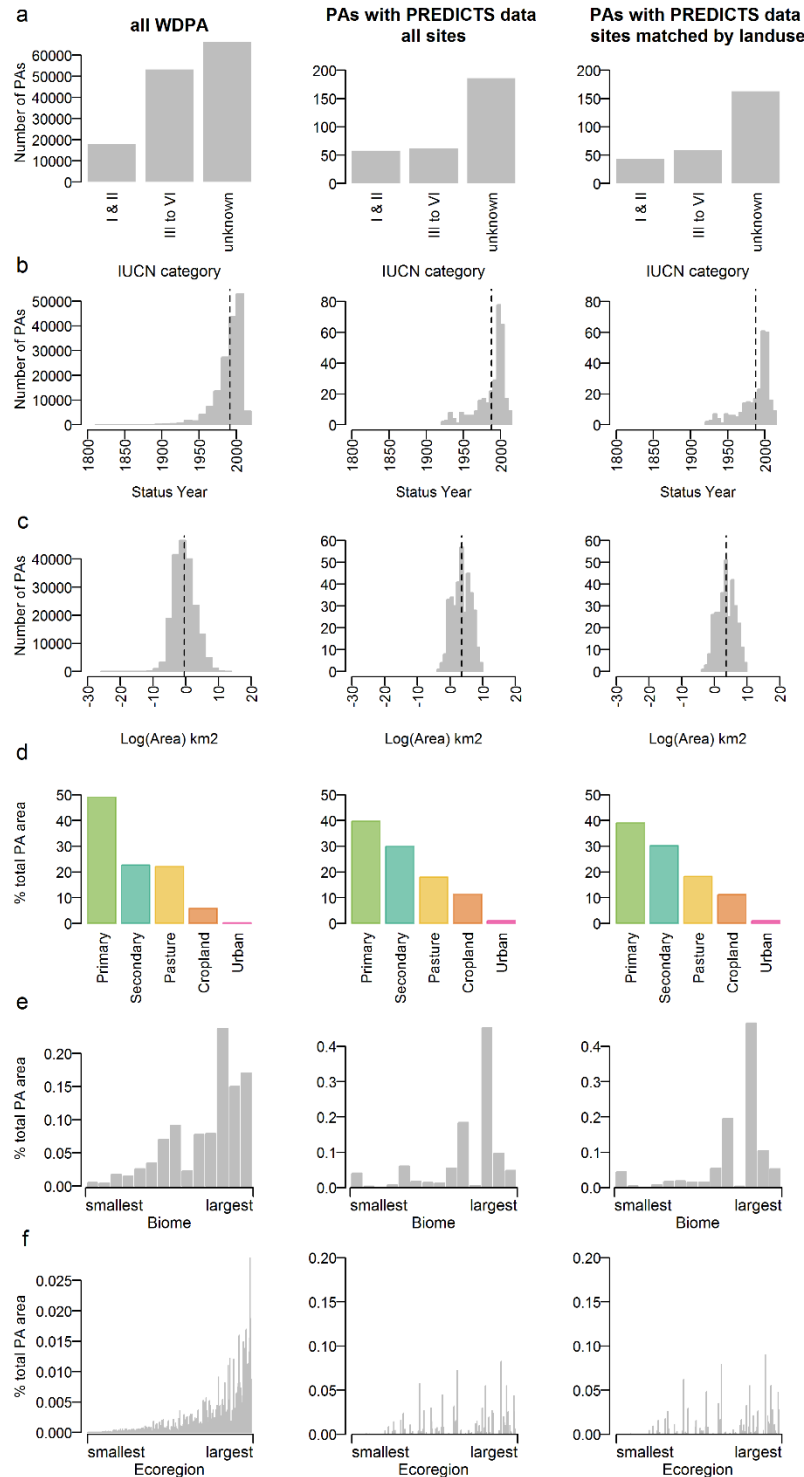
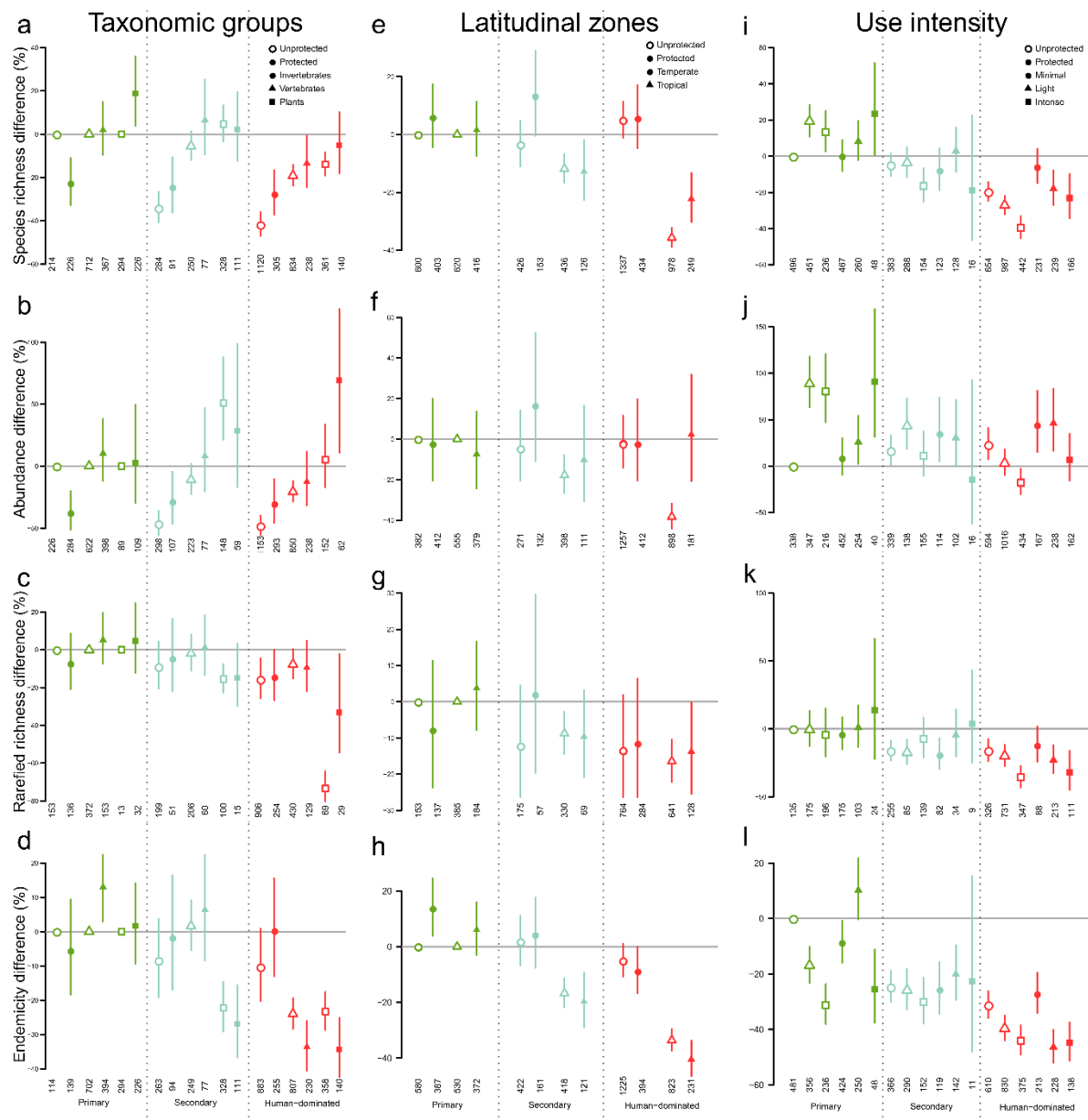


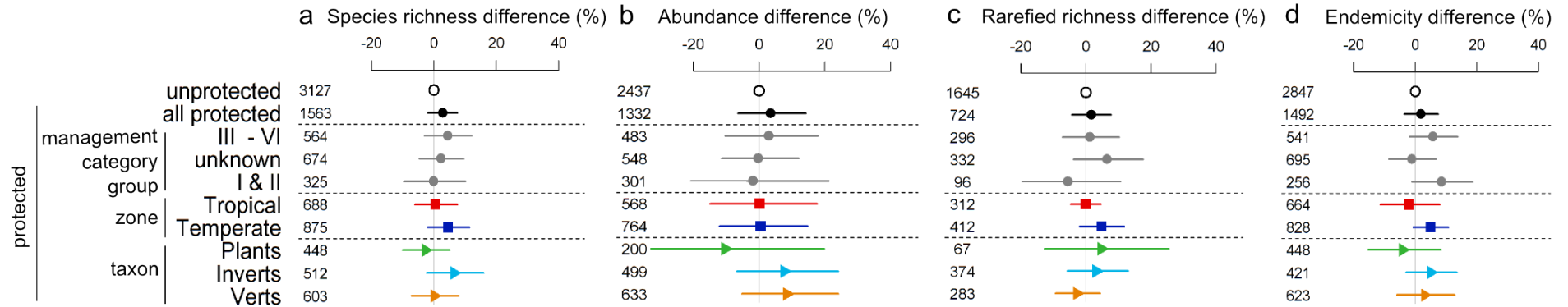
Supplementary Figures



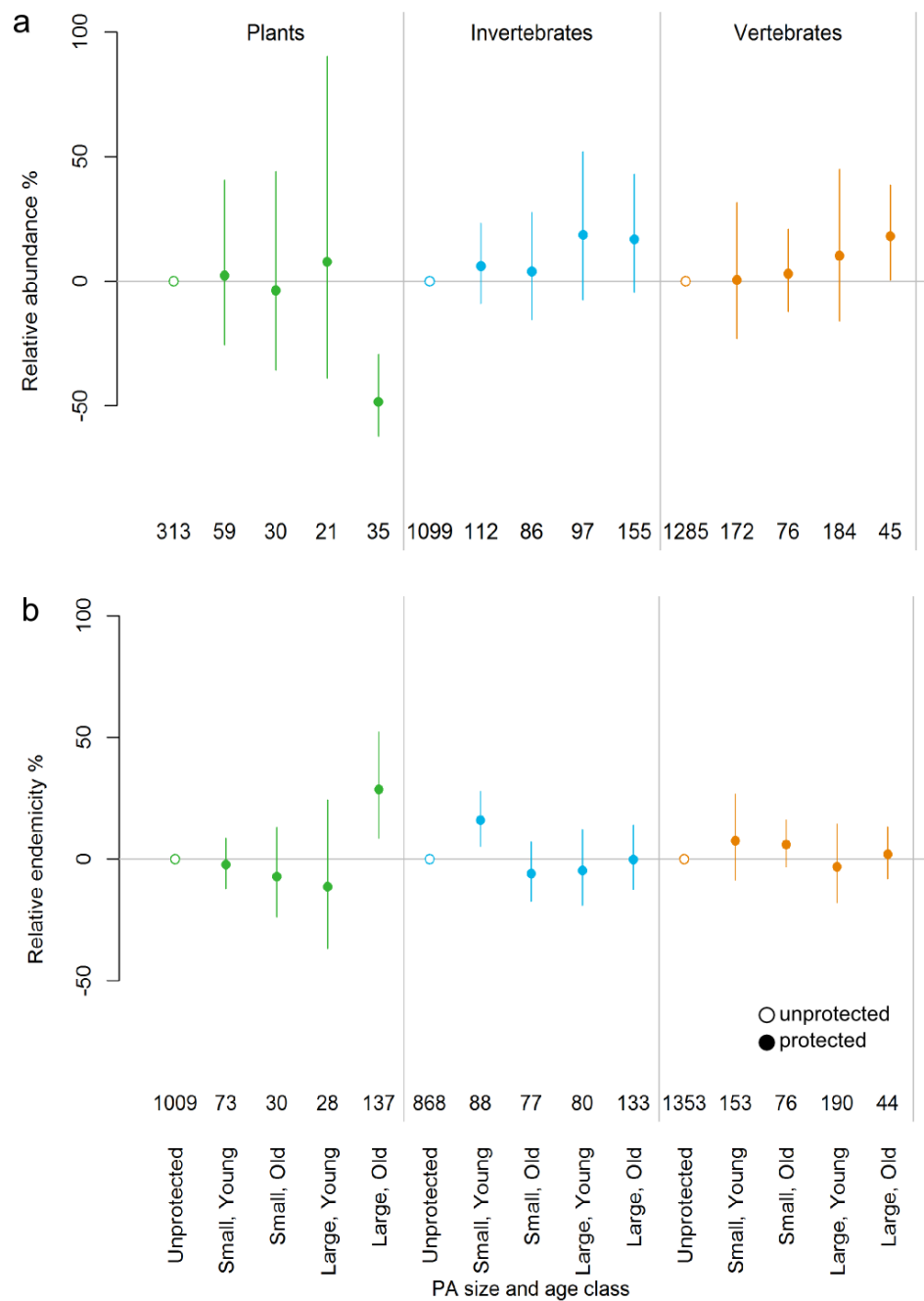
Supplementary Figure 1 | Overview of protected area data. IUCN protected area management category (a), year of establishment (status year) (b), size (c), and proportion of total land area within each of 5 land use types (d), biomes (e) and ecoregions (f) for the World Database on Protected Areas¹ (July 2014 version, $n = 194,598$; left column), all protected areas (PAs) with data in this study ($n = 359$; middle column) and the PAs for which sites could be matched by land use within the same study ($n = 313$; right column). Dashed lines show mean values.



Supplementary Figure 2 | Effects of land use types on biodiversity measures. Effects of three land use types (primary [green], secondary [blue] and human dominated [red]) and protection (unprotected = open, protected = filled symbols) on species richness (**a**), abundance (**b**), rarefied richness (**c**) and endemism (**d**) of invertebrates (circles), vertebrates (triangles) and plants (squares), in temperate (circles) and tropical (triangles) zones (**e – h**) and for three levels of use intensity: minimal (circles), light (triangles), and intense (squares) (**i – l**). Error bars show 95% confidence intervals. The number of sites in each land use type and protection status is given underneath the corresponding data point.



Supplementary Figure 3 | Effects of terrestrial protected areas on four biodiversity measures. Effects of terrestrial protected areas on four local biodiversity measures when data from each study is restricted to sites in the same land use. Response of species richness (a), total abundance (b), rarefied richness (c), and endemicity (d) to protection (black circles) relative to unprotected (open). Estimates are given separately for protected areas with different management regimes (grey circles; the least restrictive [IUCN categories III-VI], unknown [missing IUCN category, potentially a mixture of categories], and the most restrictive land management regimes [IUCN categories I & II]); for tropical (red squares) and temperate zones (blue squares) and for different taxonomic groups (triangles). Error bars show 95% confidence intervals. Sample sizes (number of sites) shown.



Supplementary Figure 4 | Effects of protected area age and size on abundance and endemicity. Effects of protected area age and size class on abundance (**a**) and endemicity (**b**) for three broad taxonomic groups, plants (green), invertebrates (blue) and vertebrates (orange). The number of sites in each age and size combination is given underneath each data point, with unprotected sites (open) and protected (filled triangles).

Supplementary Tables

Supplementary Table 1 | Statistics from the minimum adequate models for which the results are presented in Fig. 2. The first column specifies the data subset used in the model. The datasets “>80% known range”, “All data rar. richness”, “No small studies” and “No PA focus” refer to the four sensitivity analyses. In these cases we report only the results for the term of interest, not the confounding variables. χ^2 , df and p-values are given for the comparison of the model with and without the term specified in the second column. Protection was a two-level factor specifying whether each site was protected or unprotected, management category group was a four-level factor specifying whether each site was: unprotected, in a protected area with IUCN category I & II, IUCN category III to VI, or in a protected area with IUCN category unknown. Agricultural suitability, slope and elevation were all continuous variables, for which cubic, quadratic and linear terms were tested sequentially. The polynomial term (poly) retained in the final model is given for the continuous variables. dAIC gives the change in AIC from a model with the term specified to one without.

Dataset	Term removed	Species richness					Abundance					Rarefied richness					Endemicity				
		poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC
All-sites	protection		9.99	1	0.002	7.99		5.09	1	0.024	3.09		1.33	1	0.248	-0.67		2.99	1	0.084	0.99
	slope	1	0.40	1	0.529	-1.60	1	0.17	1	0.681	-1.83	1	0.06	1	0.813	-1.94	3	6.73	1	0.009	4.73
	elevation	1	46.90	1	<0.001	44.90	1	0.76	1	0.382	-1.24	3	9.15	1	0.002	7.15	2	35.14	1	<0.001	33.14
	ag.suitability	1	7.82	1	0.005	5.82	1	1.58	1	0.209	-0.42	3	10.17	1	0.001	8.17	3	9.8/9	1	0.002	7.89
All-sites	management category		11.18	3	0.011	5.18		5.04	3	0.169	-0.96		3.21	3	0.360	-2.79		3.67	3	0.299	-2.33
	slope	1	0.58	1	0.448	-1.42	1	0.04	1	0.847	-1.96	1	0.09	1	0.764	-1.91	3	5.90	1	0.015	3.90
	elevation	2	4.32	1	0.038	2.31	1	1.21	1	0.271	-0.79	1	4.01	1	0.022	3.22	2	36.78	1	<0.001	34.78
	ag.suitability	1	8.51	1	0.004	6.51	1	1.81	1	0.178	-0.19	1	11.42	1	<0.001	9.43	3	7.11	1	0.008	5.11
>80% known range	protection																	1.19	1	0.275	-0.81
	management category																	4.38	3	0.223	-1.62
All data rar. richness	protection		4.41	1	0.036	2.41															
	management category		7.03	3	0.071	1.03															
No small studies	protection		7.95	1	0.005	5.95		6.34	1	0.012	4.34		1.58	1	0.208	-0.41		2.96	1	0.085	0.96
	management category		8.68	3	0.034	2.68		5.44	3	0.142	-0.55		3.21	3	0.360	-2.79		5.00	3	0.172	-0.10
No PA focus	protection		6.43	1	0.011	4.44		3.91	1	0.048	1.91		0.88	1	0.349	-1.12		1.74	1	0.187	-0.26
	management category		8.21	3	0.042	2.21		4.27	3	0.234	-1.73		3.30	3	0.347	-2.70		2.16	3	0.541	-3.84

Supplementary Table 2 | Statistics from mixed effects models testing for effect of land use and protection, using all data from studies with at least one site inside and outside a protected area. The first column specifies the data used. The datasets “>80% known range”, “All data rar. richness”, “No small studies” and “No PA focus” refer to the four sensitivity analyses. In these cases we report only the results for the term of interest, not the confounding variables. χ^2 , df and p-values are given for the comparison of the model with and without the term specified. Protection was a two level factor specifying whether each site was protected or unprotected, LU8 was an eight level factor describing the land use of each site (primary, mature secondary, intermediate secondary, young secondary, plantation, cropland, pasture, urban). LU3 was a three level factor grouping each level from land use (8) into one of three coarser categories: primary, secondary or human dominated land use. Use intensity was a three level factor (intense, medium and light use). Taxon was a three level factor (plants, vertebrates and invertebrates) and latitudinal zone was a two level factor (tropical and temperate). LUPA refers to the compound variable used to express the land use (3):protection interaction, with six levels, one for each possible combination of protection and land use (3). LUUI refers to the compound variable used to express the land use (3):use intensity interaction, with nine levels, one for each possible combination of land use (3) and use intensity. Agricultural suitability, slope and elevation were all continuous variables (for which cubic, quadratic and linear terms were tested sequentially) with “poly” giving the polynomial term retained in the final model. Where the term was not significant, χ^2 , df and p-value are given for the linear term only. dAIC gives the change in AIC from a model with the term specified to one without.

Dataset	Term removed	Species richness					Abundance					Rarefied richness					Endemicity				
		poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC
All-sites	LU8		246.49	7	<0.001	232.49		103.58	7	<0.001	89.58		61.84	7	<0.001	47.84		298.61	7	<0.001	284.61
	protection		4.80	1	0.028	2.80		2.58	1	0.11	0.58		0.54	1	0.464	-1.46		0.17	1	0.681	-1.83
	slope	1	0.06	1	0.814	-1.94	1	0.06	1	0.799	-1.94	1	0.72	1	0.395	-1.28	3	11.29	3	0.010	5.29
	elevation	3	314.29	3	<0.001	25.29	1	2.77	1	0.096	0.77	3	13.21	3	0.004	7.21	3	105.48	3	<0.001	99.48
	ag.suitability	3	10.78	3	0.013	4.78	1	1.87	1	0.171	-0.13	3	33.18	3	<0.001	27.16	3	11.53	3	0.009	54.53
	taxon		10.10	2	0.006	6.10		21.51	2	<0.001	17.51		4.21	2	0.122	0.21		45.39	2	<0.001	41.39
	latitudinal zone		5.29	1	0.02	3.29		4.44	1	0.035	2.44		6.32	1	0.012	4.32		63.69	1	<0.001	61.69
	LU8:protection		15.26	7	0.033	1.26		19.12	7	0.008	54.12		1.74	7	0.973	-12.26		25.05	7	0.001	11.05
>80% known range	LU8: protection																	25.38	7	<0.001	11.38
All data rar. richness	LU8: protection		15.64	7	0.029	1.64															
No small studies	LU8: protection		17.29	7	0.016	3.29		18.79	7	0.009	4.79		4.10	7	0.770	-9.90		32.45	7	<0.001	18.45
No PA focus	LU8: protection		23.08	7	0.002	9.08		16.61	7	0.020	2.61		4.51	7	0.719	-9.49		20.73	7	0.004	6.73
All-sites	LU3		243.38	2	<0.001	239.40		58.80	2	<0.001	54.80		48.52	2	<0.001	44.52		238.22	2	<0.001	234.22
	protection		3.63	1	0.056	1.64		2.44	1	0.118	0.44		0.65	1	0.418	-1.35		0.36	1	0.550	-1.64
	slope	1	0.03	1	0.871	-1.97	1	0.00	1	0.995	-2.00	1	0.76	1	0.383	-1.24	3	10.50	3	0.015	4.50
	elevation	3	26.54	3	<0.001	20.54	1	2.55	1	0.110	0.55	3	15.69	3	0.001	9.69	3	108.34	3	<0.001	102.34
	ag.suitability	3	11.04	3	0.011	5.04	1	2.13	1	0.144	0.13	3	28.82	3	<0.001	22.81	3	11.56	3	0.009	5.56
	taxon		10.47	2	0.005	6.47		18.09	2	<0.001	14.09		4.05	2	0.131	0.06		44.59	2	<0.001	40.59
	latitudinal zone		5.37	1	0.020	3.37		3.83	1	0.501	1.83		6.19	1	0.013	4.19		61.77	1	<0.001	59.78
	LUPA		106.00	10	<0.001	86.00		103.12	10	<0.001	83.12		87.74	10	<0.001	67.44		89.84	10	<0.001	69.84
	LUPA:taxon		77.04	10	<0.001	57.04		105.94	10	<0.001	81.94		95.02	10	<0.001	75.02		74.99	10	<0.001	54.99
All-sites		statistics for main terms are the same as rows 13 – 19 of this table																			
	LUPA		94.73	6	<0.001	82.74		40.70	6	<0.001	28.70		0.37	6	0.588	-3.63		107.65	6	<0.001	95.65
	LUPA: latitudinal zone		66.16	5	<0.001	56.16		32.15	5	<0.001	22.15		4.29	5	0.508	-5.71		91.27	5	<0.001	81.27
All-sites	LUUI		329.08	8	<0.001	313.08		148.63	8	<0.001	132.63		78.07	8	<0.001	65.07		338.95	8	<0.001	322.95
	protection		2.31	1	0.128	0.31		2.38	1	0.123	0.38		0.40	1	0.529	-1.60		0.15	1	0.701	-1.85
	slope	1	0.56	1	0.455	-1.44	1	0.069	1	0.794	-1.93	1	0.91	1	0.339	-1.09	3	12.68	3	0.005	6.68
	elevation	3	28.11	3	<0.001	22.11	1	2.41	1	0.120	0.41	3	14.80	3	0.002	8.80	3	84.50	3	<0.001	78.50
	ag.suitability	3	11.29	3	0.010	5.29	1	2.02	1	0.155	0.02	3	30.43	3	<0.001	24.43	3	7.93	3	0.048	1.93
	taxon		10.69	2	0.005	6.70		24.46	2	<0.001	20.46		4.71	2	0.095	0.71		45.25	2	<0.001	41.25
	latitudinal zone		4.83	1	0.028	2.83		5.97	1	0.015	3.97		5.96	1	0.015	3.96		60.01	1	<0.001	58.01
	LUUI: protection		27.07	8	<0.001	12.07		39.75	8	<0.001	23.75		6.23	8	0.621	-9.77		52.51	8	<0.001	36.51

Supplementary Table 3 | Statistics from mixed effects models testing for effect of protection, using only data from sites matched by land use (as in main text Fig. 1d). Right hand column and χ^2 , df and p-values given for removal of term specified. Protection was a two level factor specifying whether each site is protected vs unprotected, management category group was a four-level factor specifying whether each site was: unprotected, in a protected area with IUCN category I & II, IUCN category unknown or IUCN category III to VI. AGSZ was a five level factor for age and size groups (unprotected, small and young, small and old, large and young, large and old). Taxon was a three level factor for taxonomic groups (plants, vertebrates and invertebrates) and latitudinal zone was a two level factor (tropical and temperate). Agricultural suitability, slope and elevation were all continuous variables (for which cubic, quadratic and linear terms were tested sequentially) and the polynomial term retained in the final model is given in “poly”. dAIC gives the change in AIC from a model with the term specified to one without.

Dataset	Term removed	Species richness					Abundance					Rarefied richness					Endemicity				
		poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC	poly	χ^2	df	p	dAIC
Matched-sites	protection		1.28	1	0.258	-0.72		0.42	1	0.517	-1.58		0.31	1	0.589	-1.69		0.31	1	0.575	-1.69
	slope	1	0.13	1	0.714	-1.87	1	0.87	1	0.352	-1.13	2	4.01	1	0.045	2.01	3	10.74	1	0.001	8.74
	elevation	1	44.74	1	<0.001	42.74	1	4.57	1	0.033	2.57	3	5.65	1	0.017	3.65	2	46.33	1	<0.001	44.33
	ag.suitability	3	13.28	1	<0.001	11.28	1	3.98	1	0.046	1.97	3	8.69	1	0.003	6.69	3	9.70	1	1.839	7.70
Matched-sites	management category		3.24	3	0.356	-2.76		0.18	3	0.980	-5.81		1.88	3	0.598	-4.12		4.63	3	0.201	-1.37
	slope	1	0.21	1	0.649	-0.76	1	3.80	1	0.051	1.80	2	4.58	1	0.599	2.57	1	5.41	1	0.020	3.41
	elevation	1	41.07	1	<0.001	39.07	1	1.09	1	0.296	-0.91	3	3.86	1	0.049	1.86	1	93.88	1	<0.001	91.88
	ag.suitability	1	1.24	1	0.265	-0.76	1	3.92	1	0.048	1.92	1	8.79	1	0.003	6.78	1	0.22	1	0.637	-1.78
Matched-sites tropical	protection		0.04	1	0.846	-1.96		<0.01	1	0.999	-2.00		0.04	1	0.839	-1.96		0.20	1	0.658	-1.80
	slope	1	0.88	1	0.348	-1.12	3	7.84	1	0.005	5.84	2	15.92	1	<0.001	13.92	1	2.05	1	0.152	0.05
	elevation	3	13.89	1	<0.001	11.89	3	9.15	1	0.002	7.15	1	4.57	1	0.033	2.57	3	8.04	1	0.005	6.04
	ag.suitability	3	19.17	1	<0.001	17.17	3	4.22	1	0.040	2.22	3	3.89	1	0.049	1.89	2	6.58	1	0.010	4.58
Matched-sites temperate	protection		1.57	1	0.211	-0.43		1.08	1	0.299	-0.92		0.57	1	0.450	-1.43		2.23	1	0.136	0.23
	slope	1	0.07	1	0.799	-1.93	1	0.36	1	0.549	-1.64	1	1.61	1	0.205	-0.39	3	8.90	1	0.003	6.90
	elevation	1	19.25	1	<0.001	17.25	1	<0.01	1	0.926	-1.99	1	0.03	1	0.871	-1.97	3	7.89	1	0.005	5.89
	ag.suitability	1	0.29	1	0.593	-1.71	1	0.48	1	0.490	-1.52	1	0.82	1	0.365	-1.18	3	17.97	1	<0.001	15.97
Matched-sites plants	protection		0.55	1	0.457	-1.45		0.70	1	0.404	-1.30		4.48	1	0.034	2.48		0.60	1	0.440	-1.40
	slope	1	1.43	1	0.231	-0.57	3	7.50	1	0.006	5.50	1	0.35	1	0.553	-1.65	1	2.13	1	0.144	0.13
	elevation	2	9.38	1	0.002	7.38	1	5.45	1	0.020	3.45	1	2.94	1	0.087	0.94	3	7.76	1	0.005	5.76
	ag.suitability	1	5.13	1	0.023	3.13	1	0.70	1	0.401	-1.30	3	1.12	1	<0.001	9.08	1	2.76	1	0.097	0.76
Matched-sites invertebrates	protection		1.58	1	0.209	-0.42		0.95	1	0.329	-1.05		0.17	1	0.678	-1.83		1.10	1	0.295	-0.90
	slope	1	0.86	1	0.354	-1.14	1	0.36	1	0.551	-1.64	3	4.12	1	0.012	2.12	1	0.67	1	0.414	-1.33
	elevation	1	6.57	1	0.010	4.57	1	2.21	1	0.137	0.21	1	0.51	1	0.476	-1.49	1	0.40	1	0.528	-1.60
	ag.suitability	1	2.55	1	0.110	0.55	1	1.26	1	0.262	-0.74	1	1.15	1	0.284	-0.85	1	0.21	1	0.644	-1.79
Matched-sites vertebrates	protection		<0.01	1	0.996	-2.00		1.50	1	0.220	-0.50		1.99	1	0.159	-0.01		0.43	1	0.511	-1.57
	slope	1	1.41	1	0.235	-0.59	2	12.47	1	<0.001	10.47	2	4.63	1	0.031	2.63	3	11.03	1	<0.001	9.03
	elevation	3	4.18	1	0.041	2.18	1	0.99	1	0.319	-1.00	1	0.09	1	0.761	-1.91	3	19.81	1	<0.001	17.81
	ag.suitability	3	12.36	1	<0.001	10.36	3	6.71	1	0.010	4.71	1	0.42	1	0.519	-1.58	3	4.61	1	0.032	2.61
Matched-sites	AGSZ		16.22	4	0.003	8.22		3.70	4	0.448	-4.30		7.33	4	0.120	-0.67		7.73	4	0.102	-0.27
	taxon		8.29	2	0.016	4.29		13.46	2	0.001	9.46		2.91	2	0.233	-1.09		49.81	2	<0.001	45.81
	latitudinal zone		4.72	1	0.030	2.72		3.05	1	0.081	1.05		5.56	1	0.018	3.56		62.70	1	<0.001	60.70
	slope	1	0.04	1	0.841	-1.96	1	3.67	1	0.056	1.67	1	<0.01	1	0.952	-2.00	3	9.53	1	0.002	7.53
	elevation	2	7.29	1	0.007	5.29	1	0.91	1	0.339	-1.09	3	9.29	1	0.002	7.29	2	26.61	1	<0.001	24.61
	ag.suitability	3	15.58	1	<0.001	13.59	1	4.00	1	0.046	2.00	3	8.87	1	0.003	6.87	3	4.60	1	0.030	2.70
	AGSZ :taxon		10.04	8	0.262	-5.95		25.38	8	0.001	9.37		8.58	8	0.380	-7.42		16.64	8	0.034	0.65
	AGSZ: latitudinal zone		5.81	4	0.214	-2.19		7.19	4	0.126	-0.81		4.50	4	0.343	-3.50		3.28	4	0.511	-4.72

Supplementary Notes

List of data sources.

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Supplementary Methods

Data. The PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) database collates spatial comparisons of community composition and site-level biodiversity from terrestrial sites around the world². The primary aim of the PREDICTS project is to model and project how biodiversity in terrestrial communities responds to human activity^{2,3}. We used data entered into the PREDICTS database up to the 13th November 2014. These data were obtained from studies identified through a review of conservation and ecology literature (including primary literature and databases) and requests to authors². Criteria for inclusion in the dataset were 1) data were published, in press or obtained using a published methodology 2) sampling took place post 2000, 3) studies sampled more than one land use, and 4) geographical coordinates of sampling locations are available². Data on coordinates and site specific abundances or presence/absence data for individual species were obtained from the original publication or directly from the authors.

For sites where data on the abundance of individuals in each species were available we calculated the species richness, total abundance, rarefaction-based richness (hereafter ‘rarefied richness’) and mean community endemism (1/community weighted mean range size ($\log_{10} \text{ km}^2$), hereafter endemism). We selected these response variables as species richness and total abundance are easily understood by a broad audience, and because endemism and rarefied richness indicate aspects of ecological communities that are often considered to be a conservation priority (higher numbers of species with small range sizes and a higher “concentration” of species for a given number of individuals). Species range sizes were measured as in ref 4, using the total land area of the 1° grid cells with records in the Global Biodiversity Information Facility (GBIF) database (<http://www.gbif.org/>, downloaded August 2014). Where range size data was not available for one or more of the species’ sampled, the community mean range size was calculated from species for which data were available. However, to check that these missing data did not affect our results, we also repeated our analyses using only the sites for which at least 80% of the individuals had known range data (see sensitivity analyses below). We recognise that the numbers of species records in GBIF are not consistent across geographic areas and taxonomic groups. However, most studies whose data we included in our analysis sampled a relatively confined taxonomic group and geographic spread. As our analyses used mixed-effects models (see below), our results are driven by within-study differences between protected and unprotected sites, which are much less likely to be affected by the biases in the GBIF database. In addition, we have

also found that differences in the grain size used (1, 0.1 or 0.01° grid cells) do not affect the estimates of species' range size, and that our GBIF occupancy measure gives similar range estimates to those derived from IUCN extent-of-occurrence maps⁵.

To calculate rarefied richness, we applied the same rarefaction procedure to each study that had data on species' abundance. First, we calculated the minimum abundance, n_{min} , recorded at any one site in the study. We then took a random sample (without replacement) of n_{min} individuals from the pool of individuals recorded at each site in that study. Rarefied richness was the count of species in this random sample. We repeated this process 1000 times and calculated one overall mean rarefied richness, rounded to the nearest integer. For some studies we only had data on species occurrence; a binary variable describing whether or not a species was detected in the sample at a given site, for all species observed in that study. For these sites we calculated only species richness and endemism. Site land use was classified from habitat descriptions in the literature and from contact with authors, as primary vegetation, secondary vegetation (mature, intermediate, young), plantation, pasture, cropland or urban. We used these habitat descriptions to allocate land use rather than obtaining information on land cover from global satellite imagery products, as the latter cannot easily distinguish certain land uses (e.g. forest and plantation, grassland and pasture), and generally have lower spatial and temporal resolution. A repeatability analysis was carried out on a subset of the PREDICTS data to ensure that the land use classifications were consistently applied – further details are given in ref 2. In addition to land use, levels of intensity of use (minimal, light, intense, or unknown [excluded from these analyses]) were assigned based on the literature and contact with authors. Further details of the PREDICTS database and definitions of land use and use intensity are given in ref 2.

The PREDICTS database does not target protected area studies specifically. Only 10 of 115 sources included in our analyses mentioned that they were intentionally comparing sites within a protected area and those outside. The overlap between the sources used in our analysis and other meta-analyses of protected area effectiveness was very low (no overlap with the sources listed by Geldmann *et al.*⁶ and only 6 sources shared with Coetzee *et al.*⁷), so our data provide a new body of evidence that has not previously been used to answer questions about the biodiversity within protected areas.

Information on protected areas was obtained from the July 2014 release of the World Database on Protected Areas (WDPA)¹. We used all protected areas with “designated” or “proposed” status, excluded UNESCO Man and Biosphere reserves because these include buffer and transition areas which do not meet the IUCN definition of protected areas. For

protected areas with known locations and reported areas but unknown boundaries (14 of 359 protected areas, containing 245 of 6531 sites in our analyses [3.8%]), we created circular buffers with an area equal to the reported value. For each PREDICTS site falling within a protected area, we extracted the year the protected area was designated (STATUS_YR), size (GIS area) and IUCN Protected Area Management Category (henceforth IUCN category). Where a PREDICTS site fell into more than one protected area, we selected the size of the largest protected area, the status year of the oldest protected area and the IUCN category of the protected area with the most restrictive management objectives (where Ia > Ib > II > III > IV > V > VI). Where countries have not used the IUCN system to classify their protected areas, or the IUCN category was unreported (IUCN_CAT = "Not Applicable" or "Not Reported"), we set our IUCN category variable to "unknown". As studies were carried out in different years, we calculated the duration of protection at each site when it was sampled: the difference between the year of earliest sampling at the site and the STATUS_YR. If STATUS_YR was unknown, we treated this as missing data and set protected area age to "NA"; these data points were excluded from analyses of age and size class but included in all other analyses. Sites with a duration of protection less than or equal to zero were considered to be unprotected.

We assessed whether our sites and the protected areas sampled are randomly placed with respect to latitude and longitude and found no bias towards higher or lower latitudes ($P = 0.51$, $\chi^2 = 0.44$, $df = 1$) or longitudes ($P = 0.12$, $\chi^2 = 2.47$, $df = 1$), using a mixed effect model approach with either latitude or longitude as a response variable, protection status (in vs out) as a fixed effect and study as a random effect (with a study-specific gradient for protection).

We obtained data on three covariates that may affect biodiversity response: 1) Mean elevation at 30 arc-second (approximately 1 km² grid cell size) resolution⁸; 2) Slope, calculated from elevation data at 30 arc-second (approximately 1 km² grid cell size) resolution; 3) Agricultural suitability, available at 5 arc-minute (approximately 10 km² grid cell size) resolution⁹. For each site, we calculated the mean elevation and slope across a buffer with 1 km radius. Due to the lower spatial resolution of the dataset, for agricultural suitability we took the absolute value of the raster at each site location. There are other factors that may influence biodiversity that we purposely did not incorporate as covariates in our models, such as human population density, accessibility (travel time to the nearest city > 5000 people), distance to market, or distance to roads. These factors may have been influenced by the presence of a protected area, so we did not consider them to be fully

independent confounding effects. Other potential confounding variables, such as evapotranspiration, precipitation and mean temperature are included in the agricultural suitability layer⁹ and thus including these variables separately would entail collinearity between explanatory and confounding variables. The latitudinal zone (tropical or temperate) of each site was allocated based on whether sites fell between tropical latitudes (approximately $\pm 23.5^\circ$ from the equator^{10,11}, Fig. 1). All studies fell into either the tropical or temperate zone.

All spatial calculations were carried out in ESRI ArcMap (version 10.0, ref 12) using an equal-area Mollweide projection. The package `rgdal`¹³ was used to plot data in R.

All-sites data. To test whether the effect of protected areas differed between land uses, we included data from all PREDICTS studies with at least one site inside and one site outside a protected area (Fig. 1B). To ensure that there were sufficient sites to make a robust estimate of the effects of land use inside and outside protected areas we had to retain all sites within these studies. To avoid artefactual differences arising because of comparisons between sites with extremely large distances between them, any sites that were on average more than 150 km away from other sites in their study were dropped. This distance was selected as it formed a clear break in the histogram of distances between sites, above which frequencies were consistently low. Each site was allocated to a unique taxonomic group (vertebrates, invertebrates, or plants), with two studies that sampled more than one major taxonomic group at each site divided accordingly. The all-sites data included data for 6531 sites from 156 studies and covers 13,669 species, 48 countries, 101 ecoregions, 13 biomes¹⁴, 23 hotspots and 359 protected areas.

Matched-sites data. In the all-sites data, sites within a protected area may be in a different land use to sites outside a protected area, but within the same study. We therefore applied an additional, stricter data selection process to assess whether protected areas have an effect within a given land use and which protected area characteristics alter this effect. The matched-sites data retained only sites within the same land uses that occurred both inside and outside the protected area(s) within any given study (Fig. 1d). The matched-sites data included data for 5015 sites from 144 studies and covers 12,898 species, 44 countries, 85 ecoregions, 21 hotspots and 313 protected areas.

Statistical analyses. Both abundance and occurrence records will have been influenced by study-specific sampling methodologies; we used mixed effect models to control for these differences. We compared nested random factor structures containing source ID, study ID (studies were separated by sampling method, and more than one study may have been presented within the same source), and block (derived from grouping structures where reported in the original study). See equations A to E (below) for model structures used in each analysis. We also compared random factor structures with and without a random slope for protection status (two-level factor, protected vs unprotected) or management category (four-level factor: unprotected, IUCN category I & II, IUCN category unknown, and IUCN category II to VI) at the study level, depending on which of these factors was included as a fixed effect. The best random factor structure was selected using Akaike Information Criterion (AIC) values.

The geographical coverage of the PREDICTS database did not allow us to apply the strict counterfactual matching approach, so instead we included slope, elevation and agricultural suitability as covariates in our models. There are other factors that may influence biodiversity that we purposely did not match for, or incorporate as covariates in our models, such as fragmentation, human population density or distance to roads. These may have been influenced by the presence of a protected area, so we did not consider them to be fully independent confounding effects.

Selection of fixed effects was based on p-values, using a threshold of 0.05. Changes in AIC for each term dropped from the model are also given in results tables for comparison. As a result of corrections for sampling efforts, not all abundance values were integers, so we log-transformed abundance data. Species richness and rarefied richness data were modelled using Poisson errors (log link function). Observation level random effects were included where needed to account for overdispersion. Any studies that focussed on only one species [7 studies (4% of all studies) accounting for 2% of all the sites in the all-sites data] were excluded from analyses where species richness or rarefied richness was the response variable. Sites without complete data were dropped.

All analyses were carried out in R¹⁵ using the lme4¹⁶ and influence.ME¹⁷ packages.

Analyses for “Local biodiversity inside and outside protected areas” Models were run on the all-sites data and included protection status (PS, inside versus outside a protected area) as a fixed effect, with the confounding variables agricultural suitability (AG), elevation (EL) and slope (SL) included as covariates. Equation A gives an example of the full model structure for the response variable species richness (SR), where the random structure includes study (SS), block (SSB) and site (SSBS). Note that when random intercepts are strictly nested, the following two ways of specifying the random-effects structure are exactly equivalent: (1|SS) + (1|SSB) + (1|SSBS) and (1|SS/SSB/SSBS):

```
M1 <- glmer(SR ~ PS + poly(AG,3) + poly(SL,3) + poly(EL,3) +  
  (1+PS|SS) + (1|SSB) + (1|SSBS), family = "poisson")
```

 (A)

To test for differences between IUCN categories we replaced the variable describing protection status with one describing management category group (factor with four levels; unprotected, IUCN category I & II, IUCN category III to VI and IUCN category unknown), again including all three confounding variables as fixed effects. To confirm that results were not driven by differences in underlying datasets, the influence of small studies or studies specifically focussing on protected areas, we repeated these models with appropriate subsets of the data (see sensitivity analyses below).

Analyses for “Effects of protection within and among land uses” Biodiversity measures and protection status across different land-uses were also modelled using the all-sites data. Here we included PS, land use (LU_8: eight level factor; primary, secondary mature, secondary intermediate, secondary young, plantation, cropland, pasture and urban), taxonomic group (TG), latitudinal zone (LZ), AG, SL, EL, and the land-use: protection interaction as fixed effects in our model selection process. Equation B gives an example of this full model structure for SR, with the random structure as above:

```
M1 <- glmer(SR ~ LU_8 + PS + TG + LZ + LU_8:PS +  
  poly(AG,3) + poly(SL,3) + poly(EL,3) +  
  (1+PS|SS) + (1|SSB) + (1|SSBS), family = "poisson")
```

 (B)

To achieve sufficient numbers of observations in each comparison group when modelling the effects of land use intensity, we created a nine-level factor (LUUI) expressing the land use

intensity at each site, and whether the land use was primary vegetation, secondary vegetation (any age class) or human-dominated (plantation, cropland, pasture, urban). We then tested for an interaction between this nine-level factor and PS. Equation C gives an example of this full model structure for SR, with the same random factor structure as in equation B above:

```
M1 <- glmer(SR ~ PS + LUUI + LUUI:PS + TG + LZ +
  poly(AG,3) + poly(SL,3) + poly(EL,3) +
  (1+PS|SS) + (1|SSB) + (1|SSBS), family = "poisson")
```

 (C)

To model responses to protection across land-uses in different LZ and TG we created a compound variable (LUPA) with six levels, one for each combination of land use (primary, secondary or human dominated) and PS. We then tested for the interaction between this variable and either TG (as in equation D) or LZ.

```
M1 <- glmer(SR ~ LUPA + TG + LZ + LUPA:TG
  poly(AG,3) + poly(SL,3) + poly(EL,3) +
  (1+PS|SS) + (1|SSB) + (1|SSBS), family = "poisson")
```

 (D)

To confirm that results were not driven by differences in underlying datasets, the influence of small studies or studies specifically focussing on protected areas, we repeated these models with appropriate subsets of the data (see sensitivity analyses below).

Analyses for “Effect of protection when sites are matched by land use” Using the matched-sites data, we re-ran the same models used for the first set of analyses (see equation A above), with either protection status or management category group as a fixed effect, and subsetting the data into latitudinal zones or taxonomic groups as required.

In addition, to further assess whether particular protected area characteristics might affect the biodiversity response when matching for land use, we ran models specifying the age-size class of the protected areas (AGSZ, a factor with four levels; young (< 20 years) and small (< 400 km²), young and large (400 – 12,000 km²), old (20 – 85 years) and young, old and large) and including land use (LU) as a crossed random factor.

Equation E gives an example of this full model structure for the response variable species richness (SR), where the random structure includes study (SS), block (SSB) and site (SSBS):

$$\begin{aligned}
M1 <- \text{glmer}(\text{SR} \sim \text{AGSZ} + \text{LZ} + \text{TG} + \text{AGSZ:LZ} + \text{AGSZ:TG} + \\
&\text{poly}(\text{AG},3) + \text{poly}(\text{SL},3) + \text{poly}(\text{EL},3) + \\
&(1|\text{SS}) + (1|\text{SSB}) + (1|\text{SSBS}) + (1|\text{LU}), \text{family} = \text{"poisson"})
\end{aligned}
\tag{E}$$

We further assessed the importance of land use versus protection in explaining differences in local biodiversity by comparing the R^2 values of a model with only land use or protection as fixed effects and the full model (land use, protection and their interaction). We used the marginal R^2 value following methods described by Nakagawa & Schielzeth¹⁸. 90% (species richness), 90% (abundance) and 86% (endemicity) of the variance explained by the full model (with land use, protection and their interaction) were provided by a model with just the land-use term.

Analyses for “Estimating the global effectiveness of protected areas” If protected areas are entirely effective, sites inside protected areas should have the species richness and abundance of sites in minimally-used primary vegetation regardless of land use. If protected areas are not at all effective, their species richness and abundance should average the same as sites in the same land use outside protected areas. These endpoints delimit a natural scale on which to estimate protected area effectiveness, e .

We assume that an estimate of the state of global terrestrial biodiversity, expressed as a proportion of that found in minimally-used primary vegetation, is made up of the biodiversity inside protected areas and outside protected areas. We take i as the mean value of a biodiversity measure of sites inside protected areas, expressed as a proportion of that found in minimally-used primary vegetation, and o as the corresponding mean of sites outside expressed in the same way. If a is the proportion of the Earth’s terrestrial surface inside protected areas and r the global average reduction in the mean site-level of the biodiversity measure caused by human pressures, then the state of global terrestrial biodiversity can be expressed as:

$$1 - r = ai + (1 - a) * o \tag{F}$$

Newbold *et al.*³ estimated r to be 0.129 for species richness and 0.126 for abundance for the year 2005 (we use values not weighted by spatial variation in species richness, as we did not weight sites by spatial variation in species richness in our analyses). Juffe-Bignoli *et al.*¹⁹

report that a was around 0.154 in 2014. To obtain an estimate of biodiversity in protected relative to unprotected sites (i.e. estimates of i/o), we used the coefficients from the model described by equation B as follows:

$$i = \beta_{pri_in} * p_{pri_in} + \beta_{sec_in} * p_{sec_in} + \beta_{crop_in} * p_{crop_in} + \beta_{pas_in} * p_{pas_in} + \beta_{urb_in} * p_{urb_in} \quad (G)$$

$$o = 1 * p_{pri_out} + \beta_{sec_out} * p_{sec_out} + \beta_{crop_out} * p_{crop_out} + \beta_{pas_out} * p_{pas_out} + \beta_{urb_out} * p_{urb_out} \quad (H)$$

where β_{x_in} is the coefficient for land use x inside protected areas and p_{x_in} is the proportion of total land area inside protected areas that is land use x , and likewise for outside protected areas.

To calculate the proportion of total land area in each land use, we used a fine-grained (30 arc-seconds; approximately 1 km) resolution land use map derived by downscaling the Harmonised Land Use dataset²⁰. The downscaling algorithm used the Harmonised Land Use dataset²¹ (50 km resolution) and higher resolution (1 km) predictor covariates describing climate (evapotranspiration²², temperature and precipitation²³, topographic wetness²⁴), landform and substrate (slope²⁴, soil carbon²⁵), anthropogenic factors (accessibility²⁶, population density²⁷) and land cover²⁸. Pixels under water²⁹ or permanent ice cover (Rock and Ice classification in¹⁴) were masked out of these data layers. Initially, a GAM with a quasibinomial error structure and logistic link was fitted to each of the five coarse grained Harmonised Land Use datasets (response variables) using the fine-grained covariates as predictors. The fine-grained fitted values from these GAMs were then rescaled multiplicatively so that the aggregated mean for each coarse-grained cell matched that of the Harmonised Land Use estimate. We then passed these rescaled fitted values to a constrained optimisation algorithm to produce an estimate of land use for each fine-grained grid cell that obeyed the constraints of being in the range of 0 - 1 and where all five estimates (one for each of five land use types: primary habitat, secondary habitat, cropland, pasture and urban) within a cell sum to 1. These estimates were then fed back into the GAMs as response variables and the procedure iterated until a convergence criterion was met. The result is fine-grained downscaled proportion of five land use types that sum to 1 within each grid cell. This analysis was performed on the entire 2005 global data layer of the Harmonised Land Use

dataset to give estimates of the proportion of all five land uses from the Harmonised Land Use dataset for every fine grained terrestrial grid cell between 90°N and 60°S.

As the downscaled proportions of land use do not separate different ages of secondary vegetation, we re-ran the models including land use (equation B) using the all-sites data, but having combined all ages of secondary vegetation to give land use as a 6 level factor (primary, secondary, plantation, pasture, cropland and urban).

We then solved equation F for i and o and calculated the effectiveness of protected areas, e , from:

$$e = 1 - (1 - i)/(1 - o) \quad (I)$$

We calculated 95% confidence intervals using the upper and lower bounds for the estimate of site level biodiversity in unprotected and protected sites relative to primary unprotected.

Analyses for “How to improve the global protected area network”. We used the models of biodiversity response to different management category groups to obtain an estimate of effectiveness, e , under the hypothetical circumstance that all existing protected areas showed the same biodiversity response as those in IUCN category I & II ($e_{I \& II}$). We assumed that the observed differences in local biodiversity measures among management category groups could be obtained by altering management objectives. However, some protected areas (e.g. in IUCN category I & II) have been specifically located in areas of high species richness, which will contribute to observed differences. We used the same effectiveness calculations described above, but i/o was given by the estimates for biodiversity at unprotected sites and those in protected areas with IUCN category I & II (from GLMMs with IUCN category as a fixed effect, equation A). We also obtained an estimate of e given a value of i/o derived from the estimates for unprotected sites and sites in IUCN categories III to VI ($e_{III \text{ to } VI}$). Our data were insufficiently resolved to test for effects of management category group in different land uses, so we could not adjust these estimates to reflect the distribution of land uses within PAs.

We then estimated the increase in protected area required to achieve the same biodiversity outcome as that given if all current protected areas are assigned IUCN category I & II. To do this, we used equation F to estimate the total biodiversity loss, r , if the area under protection, a , remains at 15.4%, the value of biodiversity outside protected areas relative to pristine, i , is the same as that estimated given the current protected area network and the biodiversity at unprotected relative to protected sites, i/o , is given by the difference between

unprotected sites and those in IUCN category I & II. We then rearranged equation F to estimate the proportion of land area (a) that would be needed given this new value of r , given the same value of biodiversity outside protected areas relative to pristine, i , as that estimated given the current protected area network and where i/o was determined by the difference between unprotected and protected sites given the current network of protected areas with a mix of IUCN categories.

Sensitivity Analyses. We carried out four sets of analyses to explore whether our results were sensitive to particular features of the data:

- 1) Were differences between species richness and rarefied richness caused by differences in the data used? We removed data from sites where total species richness was known, but not the abundance of individuals from each species; these are the sites for which rarefied richness cannot be calculated. When land use was not included in the models, sites inside protected areas still showed higher species richness than those outside (Supplementary Tables 1 and 2). The only differences were that the estimate for plant species richness had much larger confidence intervals, and that the species richness of vertebrates and invertebrates were no longer significantly higher at sites inside protected areas, though there was still a positive trend towards this. When land use was included within the model, the trends were broadly similar to those found with the full species richness data set; protection status made the largest difference to sites in human-dominated land uses.
- 2) Is a publication bias towards studies reporting a positive effect of protection affecting our results? 9% of our studies were designed to compare biodiversity inside and outside a protected area and could potentially bias results. To address this possible sampling bias, we re-ran our models without studies that explicitly focussed on protected area effects. Again, no notable changes in the results occurred (see Supplementary Tables 1 and 2).
- 3) Is a publication bias towards studies reporting a strong effect of land use affecting our results? Small studies are more likely to suffer from publication bias towards significant results³⁰ and therefore a strong effect of land use, so we re-ran the models used to produce Fig. 2 and 3 without small studies (those with fewer than 10 sites, 32 studies or 13% of all studies). Apart from small increases in the size of some confidence intervals, there were no notable changes in the results (see Supplementary Tables 1 and 2).

- 4) Does incomplete data on range size affect our results? Our measure of endemism is based on range sizes derived from GBIF data and not available for all species. We re-ran the analyses of endemism (Fig. 2 and 3), using only data from the sites for which at least 80% of the individuals had known ranges. Overall, results were very similar (Supplementary Tables 1 and 2), although confidence intervals were wider. We have also checked that ranges for vertebrates derived from GBIF and IUCN data are broadly comparable for species in the PREDICTS database.

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