

Biodiversity hotspots for conservation priorities

Norman Myers*, Russell A. Mittermeier†, Cristina G. Mittermeier†, Gustavo A. B. da Fonseca‡ & Jennifer Kent§

* Green College, Oxford University, Upper Meadow, Old Road, Headington, Oxford OX3 8SZ, UK

† Conservation International, 2501 M Street NW, Washington, DC 20037, USA

‡ Centre for Applied Biodiversity Science, Conservation International, 2501 M Street NW, Washington, DC 20037, USA

§ 35 Dorchester Close, Headington, Oxford OX3 8SS, UK

Conservationists are far from able to assist all species under threat, if only for lack of funding. This places a premium on priorities: how can we support the most species at the least cost? One way is to identify 'biodiversity hotspots' where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. As many as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots comprising only 1.4% of the land surface of the Earth. This opens the way for a 'silver bullet' strategy on the part of conservation planners, focusing on these hotspots in proportion to their share of the world's species at risk.

The number of species threatened with extinction far outstrips available conservation resources, and the situation looks set to become rapidly worse¹⁻⁴. This places a premium on identifying priorities. How can we protect the most species per dollar invested? This key question is at the forefront of conservation planning, and forms the focus of this article. By concentrating on areas where there is greatest need and where the payoff from safeguard measures would also be greatest, conservationists can engage in a systematic response to the challenge of large-scale extinctions ahead.

A promising approach is to identify 'hotspots', or areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat⁵⁻⁹. Here we focus on species, rather than populations or other taxa, as the most prominent and readily recognizable form of biodiversity. This is not to suggest that

populations and even ecological processes are not important manifestations of biodiversity, but they do not belong in this assessment. There are other types of hotspot^{10,11}, featuring richness of, for example, rare^{12,13} or taxonomically unusual species^{14,15}. This article considers only hotspots as defined above. Concentrating a large proportion of conservation support on these areas would go far to stem the mass extinction of species that is now underway.

The hotspots' boundaries have been determined by 'biological commonalities'. Each of the areas features a separate biota or community of species that fits together as a biogeographic unit. This is apparent in the case of islands or island groups such as New Caledonia, New Zealand, the Caribbean, Polynesia/Micronesia, Madagascar and the Philippines. Much the same applies to 'ecological islands' in clearly defined continental units such as the Cape

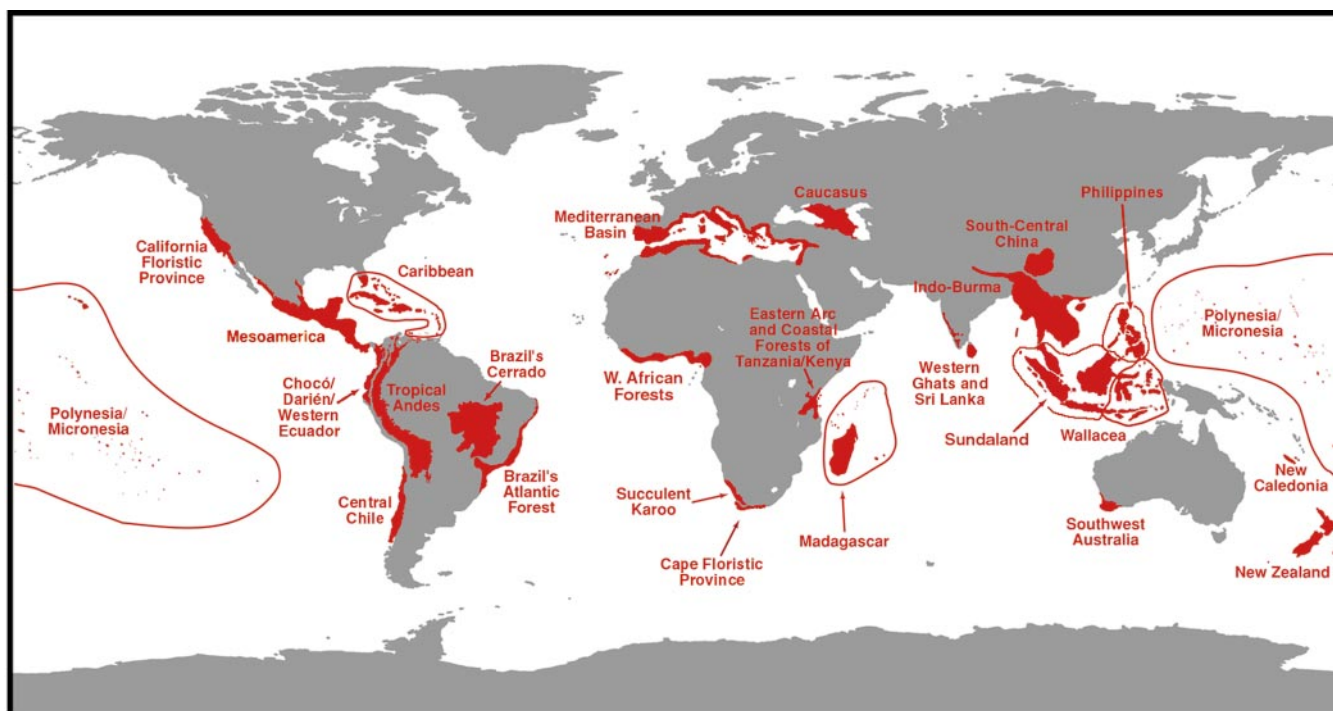


Figure 1 The 25 hotspots. The hotspot expanses comprise 30–3% of the red areas.

Floristic Province, the Eastern Arc and Coastal Forests of Tanzania/Kenya (hereafter abbreviated to 'Eastern Arc'), southwestern Australia and Caucasus. In other areas the definition of a hotspot's boundaries derives from recognized divisions such as Wallace's line between Sundaland and Wallacea, or the Kangar–Pattani line between Indo-Burma and Sundaland. In still other areas, the definition reflects a best-judgement opinion from experts in the field. Were larger hotspots, for example, the Tropical Andes, Mesoamerica, Indo-Burma and Sundaland to be subdivided into areas the size of the smaller hotspots, they would still meet the criterion of biological commonalities; and the result would be a far larger number of mini-hotspots, making for a much more complicated assessment and diffusing the essential strategy of just 25 hotspots designated for priority conservation.

This article is a qualitative as well as a quantitative advance on a preliminary effort^{5,6}, which limited itself to vascular plants in 18 hotspots. The number of hotspots has been increased to 25. More importantly, the expanded criteria require that a hotspot contains endemic plant species comprising at least 0.5% of all plant species world-wide. Here we include four categories of vertebrate species, bringing the number of endemics to almost three times more than in the earlier papers. We analyse key questions of species/area ratios and congruence among taxa. Finally, we present a way to determine the hottest hotspots and thus to pinpoint super priorities.

Analytic methods

The basic analysis is driven by two criteria: species endemism and degree of threat. The main source of data for both plants and vertebrates has been more than 100 scientists with abundant experience in countries concerned and around 800 references in the professional literature (see Supplementary Information). Additional details are available in ref. 16; supplementary sources on plants include refs 17–19. The species dimension is based in the first instance on vascular plants (comprising around 90% of all plants, and hereafter referred to as 'plants'), as they are essential to virtually all forms of animal life and are fairly well known scientifically. To qualify as a hotspot, an area must contain at least 0.5% or 1,500 of the world's 300,000 plant species²⁰ as endemics. In fact,

15 of the 25 hotspots contain at least 2,500 endemic plant species, and 10 of them at least 5,000.

The four vertebrate groups, mammals, birds, reptiles and amphibians, comprise 27,298 species, consisting of 4,809 mammals²¹, 9,881 birds²², 7,828 reptiles²³ and 4,780 amphibians²⁴. The other vertebrate group, fishes, is excluded because data are generally poor (there could well be at least 5,000 species waiting to be discovered²⁵, or more than all mammals). Hereafter 'vertebrates' refers to all vertebrates except fishes. Vertebrates do not serve as an alternative determinant of hotspot status, nor do their endemics have to comprise 0.5% of global totals. If an area qualifies by the 0.5% plants criterion (and the habitat threat criterion), it makes the list. Vertebrates serve as back-up support, and also to determine congruence and to facilitate other comparisons among the hotspots.

The analysis omits invertebrates, which are largely undocumented but probably make up at least 95% of all species, the bulk of them insects. To the extent that the five categories of endemic species assessed are sometimes matched by similar concentrations of endemic insect species, the hotspots thesis can be applied to invertebrates as well. In any case, if we were to lose, say, half of endemic plant species, we could well lose a large and perhaps similar proportion of insect species. The fig genus, for example, being the most widespread of plant genera in the tropics, comprises more than 900 species, each of which is pollinated by a single wasp species; conversely, the wasps depend on the figs' ovaries as sites for their larvae to develop²⁶. Although the plant/insect connection is variable in general application^{27–30}, it is supported by the many pollination, herbivory and other relationships between plants and insects.

The endemism data tend to be minimalist for two reasons. One is the lack of recent documentation in the form of, for example, modern floras. For instance, there is no up-to-date account of Brazil's plant species even though the country is believed to harbour the Earth's richest flora, at least 50,000 species or one-sixth of the planetary total. Second, and more importantly, endemism data almost always relate only to individual countries or parts of countries, whereas 12 of the hotspots extend across two or more countries and six across four or more countries. In these cases, it has been difficult to compute regional totals for hotspot-wide endemics,

Table 1 The 25 hotspots

Hotspot	Original extent of primary vegetation (km ²)	Remaining primary vegetation (km ²) (% of original extent)	Area protected (km ²) (% of hotspot)	Plant species	Endemic plants (% of global plants, 300,000)	Vertebrate species	Endemic vertebrates (% of global vertebrates, 27,298)
Tropical Andes	1,258,000	314,500 (25.0)	79,687 (25.3)	45,000	20,000 (6.7%)	3,389	1,567 (5.7%)
Mesoamerica	1,155,000	231,000 (20.0)	138,437 (59.9)	24,000	5,000 (1.7%)	2,859	1,159 (4.2%)
Caribbean	263,500	29,840 (11.3)	29,840 (100.0)	12,000	7,000 (2.3%)	1,518	779 (2.9%)
Brazil's Atlantic Forest	1,227,600	91,930 (7.5)	33,084 (35.9)	20,000	8,000 (2.7%)	1,361	567 (2.1%)
Choc/Darien/Western Ecuador	260,600	63,000 (24.2)	16,471 (26.1)	9,000	2,250 (0.8%)	1,625	418 (1.5%)
Brazil's Cerrado	1,783,200	356,630 (20.0)	22,000 (6.2)	10,000	4,400 (1.5%)	1,268	117 (0.4%)
Central Chile	300,000	90,000 (30.0)	9,167 (10.2)	3,429	1,605 (0.5%)	335	61 (0.2%)
California Floristic Province	324,000	80,000 (24.7)	31,443 (39.3)	4,426	2,125 (0.7%)	584	71 (0.3%)
Madagascar*	594,150	59,038 (9.9)	11,548 (19.6)	12,000	9,704 (3.2%)	987	771 (2.8%)
Eastern Arc and Coastal Forests of Tanzania/Kenya	30,000	2,000 (6.7)	2,000 (100.0)	4,000	1,500 (0.5%)	1,019	121 (0.4%)
Western African Forests	1,265,000	126,500 (10.0)	20,324 (16.1)	9,000	2,250 (0.8%)	1,320	270 (1.0%)
Cape Floristic Province	74,000	18,000 (24.3)	14,060 (78.1)	8,200	5,682 (1.9%)	562	53 (0.2%)
Succulent Karoo	112,000	30,000 (26.8)	2,352 (7.8)	4,849	1,940 (0.6%)	472	45 (0.2%)
Mediterranean Basin	2,362,000	110,000 (4.7)	42,123 (38.3)	25,000	13,000 (4.3%)	770	235 (0.9%)
Caucasus	500,000	50,000 (10.0)	14,050 (28.1)	6,300	1,600 (0.5%)	632	59 (0.2%)
Sundaland	1,600,000	125,000 (7.8)	90,000 (72.0)	25,000	15,000 (5.0%)	1,800	701 (2.6%)
Wallacea	347,000	52,020 (15.0)	20,415 (39.2)	10,000	1,500 (0.5%)	1,142	529 (1.9%)
Philippines	300,800	9,023 (3.0)	3,910 (43.3)	7,620	5,832 (1.9%)	1,093	518 (1.9%)
Indo-Burma	2,060,000	100,000 (4.9)	100,000 (100.0)	13,500	7,000 (2.3%)	2,185	528 (1.9%)
South-Central China	800,000	64,000 (8.0)	16,562 (25.9)	12,000	3,500 (1.2%)	1,141	178 (0.7%)
Western Ghats/Sri Lanka	182,500	12,450 (6.8)	12,450 (100.0)	4,780	2,180 (0.7%)	1,073	355 (1.3%)
SW Australia	309,850	33,336 (10.8)	33,336 (100.0)	5,469	4,331 (1.4%)	456	100 (0.4%)
New Caledonia	18,600	5,200 (28.0)	526.7 (10.1)	3,332	2,551 (0.9%)	190	84 (0.3%)
New Zealand	270,500	59,400 (22.0)	52,068 (87.7)	2,300	1,865 (0.6%)	217	136 (0.5%)
Polynesia/Micronesia	46,000	10,024 (21.8)	4,913 (49.0)	6,557	3,334 (1.1%)	342	223 (0.8%)
Totals	17,444,300	2,122,891 (12.2)	800,767 (37.7)	†	133,149 (44%)	†	9,645 (35%)

Documentation of plant and vertebrate species and endemism can be found in Supplementary Information.

* Madagascar includes the nearby islands of Mauritius, Reunion, Seychelles and Comores.

† These totals cannot be summed owing to overlapping between hotspots.

and we have often had to depend on best-judgement estimates by over 100 scientists with abundant experience in the countries concerned. In a few instances, we have had to accept a simple summation of country-by-country totals, which surely underestimates regional totals. To this extent, many of the endemism estimates are distinctly conservative.

A second determinant of hotspot status, applied only after an area has met the 'plants' criterion, is the degree of threat through habitat loss. To qualify, a hotspot should have lost 70% or more of its primary vegetation, this being the form of habitat that usually contains the most species, especially endemics. Eleven hotspots have already lost at least 90% and three have lost 95%. The 70% cutoff is justified on the grounds that most large-scale concentrations of endemic plant species occur within the 25 hotspots as delineated. Other concentrations of plant endemics with perhaps another 15% of the Earth's plant species occur in three regions designated as 'major tropical forest wilderness areas', each retaining 75% of its primary vegetation (see below). There are few other areas with comparable concentrations. Moreover, were the 70% cutoff to be replaced with 60%, this would admit hardly any other hotspots, whereas a 90% cutoff would exclude 11 of the hotspots.

Finally, the analysis is limited to the terrestrial realm (Conservation International is preparing an analysis of marine species and conservation priorities).

The area-by-area findings are presented in Tables 1–6 and Fig. 1. For further information regarding the sources of our statistics, see the list of references and experts in Supplementary Information.

There is variability in the precision and accuracy of data. This is to be expected given the range of areas and the degree of documentation available. In many instances, the statistical information is considered to be accurate to within 5%. In most others, it is sufficiently accurate to rank as sound support for working estimates. For example, the Tropical Andes is believed to contain at least 20,000 known plant endemics, this being a rounded figure (many more species, probably thousands, remain to be discovered there). Another 14 such totals are rounded. The Cape Floristic Province, by contrast, is considered to contain exactly 5,682 known plant endemics; the same precision applies to another nine hotspots. Similar considerations apply to vertebrate data and to estimates of remaining primary vegetation.

This overall approach, uneven as it is, is justified for an analysis that seeks to convert a profound problem into a fine opportunity. After all, to decide that a potential hotspot should not be evaluated because it lacks a conventional degree of accurate data is effectively to decide that its conservation needs cannot be evaluated either, in which case its cause tends to go by default. Uncertainty can cut both ways.

Chief findings

The 25 hotspots contain the remaining habitats of 133,149 plant species (44% of all plant species world-wide; Table 1) and 9,645 vertebrate species (35%; Table 2). These endemics are confined to an aggregate expanse of 2.1 million square kilometres, or 1.4% of the Earth's land surface. They formerly occupied 17.4 million square kilometres or 11.8% of the Earth's land surface. They are so threatened that, having already lost an aggregate of 88% of their primary vegetation, they all seem likely, in the absence of greatly increased conservation efforts, to lose much if not most of their remaining primary vegetation within the foreseeable future.

The 25 hotspots feature several habitat types at global scale. Predominant are tropical forests, appearing in 15 hotspots, and Mediterranean-type zones, in five. Nine are mainly or completely made up of islands; almost all tropical islands fall into one or another hotspot. Sixteen hotspots are in the tropics, which largely means developing countries where threats are greatest and conservation resources are scarcest.

Leading hotspots

Some hotspots are much richer than others in terms of their numbers of endemics (Table 3). (Three other modes of comparison are presented below.) Each of five hotspots—the Tropical Andes, Sundaland, Madagascar, Brazil's Atlantic Forest and the Caribbean—contains endemic plants and vertebrates amounting to at least 2% of total species world-wide. Together, they comprise 20% and 16%, respectively, of all plants and vertebrates, and 45% of all the hotspots' endemic plants and vertebrates alike, but they comprise a mere 0.4% of the Earth's land surface. At the same time, they feature some of the most depleted habitats: the Caribbean retains only 11.3% of its primary vegetation, Madagascar 9.9%, Sundaland 7.8% and Brazil's Atlantic Forest 7.5%. These five hotspots, with

Table 2 Vertebrate species and endemism

Hotspot	Bird species and endemism		Mammal species and endemism		Reptile species and endemism		Amphibian species and endemism		Total species and endemism	
Tropical Andes	1,666	677	414	68	479	218	830	604	3,389	1,567
Mesoamerica	1,193	251	521	210	685	391	460	307	2,859	1,159
Caribbean	668	148	164	49	497	418	189	164	1,518	779
Brazil's Atlantic Forest	620	181	261	73	200	60	280	253	1,361	567
Choco/Darién/W. Ecuador	830	85	235	60	210	63	350	210	1,625	418
Brazil's Cerrado	837	29	161	19	120	24	150	45	1,268	117
Central Chile	198	4	56	9	55	34	26	14	335	61
California Floristic Province	341	8	145	30	61	16	37	17	584	71
Madagascar	359	199	112	84	327	301	189	187	987	771
Eastern Arc and Coastal Forests of Tanzania/Kenya	585	22	183	16	188	50	63	33	1,019	121
West African Forests	514	90	551	45	139	46	116	89	1,320	270
Cape Floristic Province	288	6	127	9	109	19	38	19	562	53
Succulent Karoo	269	1	78	4	115	36	10	4	472	45
Mediterranean Basin	345	47	184	46	179	110	62	32	770	235
Caucasus	389	3	152	32	76	21	15	3	632	59
Sundaland	815	139	328	115	431	268	226	179	1,800	701
Wallacea	697	249	201	123	188	122	56	35	1,142	529
Philippines	556	183	201	111	252	159	84	65	1,093	518
Indo-Burma	1,170	140	329	73	484	201	202	114	2,185	528
South Central China	686	36	300	75	70	16	85	51	1,141	178
Western Ghats/Sri Lanka	528	40	140	38	259	161	146	116	1,073	355
SW Australia	181	19	54	7	191	50	30	24	456	100
New Caledonia	116	22	9	6	65	56	0	0	190	84
New Zealand	149	68	3	3	61	61	4	4	217	136
Polynesia/Micronesia	254	174	16	9	69	37	3	3	342	223
Total endemics and % of global total	*	2,821	*	1,314	*	2,938	*	2,572		9,645
		28.5%		27.3%		37.5%		53.8%		35.3%

* These totals cannot be summed owing to overlapping between hotspots.

four others, contain endemics amounting to 30.1% and 25.0% of the global totals for plant and vertebrate species, respectively, in 0.7% of the Earth's land surface.

Some hotspots are likewise significant in having their endemic species concentrated in exceptionally small areas (Table 4). The Eastern Arc contains 1,500 endemic plants in 2,000 square kilometres, giving a ratio of 75 species to 100 square kilometres, represented as 75:1, and 121 endemic vertebrates for a ratio of 6.1:1, both ratios topping the lists for all hotspots. Similarly, New Caledonia, with 5,200 square kilometres, works out at 49:1 and 1.6:1, and the Philippines with 9,023 square kilometres at 64.7:1 and 5.7:1. The rest range from 33.3:1 to 1.2:1 for plants and 2.9:1 to 0.03:1 for vertebrates.

Congruence among species categories

In several hotspots there is species congruence insofar as high counts for endemic plants are matched by high counts for endemic vertebrates (Table 5). (For analysis of congruence in other areas, see refs 12 and 31.) This factor reinforces the conservation priority thesis, especially in those hotspots with the most endemic species (Table 3). There can also be high congruence in areas with lower species counts, for example, 80% in the Eastern Arc with 0.5% of plant species and 0.4% of vertebrate species.

Endemic plants in the Tropical Andes comprise 6.7% of all plant species world-wide, and its endemic vertebrates 5.7%, with 85% congruence; Madagascar's species comprise 3.2% and 2.8%, respectively, with 88% congruence; and the Caribbean's 2.3% and 2.9%, with 79%. (The first is a large area where one could expect high congruence; the other two are only one-fifth and one-tenth as big, respectively.) In contrast, Cape Floristic Province possesses 1.9% of all plants but only 0.2% of all vertebrates, for 11% congruence, and the Mediterranean Basin possesses 4.3% of all plants but only 0.9% of all vertebrates, for 21%. Congruence tends to be high in tropical forest hotspots, and generally low in Mediterranean-type hotspots and other drier areas with their meagre counts for endemic vertebrates.

The hottest hotspots

The analysis so far has considered five key factors: numbers of endemics and endemic species/area ratios for both plants and vertebrates, and habitat loss. These factors do not carry equal weight, so they cannot be combined into a single quantitative ranking. For comparative purposes in qualitative fashion, Table 6 lists the eight 'hottest hotspots', which appear at least three times in the top ten listings for each factor. The leaders are Madagascar, the Philippines and Sundaland, appearing for all five factors, followed by Brazil's Atlantic Forest and the Caribbean, appearing for four. Three of these hotspots, Madagascar, the Philippines and the Caribbean, have small areas, which further highlights their importance.

Table 3 Leading hotspots in terms of endemics

Hotspot	Endemic plants (% of global total, 300,000)	Endemic vertebrates (% of global total, 27,298)
Tropical Andes*	20,000 (6.7)	1,567 (5.7)
Sundaland*	15,000 (5.0)	701 (2.6)
Madagascar*	9,704 (3.2)	771 (2.8)
Brazil's Atlantic Forest*	8,000 (2.7)	567 (2.1)
Caribbean*	7,000 (2.3)	779 (2.9)
Sub-totals (% rounded)	59,704 (19.9)	4,385 (16.1)
Mesoamerica	5,000 (1.7)	1,159 (4.2)
Mediterranean Basin	13,000 (4.3)	235 (0.9)
Indo-Burma	7,000 (2.3)	528 (1.9)
Philippines	5,832 (1.9)	519 (1.9)
Totals	90,536 (30.1)†	6,826 (25.0)

* Hotspots with at least 2% of the world's endemic plants and vertebrates, and comprising only 0.4% of the Earth's land surface (all nine amount to 0.7% of the Earth's land surface).
 † This would total 30.2% but for rounding of numbers in the individual hotspots.

Two additional hotspots, the Tropical Andes and the Mediterranean Basin, should be considered as hyper-hot candidates for conservation support in light of their exceptional totals of endemic plants: 20,000 and 13,000, respectively. The Tropical Andes is at the top for endemic vertebrates too, and the Mediterranean third after Sundaland for endemic plants, with 34% more than the fourth hotspot. But they do not rank in more than two of the five factor listings. Similarly, Mesoamerica is second for endemic vertebrates (49% more than the third highest), but it scores only tenth for endemic plants.

Higher taxa assessment

The analysis can be complemented by an assessment of endemism among higher taxa such as families and genera. Madagascar (including nearby Indian Ocean islands) possesses 11 endemic families and 310 endemic genera of plants, 5 endemic families and 14 endemic genera of primates, and 5 endemic families and 35 endemic genera of birds. Cape Floristic Province has 6 endemic families and 198 endemic genera of plants; and New Caledonia has 5 endemic families and 112 endemic genera of plants, and 1 endemic family and 3 endemic genera of birds. In contrast, the United States and Canada, with an expanse 8.8 times larger than the 25 hotspots combined, have only two endemic families of plants. Moreover, plant family richness can often serve as a predictor of species richness for certain animal taxa such as mammals, amphibians and reptiles³².

Action responses

In sum, the 25 hotspots contain the sole remaining habitats of 44% of the Earth's plant species and 35% of its vertebrate species, and these habitats face a high risk of elimination. Many of the hotspots could well contain sizeable proportions of endemic invertebrates. It is often supposed¹⁻⁴ that, were the present mass extinction of species to proceed virtually unchecked, between one-third and two-thirds of all species would be likely to disappear within the foreseeable future. The hotspots analysis indicates that much of this problem could be countered through protection of the 25 hotspots.

An aggregate expanse of 800,767 square kilometres, 38% of the hotspots total, is already protected in parks and reserves. True, some of these are little better than 'paper parks', but they offer a modicum of legal status. All are in urgent need of stronger safeguards, including those five hotspots where the protected expanse is as large as the hotspot itself. The areas without any protection at all

Table 4 Species/area ratios per 100 km² of hotspots

Hotspot	Endemic plants	Endemic vertebrates
Tropical Andes	6.4	0.5
Mesoamerica	2.2	0.5
Caribbean	23.5	2.6
Brazil's Atlantic Forest	8.7	0.6
Choco/Darien/Western Ecuador	3.6	0.7
Brazil's Cerrado	1.2	0.03
Central Chile	1.8	0.06
California Floristic Province	2.7	0.09
Madagascar	16.4	1.3
Eastern Arc and Coastal Forests of Tanzania/Kenya	75	6.1
Western African Forests	1.8	0.2
Cape Floristic Province	31.6	0.3
Succulent Karoo	6.5	0.15
Mediterranean Basin	11.8	0.2
Caucasus	3.2	0.1
Sundaland	12.0	0.6
Wallacea	2.9	1.0
Philippines	64.7	5.7
Indo-Burma	7.0	0.5
South-Central China	5.5	0.3
Western Ghats/Sri Lanka	17.5	2.9
SW Australia	13.0	0.3
New Caledonia	49.1	1.6
New Zealand	3.1	0.2
Polynesia/Micronesia	33.3	2.2

Table 5 Congruence between plants and vertebrates

Hotspot	Endemic plants as % of global total (300,000)	Endemic vertebrates as % of global total (27,298)	Congruence (%) (rounded)
Tropical Andes	6.7%	5.7%	85
Mesoamerica	1.7%	4.2%	41
Caribbean	2.3%	2.9%	79
Brazil's Atlantic Forest	2.7%	2.1%	78
Choco/Darien/Western Ecuador	0.8%	1.5%	53
Brazil's Cerrado	1.5%	0.4%	27
Central Chile	0.5%	0.2%	40
California Floristic Province	0.7%	0.3%	43
Madagascar	3.2%	2.8%	88
Eastern Arc and Coastal Forests of Tanzania/Kenya	0.5%	0.4%	80
West African Forests	0.8%	1.0%	80
Cape Floristic Province	1.9%	0.2%	11
Succulent Karoo	0.6%	0.2%	33
Mediterranean Basin	4.3%	0.9%	21
Caucasus	0.5%	0.2%	40
Sundaland	5.0%	2.6%	52
Wallacea	0.5%	1.9%	26
Philippines	1.9%	1.9%	100
Indo-Burma	2.3%	1.9%	83
South-Central China	1.2%	0.7%	58
Western Ghats/Sri Lanka	0.7%	1.3%	54
SW Australia	1.4%	0.4%	29
New Caledonia	0.9%	0.3%	33
New Zealand	0.6%	0.5%	83
Polynesia/Micronesia	1.1%	0.8%	73

amount to 1.3 million square kilometres or 62% of the total area of the hotspots. This expanse surely represents the greatest biodiversity challenge of the foreseeable future, and should be safeguarded through, for example, a 'hotspots rescue fund'. In some areas, outright protection is still the best option. In other areas, this is not feasible because of human settlements and other activities long in place. These areas could receive a measure of protection as 'conservation units' that allow some degree of multiple use provided that species safeguards are always paramount.

This is not to say that protection of the hotspots would safeguard all their species indefinitely. According to the well-established theory of island biogeography³³, when an area loses a large proportion of its original habitat and especially when the remaining habitat is severely fragmented, it will eventually lose some of its species through what are technically known as 'ecological equilibration' or delayed fallout effects. There is much empirical evidence to support this; for instance, the loss of birds in Brazil's Atlantic forest³⁴, in Southeast Asia's forests³⁵, in tropical forests generally^{36,37} and in the United Kingdom³⁸, of tree species in tropical forests³⁹; of forest plants in eastern North America⁴⁰; of primates in Africa's forests⁴¹; of large mammals in Tanzania⁴²; and of species generally⁴³.

Consider the consequences for the smallest hotspot, the Eastern Arc. The remaining primary vegetation is only 6.7% of the original, and its expanse of 2,000 km² is split into no fewer than 128 patches ranging in size from over 100 to 10 or fewer square kilometres. A bigger hotspot, Cape Floristic Province, with an expanse of 18,000 km² and 24.3% of its original primary vegetation, is spread

around several thousand patches ranging from over 100 to 0.1 km².

Although most island-biogeography losses are not likely to ensue for some time, it makes sense to take immediate steps to safeguard the hotspots to avoid an exceptionally large extinction spasm through outright loss of habitat on a scale to swamp island biogeography impacts. As for past extinctions in the hotspots, all too little is known with respect to taxa across the board including invertebrates; however, if we use birds extinct since 1800 as a surrogate we find that nearly 80% of those that disappeared were from hotspot areas.

These considerations apart, the prospect of a mass extinction can be made far less daunting and much more manageable through the hotspots strategy, with its tight targeting of conservation efforts.

The hotspots findings accord well with several other priority-setting analyses. There is a 68% overlap with Birdlife International's Endemic Bird Areas⁴⁴, 82% with IUCN/WWF International's Centres of Plant Diversity and Endemism¹⁷ and 92% with the most critical and endangered eco-regions of WWF/US's Global 200 List⁴⁵. The hotspots approach is more comprehensive than the first two because it combines five categories of species, and it is more closely focused than the third.

Other areas appear to feature exceptional plant endemism and exceptional threat, but are not sufficiently documented to meet the hotspots criteria. They include the Ethiopian Highlands, the Angola Escarpment, southeastern China, Taiwan, and the forests of the Albertine Rift in eastern Democratic Republic of Congo (formerly Zaire), southwestern Uganda and northern Rwanda. Much better known and with a high species/area ratio but without sufficient endemic plant species to qualify as a hotspot is the so-called Wet Tropics and adjacent tropical forest tracts along the Queensland coast in Australia, containing around 1,200 endemic plants in less than 11,000 km². Adding these areas to the hotspots list would increase the total of plants endemics by only a few per cent.

In addition, there are a few tropical forest expanses, known as 'major wilderness areas'⁴⁶ or 'good news' areas^{5,6}. They total some 6–7 million km² and feature concentrations of endemic species while retaining at least 75% of their primary vegetation, and have fewer than five people per square kilometre. One is the island of New Guinea, with around 15,000 endemic plants. Others include the Guayana Shield of northeastern Amazonia, the lowlands of western Amazonia and the Congolian Forest, with perhaps another 30,000 endemic plants. Were these regions to compose a supplementary conservation strategy, they could increase the number of plants endemics to almost 60% of all plant species in roughly 5% of the Earth's land surface.

Funding

Since the original hotspots strategy^{5,6} began to be implemented in 1989, some \$400 million has been invested by the MacArthur Foundation, the W. Alton Jones Foundation, Conservation International, the World Wildlife Fund and other non-governmental organizations. An annual average of \$40 million over 10 years is only a tiny fraction of the amount spent per year on biodiversity

Table 6 The eight hottest hotspots in terms of five factors

Hotspot	Endemic plants	Endemic vertebrates	Endemic plants/area ratio (species per 100 km ²)	Endemic vertebrates/area ratio (species per 100 km ²)	Remaining primary vegetation as % of original extent	Times appearing in top 10 for each of five factors
Madagascar	9,704	4	16.4	8	9.9	5
Philippines	5,832	8	64.7	2	3.0	5
Sundaland	15,000	2	12.0	10	7.8	5
Brazil's Atlantic Forest	8,000	5	8.7	6	7.5	4
Caribbean	7,000	6=	7.7	3	11.3	4
Indo-Burma	7,000	6=	7.0	8	4.9	3
Western Ghats/Sri Lanka	2,180	355	17.5	7	6.8	3
Eastern Arc and Coastal Forests of Tanzania/Kenya	1,500	121	75.0	1	6.7	3

conservation by governments and international agencies, these funds being assigned mainly to across-the-board activities rather than the concentrated efforts advocated here. The traditional scattergun approach of much conservation activity, seeking to be many things to many threatened species, needs to be complemented by a 'silver bullet' strategy in the form of hotspots with their emphasis on cost-effective measures.

We could go far towards safeguarding the hotspots and thus a large proportion of all species at risk for an average of \$20 million per hotspot per year over the next five years, or \$500 million annually. Although this is 12.5 times the annual average of the \$400 million spent on hotspots over the past decade, it is still only twice the cost of a single Pathfinder mission to Mars, which has been justified largely on biodiversity grounds (the search for extraterrestrial life). The \$500 million annually is to be compared, moreover, with a recent estimate⁴⁷ for a comprehensive conservation programme to protect biodiversity world-wide costing \$300 billion annually—a total that should, in turn, be compared with subsidies of various sorts that degrade environments and economies alike, amounting to \$1.5 trillion annually world-wide⁴⁸.

Finally, recall that the mass extinction of species, if allowed to persist, would constitute a problem with far more enduring impact than any other environmental problem. According to evidence from mass extinctions in the prehistoric past, evolutionary processes would not generate a replacement stock of species within less than several million years. What we do (or do not do) within the next few decades will determine the long-term future of a vital feature of the biosphere, its abundance and diversity of species. This expanded hotspots strategy offers a large step toward avoiding an impoverishment of the Earth lasting many times longer than *Homo sapiens* has been a species.

Received 22 September; accepted 22 December 1999.

1. Ehrlich, P. R. Energy use and biodiversity loss. *Phil. Trans. R. Soc. Lond. B* **344**, 99–104 (1994).
2. Myers, N. Two key challenges for biodiversity: discontinuities and synergisms. *Biodiversity Cons.* **5**, 1025–1034 (1996).
3. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* **269**, 347–350 (1995).
4. Wilson, E. O. *The Diversity of Life* (Belknap, Cambridge, Massachusetts, 1992).
5. Myers, N. Threatened biotas: 'hotspots' in tropical forests. *Environmentalist* **8**, 187–208 (1988).
6. Myers, N. The biodiversity challenge: expanded hotspots analysis. *Environmentalist* **10**, 243–256 (1990).
7. Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I. & Williams, P. H. Beyond opportunism: key principles for systematic reserve selection. *Trends Ecol. Evol.* **8**, 124–128 (1993).
8. Prendergast, J. R., Quinn, R. M. & Lawton, J. H. The gaps between theory and practice in selecting nature reserves. *Cons. Biol.* **13**, 484–492 (1999).
9. Ginsberg, J. Global conservation priorities. *Cons. Biol.* **13**, 5 (1999).
10. Dobson, A. P., Rodriguez, J. P., Roberts, W. M. & Wilcove, D. S. Geographic distribution of endangered species in the United States. *Science* **275**, 550–553 (1997).
11. Reid, W. V. Biodiversity hotspots. *Trends Ecol. Evol.* **13**, 275–280 (1998).
12. Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335–337 (1993).
13. Williams, P. et al. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Cons. Biol.* **10**, 155–174 (1996).
14. Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. What to protect?—systematics and the agony of choice. *Biol. Cons.* **55**, 235–254 (1991).
15. Williams, P. H., Humphries, C. J. & Vane-Wright, R. I. Measuring biodiversity: taxonomic relatedness for conservation priorities. *Aust. Syst. Bot.* **4**, 665–679 (1991).
16. Mittermeier, R. A., Myers, N., Gil, P. R. & Mittermeier, C. G. *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions* (Cemex, Conservation International and Agrupacion Sierra Madre, Monterrey, Mexico, 1999).

17. Davis, S., Heywood, V. H. & Hamilton, A. C. (eds) *Centres of Plant Diversity* (three vols) (World Wide Fund for Nature and International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 1994–1997).
18. Groombridge, B. (ed.) *Global Biodiversity* (Chapman and Hall, London, 1992).
19. Heywood, V. H. (ed.) *Global Biodiversity Assessment* (Cambridge Univ. Press, Cambridge, 1995).
20. Prance, G. T., Beent J. H., Dransfield, J. & Johns, R. *The Tropical Flora Remains Undercollected* (Missouri Botanical Garden Scientific Publications, St. Louis, Missouri, in the press).
21. Nowak, R. *Walker's Mammals of the World* (Johns Hopkins Univ. Press, Baltimore, Maryland, 1999).
22. Sibley, C. G. & Monroe, B. L. *Distribution and Taxonomy of Birds of the World* (Yale Univ. Press, New Haven, Connecticut, 1990).
23. Uetz, P. & Etzold, T. The EMBL/EBI reptile database. *Herpetol. Rev.* **27**, 175 (1996).
24. Glaw, F. & Kohler, J. Amphibian species diversity exceeds that of mammals. *Herpetol. Rev.* **29**, 11–12 (1998).
25. Eschmeyer, W. M. *Catalog of Fishes* (California Academy of Sciences, San Francisco, 1998).
26. Janzen, D. H. How to be a fig. *Annu. Rev. Ecol. Systemat.* **10**, 13–51 (1979).
27. Farrell, B. D. 'Inordinate Fondness' explained: why are there so many beetles? *Science* **281**, 555–557 (1998).
28. Gaston, K. J. Regional numbers of insect and plant species. *Funct. Ecol.* **6**, 243–247 (1991).
29. Strong, D. R., Lawton, J. H. & Southwood, T. R. E. *Insects on Plants: Community Patterns and Mechanisms* (Blackwell, Oxford, 1984).
30. Price, P. W. *Insect Ecology* 3rd edition (Wiley, New York, 1997).
31. Balmford, A. & Long, A. Across-country analyses of biodiversity congruence with current conservation efforts in the tropics. *Cons. Biol.* **9**, 1539–1547 (1996).
32. Williams, P. H., Gaston, K. & Humphries, C. J. Mapping biodiversity value worldwide: combining higher-taxon richness from different groups. *Proc. R. Soc. Lond. B* **264**, 141–148 (1997).
33. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, 1967).
34. Brooks, T. & Balmford, A. Atlantic forest extinctions. *Nature* **380**, 115 (1996).
35. Brooks, T., Pimm, S. L. & Collar, N. J. Deforestation predicts the number of threatened birds in Insular Southeast Asia. *Cons. Biol.* **11**, 382–394 (1997).
36. Brooks, T. M., Pimm, S. L. & Oyugi, J. O. Time lag between deforestation and bird extinction in tropical forest fragments. *Cons. Biol.* **13**, 1140–1150 (1999).
37. Laurance, W. F. Introduction and synthesis. *Biol. Cons.* **91**, 101–107 (1999).
38. Gaston, K. J. & Nicholls, A. O. Probable times to extinction of some rare breeding bird species in the United Kingdom. *Proc. R. Soc. Lond. B* **259**, 119–123 (1995).
39. Turner, I. M. Species loss in fragments of tropical rain forests: a review of the evidence. *J. Appl. Ecol.* **33**, 200–209 (1996).
40. Pimm, S. L. & Askins, R. A. Forest losses predict bird extinctions in Eastern North America. *Proc. Natl Acad. Sci. USA* **92**, 9343–9347 (1995).
41. Cowlinshaw, G. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Cons. Biol.* **13**, 1183–1193 (1999).
42. Newmark, W. D. Insularization of Tanzanian parks and the local extinction of large mammals. *Cons. Biol.* **10**, 1549–1556 (1996).
43. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
44. Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation* (Birdlife International, Cambridge, UK, 1998).
45. Dinerstein, E. et al. *The Global 200: Key Ecoregions for Saving Life on Earth* (World Wildlife Fund-US, Washington DC, 1996).
46. Mittermeier, R. A., Myers, N., Thomsen, J. B., da Fonseca, G. A. B. & Olivieri, S. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Cons. Biol.* **12**, 516–520 (1998).
47. James, A. N., Gaston, K. J. & Balmford, A. Balancing the Earth's accounts. *Nature* **401**, 323–324 (1999).
48. Myers, N. Lifting the veil on perverse subsidies. *Nature* **392**, 327–328 (1999).

Supplementary Information is available from *Nature's* World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of *Nature*. This and further information is also available at <http://www.conservation.org>.

Acknowledgements

We thank P. Robles Gil of Agrupacion Sierra Madre and the scientists listed in Supplementary Information for their help with information and analysis; P. Chambers, S. Norris and M. Prescott for research help; and D. Duthie and J. McNeely for comments on an early draft. We also thank the Mexican company CEMEX for its major financial support, and the MacArthur Foundation and S. Concannon for additional support.

Correspondence and requests for materials should be addressed to N.M. (e-mail: myers1n@aol.com).