
Habitat Loss and Extinction in the Hotspots of Biodiversity

THOMAS M. BROOKS,*†† RUSSELL A. MITTERMEIER,†
CRISTINA G. MITTERMEIER,† GUSTAVO A. B. DA FONSECA,*
ANTHONY B. RYLANDS,* WILLIAM R. KONSTANT,† PENNY FLICK,*
JOHN PILGRIM,* SARA OLDFIELD,‡ GEORGINA MAGIN,‡
AND CRAIG HILTON-TAYLOR§

*Center for Applied Biodiversity Science, Conservation International, 1919 M Street NW, Suite 600, Washington, D.C. 20036, U.S.A.

†Conservation International, 1919 M Street NW, Suite 600, Washington, D.C. 20036, U.S.A.

‡Fauna and Flora International, Great Eastern House, Tenison Road, Cambridge CB1 2DT, United Kingdom

§Red List Programme, World Conservation Union, Species Survival Commission, 219c Huntingdon Road, Cambridge CB3 0DL, United Kingdom

Abstract: *Nearly half the world's vascular plant species and one-third of terrestrial vertebrates are endemic to 25 "hotspots" of biodiversity, each of which has at least 1500 endemic plant species. None of these hotspots have more than one-third of their pristine habitat remaining. Historically, they covered 12% of the land's surface, but today their intact habitat covers only 1.4% of the land. As a result of this habitat loss, we expect many of the hotspot endemics to have either become extinct or—because much of the habitat loss is recent—to be threatened with extinction. We used World Conservation Union [IUCN] Red Lists to test this expectation. Overall, between one-half and two-thirds of all threatened plants and 57% of all threatened terrestrial vertebrates are hotspot endemics. For birds and mammals, in general, predictions of extinction in the hotspots based on habitat loss match numbers of species independently judged extinct or threatened. In two classes of hotspots the match is not as close. On oceanic islands, habitat loss underestimates extinction because introduced species have driven extinctions beyond those caused by habitat loss on these islands. In large hotspots, conversely, habitat loss overestimates extinction, suggesting scale dependence (this effect is also apparent for plants). For reptiles, amphibians, and plants, many fewer hotspot endemics are considered threatened or extinct than we would expect based on habitat loss. This mismatch is small in temperate hotspots, however, suggesting that many threatened endemic species in the poorly known tropical hotspots have yet to be included on the IUCN Red Lists. We then asked in which hotspots the consequences of further habitat loss (either absolute or given current rates of deforestation) would be most serious. Our results suggest that the Eastern Arc and Coastal Forests of Tanzania-Kenya, Philippines, and Polynesia-Micronesia can least afford to lose more habitat and that, if current deforestation rates continue, the Caribbean, Tropical Andes, Philippines, Mesoamerica, Sundaland, Indo-Burma, Madagascar, and Chocó-Darién-Western Ecuador will lose the most species in the near future. Without urgent conservation intervention, we face mass extinctions in the hotspots.*

Pérdida de Hábitat y Extinciones en Áreas Críticas para la Biodiversidad

Resumen: *Casi la mitad del total de plantas vasculares del mundo y un tercio de los vertebrados terrestres son endémicos en 25 "áreas críticas" para la biodiversidad, cada una de las cuales tiene por lo menos 1500 especies de plantas endémicas. En ninguno de estos sitios permanece más de un tercio de su hábitat prístino. Históricamente, cubrían 12% de la superficie terrestre, pero en la actualidad su hábitat intacto cubre solo 1.4% del terreno. Como resultado de esta pérdida de hábitat esperamos que muchas de las especies endémicas a es-*

††email t.brooks@conservation.org

Paper submitted December 12, 2000; revised manuscript accepted September 26, 2001.

tos sitios estén extintas o – porque la pérdida de hábitat es reciente – se encuentren amenazadas de extinción. Utilizamos Listas Rojas de UICN para comprobar esta predicción. En general, entre la mitad y dos tercios de las plantas amenazadas y el 57% de los vertebrados terrestres amenazados son endémicos de áreas críticas para la biodiversidad. Para aves y mamíferos en general, las predicciones de extinción en las áreas críticas para la biodiversidad, basadas en la pérdida de hábitat, coinciden con el número de especies consideradas extintas o amenazadas independientemente. En dos clases de áreas críticas para la biodiversidad la coincidencia no es muy grande. En islas oceánicas, la pérdida de hábitat subestima la extinción porque las especies introducidas han causado más extinciones que las producidas por la reducción del hábitat. Por lo contrario, la pérdida de hábitat sobrestima la extinción en áreas críticas para la biodiversidad extensas, lo que sugiere una dependencia de escala (este efecto también es aparente para plantas). Para reptiles, anfibios y plantas mucho menos especies endémicas son consideradas amenazadas o extintas por pérdida de hábitat. Sin embargo, esta discordancia es pequeña en áreas críticas para la biodiversidad en zonas templadas templadas, lo que sugiere que muchas especies endémicas amenazadas en las poco conocidas áreas críticas para la biodiversidad en zonas tropicales aun están por incluirse en las Listas Rojas. Posteriormente nos preguntamos en que áreas críticas para la biodiversidad serían más serias las consecuencias de una mayor pérdida de hábitat (absoluta o con las tasas actuales de deforestación). Nuestros resultados sugieren que el Arco Oriental y los Bosques Costeros de Tanzania/Kenia, Filipinas, Polinesia/Micronesia no pueden soportar mayores pérdidas y que, si continúan las tasas de deforestación actuales, el Caribe, Andes Tropicales, Filipinas, Mesoamérica, Sundaland, Indo-Burma, Madagascar y Chocó/Darién/Ecuador Occidental perderán más especies en el futuro. Sin acciones urgentes de conservación, habrá extinciones masivas en las áreas críticas para la biodiversidad.

Introduction

Four general principles combine to present one of the greatest challenges for conservation. First, most species have small range sizes relative to the mean range size, increasing their probability of extinction by chance alone (Gaston 1994). Second, species with small ranges also tend to be scarce within those ranges (Brown 1984), so their probability of extinction is increased on two counts. Third, the consistent mechanisms underlying the evolution of small range (Fjeldsá & Lovett 1997) mean that most such species co-occur. Stattersfield et al. (1998) demonstrated this convincingly for birds. Finally, most of these areas of co-occurrence of species with small ranges—call them centers of endemism—are disproportionately threatened by human activity (Cincotta et al. 2000). Myers et al. (2000) quantified this. Twenty-five biogeographically distinctive “hotspots” each have 0.5% or more of the world’s flora completely restricted to their boundaries and have already lost 70% or more of their original geographic extent. The hotspots are therefore both irreplaceable and vulnerable (Margules & Pressey 2000). In combination, these hotspots hold the entire ranges of 44% of the world’s plants and 35% of terrestrial vertebrates in just 1.4% of the land area. Nature has put many of her eggs in a few baskets, and we are in danger of dropping even these.

Where are these hotspots? We plotted the distribution and relative densities of endemics across the 25 hotspots as presented by Myers et al. (2000) (Fig. 1). We cannot simply map numbers of endemic species, because the hotspots (and countries) are different sizes and larger areas tend to hold more endemics. Furthermore, this re-

lationship is not linear; it is probably a power function (Harte & Kinzig 1997). Therefore, we factored out area by plotting numbers of endemics against original hotspot area, fitting a power function and taking residuals about this line (Balmford & Long 1995). These residuals represent the relative density of endemics, which we plotted onto the map. The residuals are qualitatively similar if based on remaining hotspot area. Most (15) of the hotspots hold predominantly tropical rainforest; five hold Mediterranean-type vegetation, three temperate forest, one tropical dry forest (Brazil’s Cerrado), and one semidesert (Succulent Karoo).

Given these enormous concentrations of small-ranged species in places where most natural habitat has already been cleared, we expect that many of the hotspot endemics will have become extinct (Pimm et al. 1995). Habitat loss accurately predicts species loss in regions where the habitat loss occurred a long time ago (Dial 1994; Pimm & Askins 1995). However, there is a time lag between habitat loss and species loss (Brooks et al. 1999a). For well-known taxa, one can detect this time lag in the form of population declines toward extinction. Such information is compiled in the World Conservation Union (IUCN) Red Data books (Baillie & Groombridge 1996; Walter & Gillett 1998). The very act of listing a taxon as threatened should stimulate conservation measures to preempt its decline to extinction (Collar 1996). Nevertheless, for both birds and mammals, the proportion of deforestation in both insular Southeast Asia (Magsalay et al. 1995; Brooks et al. 1997, 1999b) and Brazil’s Atlantic forest (Brooks & Balmford 1996; Brooks et al. 1999c; Grelle et al. 1999) consistently pre-

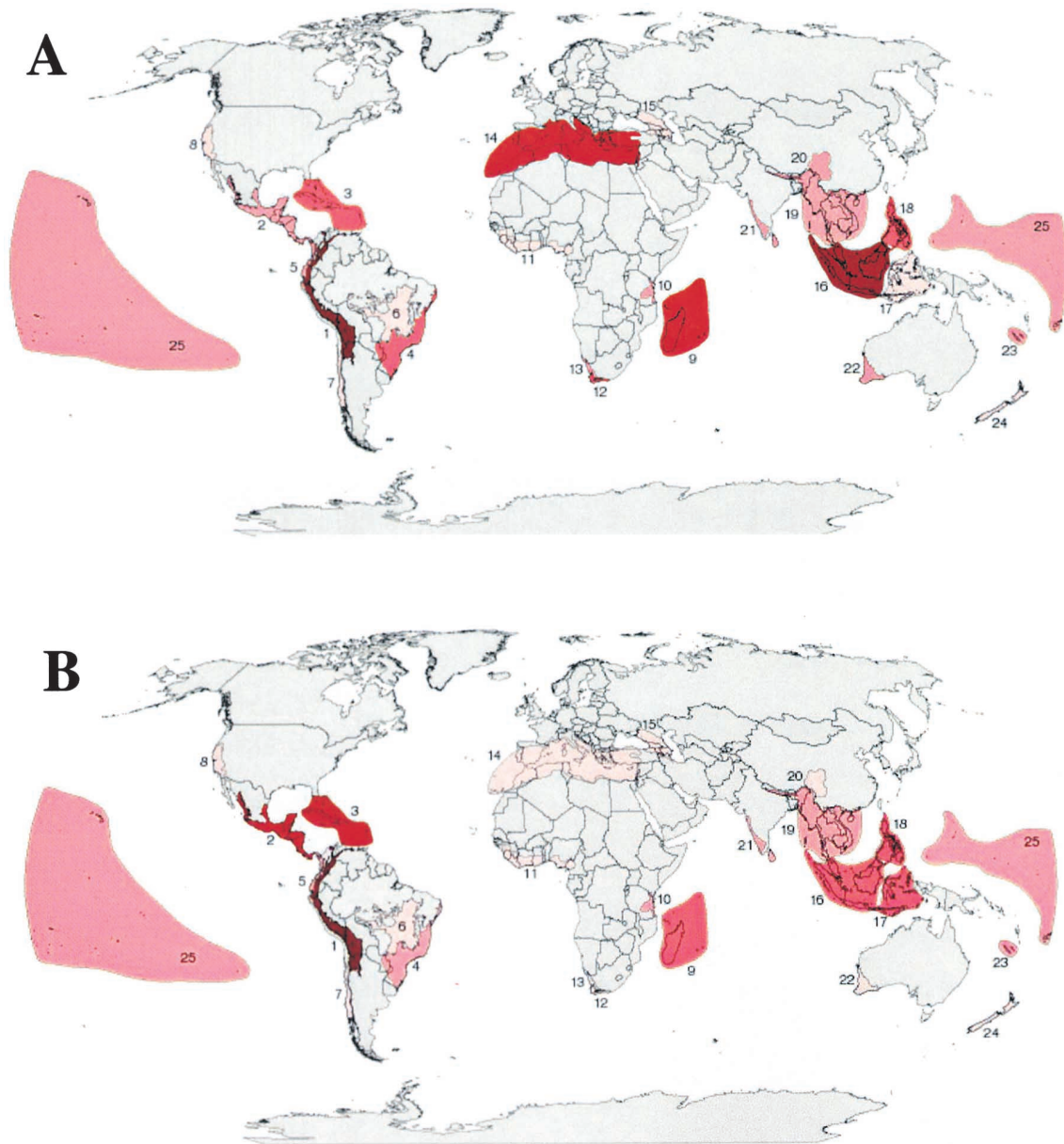


Figure 1. (a) Distribution of endemic plants across the hotspots (Myers et al. 2000) with area factored out by plotting numbers of endemics against area, fitting a power function, and taking residuals (representing relative densities of endemic plants) about this line (Balmford & Long 1995) (scale of six equal intervals of 3000, with the darkest reds representing residuals of 10,500 to 14,500 and the lightest -3500 to -1500). (b) Distribution of endemic vertebrates across the hotspots (Myers et al. 2000), with area factored out as above (scale of six equal intervals of 300, with the darkest reds representing 1150 to 1450 and the lightest -350 to -50). Numbers reference the hotspots as listed in the appendices.

dicts the numbers of threatened species. This suggests that extinctions are likely to occur in the absence of concerted conservation efforts.

We tested this expectation for the 25 global hotspots. Specifically, we predicted how many endemic species we expect to lose from each hotspot given the extent of habitat destruction to date. We then compared these predictions to actual numbers of threatened and extinct species and looked for consistent patterns in these comparisons. Finally, given this loss to date, we asked which

hotspots can least afford to lose more habitat and which are likely to suffer most given current rates of loss.

Methods

Prediction of Extinctions following Habitat Loss

The relationship between the number of species in an area and the size of that area, one of the longest-docu-

mented empirical laws of ecology (Arrhenius 1921), underpins the prediction of species loss following habitat loss. Traditionally, this relationship has been examined by considering how the number of species varies across areas of varying sizes (MacArthur & Wilson 1967). To predict extinctions following habitat loss, we applied the same relationship across time, rather than across space (Simberloff 1992). The exact form of the species-area relationship is debated (Connor & McCoy 1979), but it is most closely described by a power function, $S = cA^z$, where S is the number of species, A is area, and c and z are constants (Rosenzweig 1995). Thus,

$$S_{\text{original}} = cA_{\text{original}}^z \quad (1)$$

and

$$S_{\text{new}} = cA_{\text{new}}^z. \quad (2)$$

Dividing equation 2 by equation 1 yields

$$S_{\text{new}}/S_{\text{original}} = (A_{\text{new}}/A_{\text{original}})^z. \quad (3)$$

Multiplying equation 3 through by S_{original} yields

$$S_{\text{new}} = S_{\text{original}}(A_{\text{new}}/A_{\text{original}})^z. \quad (4)$$

Finally, subtracting from S_{original} gives our prediction of extinctions:

$$S_{\text{original}} - S_{\text{new}} = S_{\text{original}} - S_{\text{original}}(A_{\text{new}}/A_{\text{original}})^z. \quad (5)$$

The value of z varies with the system and taxon considered, but in fragmented systems such as hotspots, the value has been empirically shown to approximate 0.25 (Rosenzweig 1995). We used this value.

One important caveat underlies this method: we considered only species completely restricted to—the area A_{original} . We would never expect species not confined to this area to become extinct through habitat loss there (Pimm & Askins 1995).

Myers et al. (2000) provide, for each of the 25 hotspots, the percentage of original habitat remaining and the numbers of endemic species in each of five taxa: birds, mammals, reptiles, amphibians, and plants (Appendix 1). These data were compiled from approximately 800 references in the specialist biogeographic literature by more than 100 biologists with intimate knowledge of the hotspots (Mittermeier et al. 1999). There is considerable variability in the accuracy of these estimates, especially for plants, but in every case they can be considered conservative because many species undoubtedly remain to be described (Prance et al. 2000). This is even the case for birds, the best-known higher taxon (Peterson 1998). In addition, many species doubtless became extinct before they could be discovered (Balmford 1996).

Comparison of Predictions with Species Extinct or Threatened

How many of the hotspots' endemic species are either extinct or threatened with extinction? For all of the ver-

tebrate species on the 1996 IUCN Red List of Threatened Animals (Baillie & Groombridge 1996), we crosschecked (if not obvious) whether they were endemic to a hotspot and, if so, to which one. For birds, our distributional data source was Collar et al. (1994). For mammals, we based our classifications on those of Wilson and Reeder (1993), with further data from Eisenberg (1989), Redford and Eisenberg (1992), da Fonseca et al. (1996), Gurung and Singh (1996), Boitani et al. (1999), Eisenberg and Redford (1999), and Helin et al. (1999). For reptiles we used the European Molecular Biology Laboratory/European Bioinformatics Institute reptile database (Uetz & Etzold 1996; Uetz et al. 2001). For amphibians, we followed the relevant continental chapters in *Patterns of Distribution of Amphibians* (Borkin 1999; Duellman 1999; Inger 1999; Poynton 1999; Tyler 1999), supplemented by Frost (1985, 2000). For all terrestrial vertebrates, we excluded all species listed only under criteria A1/2d (decline due to direct exploitation) or D (naturally tiny population or range) because these would be listed as threatened even if their habitat was completely intact.

For plants, we followed the distributional information given by Walter and Gillett (1998), supplemented for tree distributions by Oldfield et al. (1998), except for the Cape Floristic Province and the Succulent Karoo, for which we took data directly from Hilton-Taylor (1996). This information varies considerably in resolution, so we used only the minimum estimate for numbers of threatened endemics per hotspot. We excluded many (10,556) species that were possible but not definite threatened hotspot endemics. We outline (by hotspot) how we classified species listed for various areas in Walter and Gillett (1998) in Appendix 2. Walter and Gillett (1998) assessed species following the pre-1994 Red List categories, and therefore for plants we included species listed in the old categories R (rare) and I (indeterminate). These categories were subsumed into one of the threatened categories, particularly under criterion D, into the category of lower risk-near threatened, and into data deficient by the standards of the IUCN (World Conservation Union [IUCN] 1994). These reclassifications cannot now be distinguished, so we followed the pre-1994 categories, with caution, for plants. The 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2000) updates the status of vertebrates, but Walter and Gillett (1998) remain the key information source for threatened plants, so we did not update any of our lists.

The red lists (Baillie & Groombridge 1996; Walter & Gillett 1998) also provided lists of extinct species. However, probably because the aim of the red lists is, by definition, to prevent extinction, those species already lost were treated rather poorly. To redress this problem, the Committee on Recently Extinct Organisms (CREO) has been formed to document recent extinctions (CREO 1999). All species listed as extinct by CREO are therefore confirmed not only to be valid taxonomically, but also to have become extinct since 1500 A.D. but remained

unrecorded despite comprehensive searching in subsequent surveys. There is a compatibility factor of only 49% between the mammal list of MacPhee and Flemming (1999) and the list of extinct mammals of Baillie and Groombridge (1996), with much of this difference being due to differing taxonomies. For birds, the compatibility factor is slightly higher at 65% (Brooks 2000). We therefore used the CREO lists for both mammals and birds, adding those species listed by the IUCN as extinct in the wild. We included as threatened the species listed as extinct by Baillie and Groombridge (1996) but as extant, mainly because of more recent information, by MacPhee and Flemming (1999) or Brooks (2000). For reptiles, amphibians, and plants, which have yet to be assessed by CREO, we followed Baillie and Groombridge (1996) and Walter and Gillett (1998).

We summed the numbers of endemics in each hotspot that were either threatened with extinction or were extinct already. Using a chi-square test, we then compared these as proportions of the total number of endemics in each hotspot to the proportions expected based on habitat loss. In cases where the expected number of extinctions was <5 , the sampling distribution of chi-square no longer approximated the chi-square distribution, so we used Yates's correction (Spiegel 1994).

Predictions of Future Losses

The comparisons—of proportions of hotspot endemics actually threatened or extinct with proportions predicted to be extinct—give an indication of the threat that has resulted from habitat loss. A pressing matter that remains, one that must be factored into consideration of conservation priority, is the question of which hotspots stand to lose the most additional species as a result of habitat loss in the future. Myers et al. (2000) addressed this

question by calculating, for each hotspot, the number of endemics per unit area. We improved on this calculation by using the species-area relationship to predict how many more endemics could be lost from each hotspot given additional habitat loss beyond that which has occurred already. We did this by assuming a given absolute amount of additional habitat loss across all hotspots and by estimating actual habitat loss over the next 5 years.

For the first method, we assumed that a further 1000 km² of each hotspot is cleared. This is an arbitrary value equivalent to half the extent of the hotspot with the least remaining habitat, the Eastern Arc and Coastal Forests of Tanzania-Kenya. To predict how many more extinctions among each hotspot's endemics this habitat destruction would cause, we subtracted this 1000 km² from the current extent of surviving habitat in each hotspot and calculated the new percent area of each hotspot. We then substituted these percentages into equation 5 to calculate the new total number of predicted extinctions. Finally, we subtracted from this value the predicted number of extinctions to date to give the additional number of extinctions we predict would be caused in each hotspot by the destruction of an additional 1000 km² of habitat.

For the second method, we estimated annual rates of deforestation based on data provided by the Food and Agriculture Organization (1997). We did this for 13 tropical forest hotspots only (Table 1). Data are not available for rates of habitat loss in the two tropical Pacific hotspots or for the nontropical forest hotspots. We then calculated the absolute amount of forest lost in a year for each hotspot and hence how much is likely to be lost and the percentage of original habitat surviving after 5 years. As in the first method, we then substituted these percentages into equation 5 to calculate the new total number of predicted extinctions; we then subtracted

Table 1. Percent annual rates of deforestation in 13 tropical forest hotspots, 1990–1995 (Food and Agriculture Organization 1997).

<i>Hotspot</i>	<i>Deforestation rate</i>	<i>Location of data collection</i>
Tropical Andes	0.94	average for Venezuela, Colombia, Ecuador, Peru, and Bolivia
Mesoamerica	2.13	average for Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama
Caribbean	4.05	average for Cuba, the Dominican Republic, Haiti, and Jamaica
Brazil's Atlantic Forest	0.5	overall for Brazil
Chocó-Darién-Western Ecuador	1.43	average for Panama, Colombia, and Ecuador
Madagascar	0.9	overall for Madagascar
Eastern Arc and Coastal Forests of Tanzania-Kenya	0.65	average for Tanzania and Kenya
West African Forests	1.21	average for Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, and Cameroon
Sundaland	1.75	average for Indonesia and Malaysia
Wallacea	1.0	overall for Indonesia
Philippines	3.6	overall for the Philippines
Indo-Burma	1.76	average for India, Bangladesh, Myanmar, Cambodia, Laos, Vietnam, and Thailand
Western Ghats-Sri Lanka	0.85	average for India and Sri Lanka

from this value the predicted number of extinctions to date to give the additional number of extinctions that we predict will occur in each tropical forest hotspot at rates of current deforestation. Ideally, we would sample rate of habitat loss multiple times per hotspot to enable us to fit confidence intervals to these predictions. Such data are not available, however, so we cautiously present single values with the caveat that these will have considerable error associated with them.

Results

Comparison of Predicted Species Extinctions with Species Extinct or Threatened

We first give the numbers of globally threatened and extinct species endemic to each hotspot, excluding those that would be listed as threatened even if their habitat was still completely intact (Table 2). Overall, the Caribbean and Madagascar (including the Indian Ocean islands) have the most extinct terrestrial vertebrates (>40 since 1500 A.D.). The Philippines have the most threatened endemics (126 species). For plants, the Caribbean and the Mediterranean basin have the highest minimum totals (both

with about 2000 threatened species). Including species listed under criteria A1/2d or D that would be listed as threatened even if their habitat was completely intact, 622 (52%) of all globally threatened or extinct mammals are hotspot endemics. For birds this total is 797 (64%), for reptiles 150 (55%), for amphibians 49 (38%), for terrestrial vertebrates as a whole 1618 (57%), and for plants a minimum of 14,246 (42%). For birds and mammals, the percentages of hotspot endemics in the top two threatened categories (critically endangered and endangered) are even higher, 82% and 58% respectively (Mittermeier et al. 1999). Except for amphibians, these proportions are all considerably greater than the proportions of all species that are hotspot endemics (Myers et al. 2000): 27% for mammals, 28% for birds, 38% for reptiles, 54% for amphibians, 35% for terrestrial vertebrates overall, and 44% for plants.

Does habitat loss predict species threat and extinction accurately, underestimate it, or overestimate it? The numbers of species of hotspot-endemic birds and mammals already considered threatened or extinct and the numbers predicted to have become extinct based on habitat loss to date are broadly similar (Figs. 2 & 3). We assessed these comparisons quantitatively (Table 3). For mammals, fewer species were predicted to have become ex-

Table 2. Total number and number of threatened and extinct endemic plants, mammals, birds, reptiles, and amphibians in biodiversity hotspots.^a

Hotspot	Plants		Mammals			Birds			Reptiles			Amphibians		
	total	tb or ex	total	tb	ex	total	tb	ex	total	tb	ex	total	tb	ex
Tropical Andes	20,000	78	68	32	0	677	90	2	218	1	0	604	1	0
Mesoamerica	5,000	951	210	35	2	251	20	1	391	5	0	307	1	1
Caribbean	7,000	2,017	49 ^b	22	27 ^b	148	35	12	418	30	4	164	8	0
Brazil's Atlantic Forest	8,000	200	73	28	0	181	61	0	60	3	0	253	5	0
Chocó-Darién-Western Ecuador	2,250	52	60	5	0	85	23	0	63	1	0	210	0	0
Brazil's Cerrado	4,400	15	19	6	0	29	14	0	24	0	0	45	0	0
Central Chile	1,605	173	9	5	0	4	1	0	34	0	0	14	0	0
California Floristic Province	2,125	1,031	30	11	0	8	1	0	16	0	0	17	0	0
Madagascar	9,704	705	84	49	5	199	47	28	301	16	12	187	3	0
Eastern Arc and Coastal Forests of Tanzania-Kenya	1,500	193	16	15	1	22	13	0	50	0	0	33	0	0
West African Forests	2,250	224	45	35	0	90	30	0	46	0	0	89	2	0
Cape Floristic Province	5,682	1,062	9	5	1	6	0	0	19	4	0	19	0	0
Succulent Karoo	1,940	674	4	4	0	1	1	0	36	5	0	4	1	0
Mediterranean Basin	13,000	1,932	46	16	2	47	5	1	110	13	0	32	6	1
Caucasus	1,600	115	32	4	0	3	0	0	21	6	0	3	0	0
Sundaland	15,000	642	115	50	0	139	28	1	268	1	0	179	0	0
Wallacea	1,500	29	123	38	0	249	38	0	122	1	0	35	0	0
Philippines	5,832	327	111	47	1	183	76	0	159	3	0	65	0	0
Indo-Burma	7,000	837	73	57	0	140	48	0	201	12	0	114	0	0
Southcentral China	3,500	30	75	19	0	36	16	0	16	0	0	51	0	0
Western Ghats-Sri Lanka	2,180	894	38	21	0	40	6	0	161	2	0	116	2	0
Southwest Australia	4,331	450	7	5	2	19	6	1	50	1	0	24	1	0
New Caledonia	2,551	486	6	3	0	22	8	1	56	0	0	0	0	0
New Zealand	1,865	203	3	2	1	68	27	16	61	6	1	4	0	0
Polynesia-Micronesia	3,334	926	9	7	2	174	50	33	37	3	1	3	1	0

^a Abbreviations: *tb*, threatened; *ex*, extinct.

^b MacPhee and Flemming (1999) list 36 extinct Caribbean endemic mammals, including 9 not included in Myers et al.'s (2000) totals, but the key point is that all of the Caribbean's endemic mammals are either threatened or already extinct (Koopman 1989; Woods 1989).

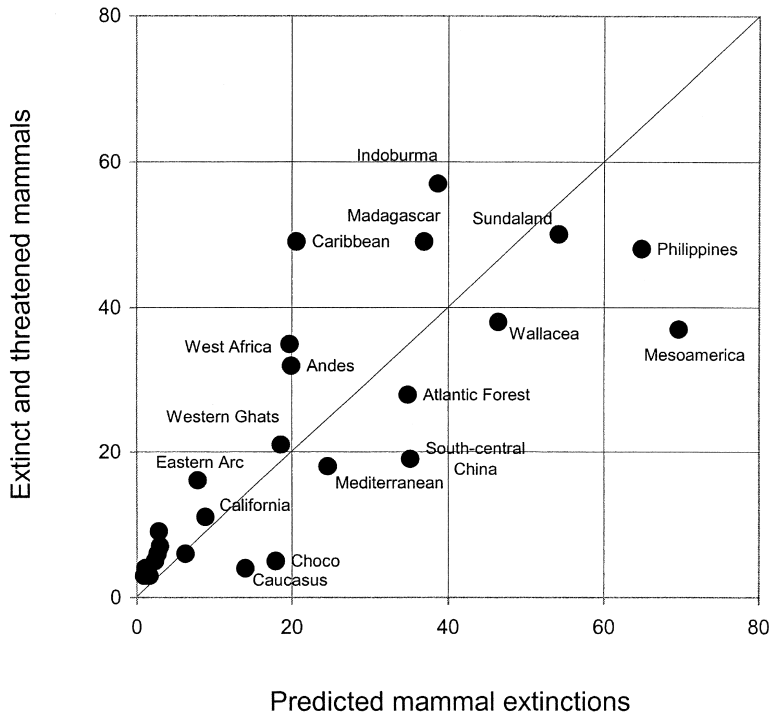


Figure 2. Comparisons of the numbers of threatened or extinct endemic mammals in hotspots with the numbers predicted to become extinct based on the extent of habitat loss to date.

tinct than are already threatened or extinct in 17 of the 25 hotspots (significantly fewer in 12 of the 25) and more in 8 of the 25 hotspots (significantly more in 5 of the 25). For birds, fewer species were predicted to have become extinct than are already threatened or extinct in 6 of the 25 hotspots (significantly fewer in 2 of the 25) and more in 19 of the 25 hotspots (significantly more in 11 of the 25). For mammals overall, habitat loss accurately predicted species threat or extinction in 8 of the 25 hotspots. For birds it was an accurate predictor in 12 of the 25 hotspots.

For reptiles, amphibians, and plants, habitat loss was a much poorer predictor of threat and extinction (Table

3). For amphibians, habitat loss predicted threat accurately in only five hotspots, four of them temperate: Cape Province, Succulent Karoo, Caucasus, New Zealand, and Polynesia-Micronesia. For reptiles, habitat loss predicted threat in only the first three of these. Far fewer amphibians and reptiles are listed as threatened by Baillie and Groombridge (1996) than we would expect to have become extinct based on habitat loss in all other hotspots. Similarly, for plants, habitat loss predicted fewer extinctions than the minimum numbers of threatened endemics listed by Walter and Gillett (1998) for the California Floristic Province and Succulent Karoo but predicted many more for all other hotspots.

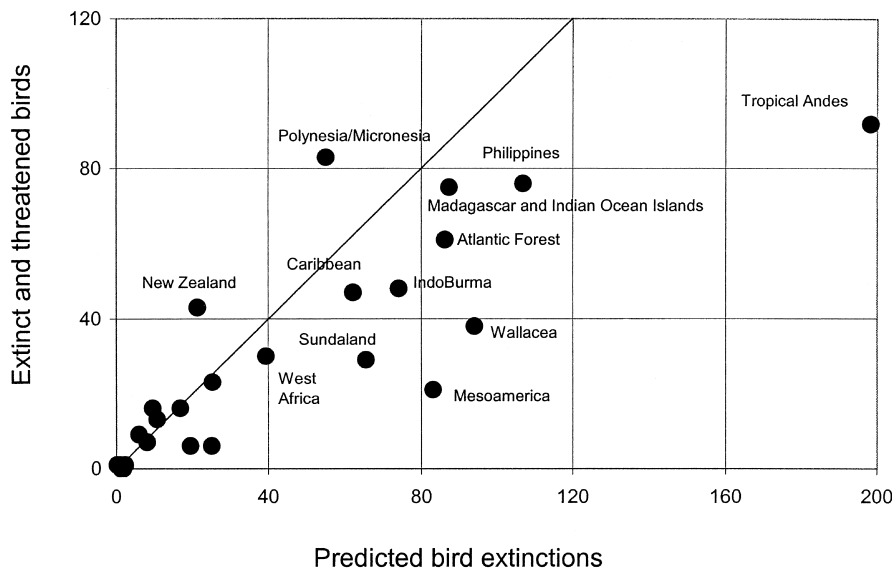


Figure 3. Comparisons of the numbers of threatened or extinct endemic birds in hotspots with the numbers predicted to become extinct based on the extent of habitat loss to date.

Table 3. Comparisons of proportions (χ^2)^a of threatened or extinct endemic birds, mammals, reptiles, and amphibians in hotspots and minimum proportions of threatened or extinct endemic plants in hotspots, with those predicted based on the extent of habitat loss to date.^b

Hotspot	Expected	Birds	Mammals	Reptiles	Amphibians	Plants
Tropical Andes	0.29	0.14 (80.6)*	0.47 (-10.4)*	0.00 (87.5)*	0.00 (247.4)*	0.00 (8065.1)*
Mesoamerica	0.33	0.08 (69.5)*	0.17 (25.7)*	0.01 (179.0)*	0.01 (146.1)*	0.19 (449.1)*
Caribbean	0.42	0.32 (6.4)*	1.00 (-67.6)*	0.08 (197.0)*	0.05 (92.9)*	0.29 (501.1)*
Brazil's Atlantic Forest	0.48	0.34 (14.2)*	0.38 (2.5)	0.07 (40.4)*	0.02 (211.7)*	0.03 (6542.8)*
Chocó-Darién-Western Ecuador	0.30	0.27 (0.3)	0.08 (13.3)*	0.02 (24.0)*	0.00 (89.4)*	0.02 (815.42)*
Brazil's Cerrado	0.33	0.48 (-3.0)	0.32 (0.0)	0.00 (11.9)*	0.00 (22.3)*	0.00 (2134.9)*
Central Chile	0.26	0.25 (0.0)	0.56 (-4.1)*	0.00 (11.9)*	0.00 (4.9)*	0.11 (193.1)*
California Floristic Province	0.30	0.13 (1.1)	0.37 (-0.7)	0.00 (6.7)*	0.00 (7.1)*	0.49 (-369.4)*
Madagascar	0.44	0.38 (3.1)	0.64 (-14.2)*	0.09 (146.4)*	0.02 (135.9)*	0.07 (5290.1)*
Eastern Arc and Coastal Forests of Tanzania-Kenya	0.49	0.59 (-0.9)	1.00 (-16.6)*	0.00 (48.3)*	0.00 (31.9)*	0.13 (789.0)*
West African Forests	0.44	0.33 (4.0)*	0.78 (-21.1)*	0.00 (35.8)*	0.02 (62.3)*	0.10 (1045.1)*
Cape Floristic Province	0.30	0.00 (2.6)	0.67 (-5.9)*	0.21 (0.7)	0.26 (0.1)	0.19 (334.7)*
Succulent Karoo	0.28	1.00 (-2.6)	1.00 (-10.3)*	0.14 (3.6)	0.25 (0.0)	0.35 (-43.1)*
Mediterranean Basin	0.53	0.13 (31.3)*	0.39 (3.8)	0.12 (76.6)*	0.22 (12.8)*	0.15 (7775.4)*
Caucasus	0.44	0.00 (2.3)	0.13 (12.7)*	0.29 (2.0)	0.00 (2.3)	0.07 (869.8)*
Sundaland	0.47	0.21 (38.6)*	0.43 (-0.6)	0.00 (235.4)*	0.00 (159.7)*	0.04 (11064.2)*
Wallacea	0.38	0.15 (53.7)*	0.31 (-2.5)	0.01 (70.9)*	0.00 (21.2)*	0.02 (819.5)*
Philippines	0.58	0.42 (21.4)*	0.43 (10.5)*	0.02 (208.9)*	0.00 (91.2)*	0.06 (6685.2)*
Indo-Burma	0.53	0.34 (19.6)*	0.78 (-18.5)*	0.06 (178.1)*	0.00 (128.3)*	0.12 (4721.9)*
Southcentral China	0.47	0.44 (0.1)	0.28 (10.7)*	0.00 (14.1)*	0.00 (44.9)*	0.01 (2969.3)*
Western Ghats-Sri Lanka	0.49	0.15 (18.4)*	0.58 (-1.2)	0.01 (146.5)*	0.02 (103.5)*	0.41 (54.8)*
Southwest Australia	0.43	0.37 (0.3)	1.00 (-9.4)*	0.02 (33.8)*	0.04 (14.5)*	0.10 (1845.1)*
New Caledonia	0.27	0.41 (-2.1)	0.50 (-1.6)	0.00 (21.0)*	—	0.19 (86.6)*
New Zealand	0.32	0.63 (-31.7)*	1.00 (-6.5)*	0.11 (11.3)*	0.00 (1.8)	0.11 (367.7)*
Polynesia-Micronesia	0.43	0.48 (-20.7)*	1.00 (-19.4)*	0.11 (7.4)*	0.33 (0.0)	0.28 (23.4)*

^aAll chi-square comparisons have 1 df; significant chi-square values ($p < 0.05$) are marked with an asterisk.

^bCases in which there is a greater proportion of threatened or extinct endemic species in a hotspot than we expected based on habitat loss are marked with a minus sign.

Predictions of Future Losses

We list predictions of likely future extinctions of endemic plants and terrestrial vertebrates in the hotspots, given loss of an additional 1000 km² of habitat in addition to the loss to date (Table 4). These predictions inform us about the sensitivity of each hotspot to a given amount of additional habitat loss. For both plants and vertebrates, the eastern arc and coastal forests of Tanzania-Kenya, with its already tiny extent of remaining forest, emerges as the hotspot likely to suffer the most extinctions from a given loss of habitat. The Philippines and Polynesia-Micronesia also stand to lose many endemics from a given incremental deforestation. In addition, the other hotspots with a small total area of habitat remaining—New Caledonia, Caribbean, Western Ghats-Sri Lanka, and Madagascar—were ranked among the top 10 for number of likely extinctions for both plants and terrestrial vertebrates.

Predicted future extinctions based on actual current rates of deforestation (in 13 tropical forest hotspots), rather than on a given incremental loss across the board, present a rather different picture (Table 5). These predictions appear driven more by deforestation rate (Table 1) than by absolute extent of remaining habitat (Table

4). For both plants and vertebrates, the Caribbean stands to lose the most endemics in the future, especially given the rapid rates of deforestation on Haiti and Jamaica (Food and Agriculture Organization 1997). The Tropical Andes, Philippines, Mesoamerica, and Sundaland also rank among the five hotspots likely to lose most plants and vertebrates as a result of forest loss continuing at its current rate, followed closely by Indo-Burma, Madagascar, and Chocó-Darién-Western Ecuador.

Discussion

In general, the extent of habitat loss in each hotspot is a remarkably good predictor of its number of threatened or extinct endemic species. The direct implication is that habitat destruction in the hotspots is leading, or in some cases has already led, to an extinction crisis. Could this result be circular? The criteria A1c, A2c, and B2a-c for red listing all involve measurements of species' habitat decline (World Conservation Union [IUCN] 1994). But although the species-area relationship produces top-down predictions of extinction, the Red Lists are bottom-up predictions: they depend on knowledge of a species'

Table 4. Predicted total number of endemic-species extinctions in each hotspot to date, total number following an additional 1000 km² of habitat loss, and additional number caused by such habitat loss.^a

Hotspot	Area (% km ²)		Plants				Vertebrates			
	now	-1000	total	predicted extinct	future extinct	extra extinct	total	predicted extinct	future extinct	extra extinct
	Tropical Andes	0.25	0.249	20000	5857.9	5869.1	11.3	1567	459.0	459.8
Mesoamerica	0.2	0.199	5000	1656.3	1659.9	3.6	1159	383.9	384.8	0.8
Caribbean	0.113	0.109	7000	2941.5	2975.9	34.4*	779	327.3	331.2	3.8*
Brazil's Atlantic Forest	0.075	0.074	8000	3813.5	3824.9	11.4	567	270.3	271.1	0.8
Chocó-Darién-Western Ecuador	0.242	0.238	2250	671.9	678.2	6.3	418	124.8	126.0	1.2*
Brazil's Cerrado	0.2	0.199	4400	1457.5	1459.6	2.1	117	38.8	38.8	0.1
Central Chile	0.3	0.297	1605	417.2	420.5	3.3	61	15.9	16.0	0.1
California Floristic Province	0.247	0.244	2125	626.9	631.6	4.7	71	20.9	21.1	0.2
Madagascar	0.099	0.097	9704	4260.7	4283.9	23.2*	771	338.5	340.4	1.8*
Eastern Arc and Coastal										
Forests of Tanzania-Kenya	0.067	0.034	1500	736.8	858.3	121.4*	121	59.4	69.2	9.8*
West African Forests	0.1	0.099	2250	984.7	987.2	2.5	0	118.2	118.5	0.3
Cape Floristic Province	0.243	0.230	5682	1692.6	1749.2	56.6*	53	15.8	16.3	0.5
Succulent Karoo	0.268	0.259	1940	544.4	555.9	11.8	45	12.6	12.9	0.3
Mediterranean Basin	0.047	0.047	13000	6947.0	6960.8	13.8	235	125.6	125.8	0.2
Caucasus	0.1	0.098	1600	700.3	704.8	4.5	59	25.8	26.0	0.2
Sundaland	0.078	0.077	15000	7072.9	7088.8	15.9*	701	330.5	331.3	0.7
Wallacea	0.15	0.147	1500	566.5	571.0	4.5	529	199.8	201.4	1.6*
Philippines	0.03	0.027	5832	3404.8	3475.1	70.2*	518	302.4	308.7	6.2*
Indo-Burma	0.049	0.049	7000	3706.6	3714.8	8.3	528	279.6	280.2	0.6
Southcentral China	0.08	0.079	3500	1638.8	1645.9	7.3	178	83.3	83.7	0.4
Western Ghats-Sri Lanka	0.068	0.063	2180	1066.8	1089.8	23.1*	355	173.7	177.5	3.8*
Southwest Australia	0.108	0.105	4331	1848.2	1867.0	18.8*	100	42.7	43.1	0.4
New Caledonia	0.28	0.226	2551	695.3	791.9	96.5*	84	22.9	26.1	3.2*
New Zealand	0.22	0.216	1865	587.7	593.1	5.4	136	42.9	43.3	0.4
Polynesia-Micronesia	0.218	0.196	3334	1055.9	1114.9	59.1*	223	70.6	74.6	4.0*

^aHotspots standing to lose the most endemic plants and vertebrates following an additional 1000 km² of habitat loss are marked with an asterisk.

ecology to assess its conservation status (Brooks et al. 1999b). If this were not the case, there would be no reason to list, say, the critically endangered Philippine Eagle (*Pithecophaga jefferyi*) differently than the common

Philippine Bulbul (*Hypsipetes philippensis*), despite the fact that both are endemics to the Philippines and have lost approximately the same amount of habitat across their ranges (Dickinson et al. 1991). This argument is

Table 5. Predicted total number of endemic-species extinctions in 13 tropical forest hotspots to date, total number in 5 years given current rates of deforestation, and additional number predicted to be caused by another 5 years of deforestation.

Hotspot	Area (% km ²)		Plants				Vertebrates			
	now	5 yrs	total	predicted extinct	future extinct	extra extinct	total	predicted extinct	future extinct	extra extinct
	Tropical Andes	0.25	0.238	20000	5857.9	6027.0	169.1	1567	459.0	472.2
Mesoamerica	0.2	0.179	5000	1656.3	1749.1	92.8	1159	383.9	405.4	21.5
Caribbean	0.113	0.090	7000	2941.5	3164.7	223.2	779	327.3	352.2	24.9
Brazil's Atlantic Forest	0.075	0.073	8000	3813.5	3839.9	26.4	567	270.3	272.2	1.9
Chocó-Darién-										
Western Ecuador	0.242	0.225	2250	671.9	700.9	29.0	418	124.8	130.2	5.4
Madagascar	0.099	0.095	9704	4260.7	4323.0	62.3	771	338.5	343.5	5.0
Eastern Arc and Coastal										
Forests of Tanzania-Kenya	0.067	0.065	1500	736.8	743.1	9.3	121	59.4	59.9	0.5
West African Forests	0.1	0.094	2250	984.7	1004.3	19.6	0	118.2	120.5	2.3
Sundaland	0.078	0.071	15000	7072.9	7252.3	179.4	701	330.5	338.9	8.4
Wallacea	0.15	0.143	1500	566.5	578.4	11.9	529	199.8	204.0	4.2
Philippines	0.03	0.025	5832	3404.8	3522.3	117.5	518	302.4	312.9	10.5
Indo-Burma	0.049	0.045	7000	3706.6	3781.6	75.0	528	279.6	285.2	5.6
Western Ghats-Sri Lanka	0.068	0.065	2180	1066.8	1078.8	12.0	355	173.7	175.7	2.0

also supported by direct evidence: the extent of habitat loss does not always predict numbers of threatened or extinct species, and this deviation from the general pattern is systematic. What causes these systematic deviations?

Underestimates of Threat to Mammals and Birds on Oceanic Islands and in Africa

For birds, the extent of habitat loss only significantly underestimates threat in two hotspots: New Zealand and Polynesia-Micronesia. For mammals, habitat loss underestimates threat in both these hotspots and also in the Caribbean, central Chile, Madagascar, eastern arc and coastal forests of Tanzania–Kenya, West African forests, Cape Floristic Province, Succulent Karoo, Indo-Burma, and southwest Australia. Thus, all hotspots for which habitat loss underestimates threat occur either on oceanic islands (birds and mammals) or in Africa, Indo-Burma, or central Chile (mammals).

There are four possible explanations for such underestimation. Three concern potential errors in the parameters used in the species-area prediction. We may have overestimated remaining habitat or percentage of threatened endemics, or we may have underestimated the z value. Predictions of extinctions following habitat loss are relatively insensitive to these errors, however (Brooks et al. 1999c). Alternatively, and more parsimoniously, habitat loss may appear to underestimate threat if species threatened by (or in synergy with) factors other than habitat loss are included in counts. This is the case both for oceanic islands and Africa. Oceanic islands have suffered massive recent extinctions due to the naivete of their species (Steadman 1995). In the case of the mainland African hotspots, the threat beyond that due to deforestation comes from introduced species (especially in dry-land hotspots) and from direct exploitation—the bushmeat trade (Wilkie et al. 1992). Exploitation for the medicinal trade causes a similar situation in Indo-Burma (Srikosamatara et al. 1992). In none of these cases is threat due to direct exploitation the sole cause of species' declines (in which case they would be excluded under criteria A1/2c); rather, threat acts in conjunction with habitat loss to drive extinction (Pimm 1996). In contrast, in Latin America the “empty forest” syndrome is a more common occurrence in the Amazon than in hotspots (Grelle et al. 1999).

Overestimates of Threat in Large Hotspots

Habitat loss significantly overestimates threat to birds in 10 hotspots, to mammals in 5 hotspots, and to reptiles, amphibians, and plants in nearly all hotspots. Again, various hypotheses could explain these cases. First, our estimates of remaining habitat may be too low. This is in fact likely because Myers et al. (2000) used data for the

extent of surviving primary habitat only, which explains why their data for percentages of remaining habitat are so much lower than those used by Brooks et al. (1997). This causes habitat loss to overestimate threat unless only strict habitat endemics are included in the calculation (Brooks et al. 1999c). Alternatively, our estimates of the ratio between threatened and total endemic species may be too low, for example, if the hotspots have passed through “extinction filters” and lost many of their endemics unnoticed (Balmford 1996). This is especially likely to be the case in those hotspots that have been exposed to intensive agriculture for many thousands of years, such as the Mediterranean basin (Greuter 1994). It could also apply to island hotspots such as Polynesia-Micronesia, which hold naive endemics particularly vulnerable to depredation by introduced species (Pimm et al. 1994), but the fact that habitat loss tends to underestimate extinction on these oceanic-island hotspots suggests that this is not a major factor.

More likely is the possibility of scale dependence (Palmer & White 1994): habitat loss underestimates threat to large areas more than to small areas (Brooks et al. 1997; Grelle et al. 1999). We tested this by assessing the correlations (all had 24 df) between the remaining area of each hotspot and its chi-square values, retaining negative values (Table 3). The relationship was significant for birds ($r = 0.53$, $p < 0.01$), amphibians ($r = 0.42$, $p < 0.05$), and minimum plant estimates ($r = 0.33$, $p < 0.05$) but not for mammals or reptiles ($r = 0.19$ and 0.07 , respectively, $p > 0.05$). This means that the z value we used was too large for our predictions of extinction in large hotspots.

Overestimates of Threat to Poorly Known Taxa

If the parameters of the species-area relationship cannot provide an explanation for overestimates of threat to poorly known taxa, we must again turn to the Red Lists for answers. One possibility is that the Red Lists are accurate and that reptiles, amphibians, and plants are simply highly tolerant to habitat loss. Two lines of evidence refute this suggestion. The first is that, in well-sampled habitats (e.g., in North America), these groups are much more threatened than are birds and mammals (Stein et al. 2000). The second is that, in any case, serious declines are apparent among reptiles (Gibbons et al. 2000), amphibians (Houlahan et al. 2000), and plants (Cardoso da Silva & Tabarelli 2000).

The more likely possibility is that our knowledge of threat to plant, reptile, and amphibian species is insufficient and that many more species are threatened than are currently on the red lists. For reptiles 253 species are threatened, 20% of those species assessed, whereas for amphibians 124 species are threatened, 25% of those species assessed (Baillie & Groombridge 1996). Hence, approximately 1265 reptile species (one-sixth of the to-

tal global fauna) and 496 amphibians (one-tenth of the total global fauna) were assessed. The IUCN Red List Programme (Hilton-Taylor 2000) is making a concerted effort to ensure complete coverage of all herptiles in the next few years. For plants, the paucity of information is also stated explicitly in the red list: "data, in particular for many parts of Africa, Asia, the Caribbean, and South America, are either patchy or lacking" (Walter & Gillett 1998:xix).

We tested explicitly whether this geographic bias toward the temperate zone is apparent in our results by looking for correlations between the magnitude of the (approximate modal) latitude for each hotspot and its chi-square values, again retaining negative values (Table 4). Recall that these values reveal whether the extent of habitat loss predicts numbers of extinctions significantly different than the actual numbers of threatened and extinct species. All tests had 24 df. For amphibians ($r = 0.36$, $p < 0.05$) and reptiles ($r = 0.39$, $p < 0.05$), the chi-square values were significantly lower in tropical than in temperate hotspots. Thus, the extent of habitat loss overestimated threat in tropical hotspots but predicted threat more accurately in the temperate zone. There was no significant correlation for birds or mammals ($r = 0.24$ and 0.07 , respectively, $p > 0.05$), which we would expect given that these groups are relatively well known. The correlations for plants were also not significant, probably because of the noise introduced by using minimum estimates ($r = 0.18$, $p > 0.05$). These results are not independent of the scale dependence demonstrated earlier, although there was no relationship between hotspot size (original or remaining) and latitude ($r = 0.04$ and 0.08 , respectively, $p > 0.05$). Also, in contrast, Brooks et al. (1999b) found that for birds and mammals habitat loss tends to predict threat accurately in tropical rainforest but to overestimate threat in monsoon forests. This raises the possibility that the numbers of "missing" plants, reptiles, and amphibians in the 15 tropical rainforest hotspots may be even higher than the comparison with nonforest temperate hotspots suggests.

Implications for Conservation Strategy

Our analysis supports the call of Myers et al. (2000:857) to "take immediate steps to safeguard the hotspots to avoid an exceptionally large extinction spasm." More than a half of all the planet's threatened species live on 1.4% of the land surface, which includes the hotspots. Furthermore, the number of threatened endemic birds and mammals in hotspots generally matches the number expected to become extinct following the habitat loss that has already occurred in the hotspots. These threatened species survive only thanks to the time lag between habitat loss and extinction (Brooks et al. 1999a).

For reptiles, amphibians, and plants, the extent of habitat loss consistently overestimates the numbers of

threatened or extinct species. The most likely explanation for this is simply our lack of knowledge of the conservation status of most species. This explanation is supported, for both reptiles and amphibians, by the existence of a latitudinal gradient in the degree to which habitat loss overestimates known threat. Habitat loss is a worse predictor of known threat for tropical than for temperate hotspots, which emphasizes the plea of da Fonseca et al. (2000) for the investment of far greater effort in the tropics in both the compilation of existing data and in the collection of new data in the field.

Among the 25 hotspots, the highest priorities can be identified by various parameters. Myers et al. (2000) ranked hotspots for numbers of endemic plants and vertebrates, endemic plants and vertebrates divided by area, and percentage of original vegetation remaining; they then listed as the eight hottest hotspots those ranked in the top five hotspots for at least three of these criteria. Number of endemic plants and vertebrates divided by area is a surrogate measure of the incremental species loss that a hotspot faces from a given additional habitat loss. This measure is also correlated with the endemism densities mapped in Fig. 1, although it underestimates the richness of large hotspots. Thus, the data for endemism divided by area in Table 6 of Myers et al. (2000) could be substituted with those from our Table 4. The only change resulting from this would be the addition of the Tropical Andes.

Another substitute for these parameters could be the actual measure of threat in terms of rate of habitat loss. Using these data in Myers et al.'s (2000) Table 6 adds Mesoamerica and Tropical Andes but drops Western Ghats-Sri Lanka and the Eastern Arc and Coastal Forests of Tanzania-Kenya. A clear limitation to this technique is our lack of data on rates of habitat loss for nontropical forest habitats. If these were available, using this method would undoubtedly also place the Mediterranean basin among the hottest hotspots. In any case, these 11 hotspots (Madagascar, Philippines, Sundaland, Brazil's Atlantic Forest, Caribbean, Indo-Burma, Western Ghats-Sri Lanka, Eastern Arc and Coastal Forests of Tanzania-Kenya, Tropical Andes, Mesoamerica, and Mediterranean Basin) are clearly the "hyperhot" priorities for conservation investment (Myers et al. 2000).

A concern could be raised that the hotspots strategy misses other areas of high endemism and threat. Myers et al. (2000) point to the Angola Scarp, Ethiopian Highlands, southeastern China and Taiwan, and Queensland rainforests as possible secondary hotspots. Preliminary analysis of these areas confirms that although all are certainly rich in endemics, none hold more than 1500 endemic plant species (World Wide Fund for Nature & IUCN 1994, 1995; Stattersfield et al. 1998). Other distinctive regions that also fall into this category are the Horn of Africa; the Maputaland-Pondoland region of southern Africa; the Kopetdag, Pamir and Tien-Shan mountains of middle Asia;

and the pine-oak woodlands of the southern United States and northern Mexico (Udvardy 1975; World Wide Fund for Nature & IUCN 1994, 1995, 1997; Olson & Dinerstein 1998). All of these areas probably also retain <30% of their original habitat cover (Hannah et al. 1995) and so are definite conservation priorities. Nonetheless, these areas between them hold only a few percent of the world's plants as endemics (Myers et al. 2000). All other distinct biogeographic regions appear to hold less than 500 endemic plant species, with the likely exception of the Albertine Rift of Central Africa (for which the compilation of botanical data is an urgent need). Of course, the three major tropical wilderness areas of the Greater Amazon, the Congo Basin, and New Guinea and Melanesia are also extremely species-rich and hold many endemics, but all three regions retain more than two-thirds of their original forest cover and require a different conservation strategy than do the hotspots (Mittermeier et al. 1998).

We have shown that the habitat loss that is such a feature of the world's biodiversity hotspots has left extremely large numbers of species threatened and with a high probability of extinction in the absence of immediate conservation action. In some hotspots—oceanic islands of the Caribbean, Indian Ocean, and Pacific—many of these extinctions have already occurred, and in fact we have lost even more species than we would expect based on habitat loss. Overall, the majority of the world's threatened species are endemic to hotspots. The degree to which we can effectively conserve these will determine the height of the breaking wave of the sixth extinction (Pimm & Raven 2000). If the conservation community can effectively use the hotspots approach, we have a chance to protect over half the world's species in the hotspots alone. Otherwise, we stand to lose over half of the world's threatened species in the medium-term future.

Acknowledgments

We thank an anonymous reviewer, A. Balmford, N. Burgess, J. Cannon, J. D'Amico, C. Galindo-Leal, J. Lamoreux, J. Kent, C. Kormos, J. Morrison, J. Mutke, N. Myers, S. Olivieri, D. Olson, M. Pascual, S. Pimm, C. Sugal, BirdLife International, and the rest of the staff of Conservation International for help in many aspects of this study.

Literature Cited

- Arrhenius, O. 1921. Species and area. *Journal of Ecology* **9**:95–99.
- Baillie, J., and B. Groombridge. 1996. 1996 IUCN red list of threatened animals. World Conservation Union, Gland, Switzerland.
- Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution* **11**:193–196.
- Balmford, A., and A. Long. 1995. Across-country analyses of biodiversity congruence with current conservation efforts in the tropics. *Conservation Biology* **9**:1539–1547.
- Boitani, L., F. Corsi, A. De Biase, I. D'Inzillo Carranza, M. Ravagli, G. Reggiani, I. Sinibaldi, and P. Trapanese. 1999. AMD African mammals databank: a databank for the conservation and management of the African mammals. Istituto di Ecologia Applicata, Rome.
- Borkin, L. J. 1999. Distribution of amphibians in North Africa, Europe, western Asia, and the former Soviet Union. Pages 329–420 in W. E. Duellman, editor. *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Brooks, T. M. 2000. Recent bird extinctions. Pages 695–703 in BirdLife International, editor. *Threatened birds of the world*. Lynx Edicions, Barcelona, Spain.
- Brooks, T., and A. Balmford. 1996. Atlantic forest extinctions. *Nature* **380**:115.
- Brooks, T. M., S. L. Pimm, and N. J. Collar. 1997. The extent of deforestation predicts the number of birds threatened with extinction in insular South-east Asia. *Conservation Biology* **11**:382–394.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999a. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**:1140–1150.
- Brooks, T. M., S. L. Pimm, V. Kapos, and C. Ravilious. 1999b. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology* **68**:1061–1078.
- Brooks, T., J. Tobias, and A. Balmford. 1999c. Deforestation and bird extinctions in the Atlantic Forest. *Animal Conservation* **2**:211–222.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* **124**:255–279.
- Cardoso da Silva, J. M., and M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeastern Brazil. *Nature* **404**:72–74.
- Cincotta, P. R., J. Wisniewski, and R. Engelman. 2000. Human population in the biodiversity hotspots. *Nature* **404**:990–992.
- Collar, N. J. 1996. The reasons for Red Data books. *Oryx* **30**:121–130.
- Collar, N. J., M. J. Crosby, and A. J. Stattersfield. 1994. *Birds to watch*. 2. The world list of threatened birds. BirdLife conservation series 4. BirdLife International, Cambridge, United Kingdom.
- Committee on Recently Extinct Organisms (CREO). 1999. American Museum of Natural History, New York. Available from <http://creo.amnh.org> (accessed 26 May 2001).
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *The American Naturalist* **113**:791–833.
- da Fonseca, G. A. B., G. Herrmann, Y. L. R. Leite, R. A. Mittermeier, A. B. Rylands, and J. L. Patton. 1996. Lista anotada dos mamíferos do Brasil. *Occasional Papers in Conservation Biology* **4**:1–38.
- da Fonseca, G. A. B., et al. 2000. Following Africa's lead in setting priorities. *Nature* **405**:393–394.
- Dial, R. 1994. Extinction or miscalculation? *Nature* **105**:104–105.
- Dickinson, E. C., R. S. Kennedy, and K. C. Parkes. 1991. The birds of the Philippines. Check-list 12. British Ornithologists' Union, Tring, United Kingdom.
- Duellman, W. E. 1999. Distribution patterns of amphibians in South America. Pages 255–328 in W. E. Duellman, editor. *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Eisenberg, J. F. 1989. *Mammals of the Neotropics*. 1. The northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. Chicago University Press, Chicago.
- Eisenberg, J. F., and K. H. Redford. 1999. *Mammals of the Neotropics*. 3. The central Neotropics: Ecuador, Peru, Bolivia, Brazil. Chicago University Press, Chicago, Illinois.
- Food and Agriculture Organization (FAO). 1997. *State of the world's forests 1997*. FAO, Rome, Italy.
- Fjeldså, J., and J. Lovett. 1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation* **6**:325–346.
- Frost, D. R. 1985. *Amphibian species of the world: a taxonomic and geographical reference*. Association of Systematics Collections, Lawrence, Kansas.
- Frost, D. R. 2000. *Amphibian species of the world*. American Museum of

- Natural History, New York. Available from <http://research.amnh.org/herpetology/amphibia/index.html> (accessed 26 May 2001).
- Gaston, K. J. 1994. *Rarity*. Chapman and Hall, London.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winnie. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* **50**:653–666.
- Grelle, C. E. de V., G. A. B. Fonseca, M. T. Fonseca, and L. P. Costa. 1999. The question of scale in threat analysis: a case study with Brazilian mammals. *Animal Conservation* **2**:149–152.
- Greuter, W. 1994. Extinctions in Mediterranean areas. *Philosophical Transactions of the Royal Society of London B* **344**:41–46.
- Gurung, K. K., and R. Singh. 1996. *Field guide to the mammals of the Indian subcontinent*. Academic Press, San Diego, California.
- Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation* **4**:128–155.
- Harte, J., and A. P. Kinzig. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* **80**:417–427.
- Helin, S., N. Ohtaishi, and L. Houji. 1999. *The mammalian of China*. China Forestry Publishing House, Beijing.
- Hilton-Taylor, C. 1996. *Red Data List of southern African plants. Strelitzia 4*. National Botanical Institute, Pretoria, South Africa.
- Hilton-Taylor, C., compiler. 2000. *2000 IUCN Red List of threatened species*. World Conservation Union, Gland, Switzerland. Available from <http://www.redlist.org> (accessed 26 May 2001).
- Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. *Nature* **404**:752–755.
- Inger, R. F. 1999. Distribution of amphibians in southern Asia and adjacent islands. Pages 445–482 in W. E. Duellman, editor. *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Koopman, K. F. 1989. A review and analysis of the bats of the West Indies. Pages 635–644 in C. A. Woods, editor. *Biogeography of the West Indies*. Florida Museum of Natural History, Gainesville.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- MacPhee, R. D. E., and C. Flemming. 1999. Requiem /Eternam: the last five hundred years of mammalian extinctions. Pages 333–371 in R. D. E. MacPhee, editor. *Extinctions in near time*. Kluwer Academic Publishers, New York.
- Magsalay, P., T. Brooks, G. Dutton, and R. Timmins. 1995. Extinction and conservation on Cebu. *Nature* **373**:294.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243–253.
- Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* **12**:516–520.
- Mittermeier, R. A., N. Myers, P. Robles Gil, and C. G. Mittermeier. 1999. *Hotspots*. Cemex, Mexico City, Mexico.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853–858.
- Oldfield, S., C. Lusty, and A. MacKinnon. 1998. *The world list of threatened trees*. World Conservation Press, Cambridge, United Kingdom.
- Olson, D. M., and E. Dinerstein. 1998. The Global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Conservation Biology* **12**:502–515.
- Palmer, M. W., and P. S. White. 1994. Scale dependence and the species-area relationship. *The American Naturalist* **144**:717–740.
- Peterson, A. T. 1998. New species and new species limits in birds. *Auk* **115**:555–558.
- Pimm, S. L. 1996. Lessons from a kill. *Biodiversity and Conservation* **5**:1059–1067.
- Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences of the United States of America* **92**:9343–9347.
- Pimm, S. L., and T. M. Brooks. 2000. The sixth extinction: how large, how soon, and where? Pages 46–62 in P. H. Raven and T. Williams, editors. *Nature and human society: the quest for a sustainable world*. National Academy Press, Washington, D.C.
- Pimm, S. L., and P. Raven. 2000. Extinction by numbers. *Nature* **403**:843–845.
- Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. *The American Naturalist* **132**:757–785.
- Pimm, S. L., M. P. Moulton, and L. J. Justice. 1994. Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society of London B* **344**:27–33.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* **269**:347–350.
- Poynton, J. C. 1999. Distribution of amphibians in Sub-Saharan Africa, Madagascar, and Seychelles. Pages 483–539 in W. E. Duellman, editor. *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Prance, G. T., H. Beentje, J. Dransfield, and R. Johns. 2000. The tropical flora remains undercollected. *Annals of the Missouri Botanical Garden* **87**:67–71.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the incidence of diversity hotspots, and conservation strategies. *Nature* **365**:335–337.
- Redford, K. H., and J. F. Eisenberg. 1992. *Mammals of the Neotropics. 2. The Southern Cone: Chile, Argentina, Uruguay, Paraguay*. Chicago University Press, Chicago.
- Rosenzweig, M. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, United Kingdom.
- Simberloff, D. 1992. Do species-area curves predict extinction in fragmented forest? Pages 75–89 in T. C. Whitmore and J. A. Sayer, editors. *Tropical deforestation and species extinction*. Chapman and Hall, London.
- Spiegel, M. R. 1994. *Theory and problems of statistics*. 2nd edition. McGraw-Hill, New York.
- Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998. *Endemic bird areas of the world: priorities for biodiversity conservation*. BirdLife conservation series 7. BirdLife International, Cambridge, United Kingdom.
- Steadman, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarcheology. *Science* **267**:1123–1131.
- Stein, B. A., L. S. Kutner, and J. S. Adams. 2000. *Precious heritage: the status of biodiversity in the United States*. Oxford University Press, Oxford, United Kingdom.
- Srikosamatar, S., B. Siripholdej, and V. Suteethorn. 1992. Wildlife trade in Lao P.D.R. and between Lao P.D.R. and Thailand. *Natural History Bulletin of the Siam Society* **40**:1–47.
- Tyler, M. J. 1999. Distribution patterns of amphibians in the Australo-Papuan region. Pages 541–563 in W. E. Duellman, editor. *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Udvardy, M. D. F. 1975. A classification of the biogeographical provinces of the world. Occasional paper 18. World Conservation Union, Morges, Switzerland.
- Uetz, P., and T. Etzold. 1996. The EMBL/EBI reptile database. *Herpetological Review* **27**:174–175.
- Uetz, P., T. Etzold, and R. Chenna. 2001. The EMBL reptile database. European Molecular Biology Laboratory, Heidelberg. Available from <http://www.embl-heidelberg.de/~uetz/LivingReptiles.html> (accessed 26 May 2001).
- Walter, K. S., and H. J. Gillett. 1998. 1997 IUCN Red List of threatened plants. World Conservation Union, Gland, Switzerland.
- Wilkie, D. S., J. G. Sidle, and G. C. Boundzanga. 1992. Mechanized log-

ging, market hunting, and a bank loan in Congo. *Conservation Biology* 6:570–580.

Wilson, D. E., and D. M. Reeder. 1993. *Mammal species of the world*. Smithsonian Institution Press, Washington, D.C. Available from <http://nmnhwww.si.edu/msw/> (accessed 26 May 2001).

Woods, C. A. 1989. The biogeography of West Indian rodents. Pages 741–798 in C. A. Woods, editor. *Biogeography of the West Indies*. Florida Museum of Natural History, Gainesville.

World Conservation Monitoring Centre (WCMC). 1994. *Biodiversity data sourcebook*. WCMC, Cambridge, United Kingdom.

World Conservation Union (IUCN). 1994. *IUCN Red List categories*. IUCN Species Survival Commission, Gland, Switzerland.

World Wide Fund for Nature and World Conservation Union (IUCN). 1994. *Centres of plant diversity. 1. Europe, Africa, South-west Asia and the Middle East*. World Wide Fund for Nature and IUCN, Cambridge, United Kingdom.

World Wide Fund for Nature and World Conservation Union (IUCN). 1995. *Centres of plant diversity. 2. Asia, Australasia and the Pacific*. World Wide Fund for Nature and IUCN, Cambridge, United Kingdom.

World Wide Fund for Nature and World Conservation Union (IUCN). 1997. *Centres of plant diversity. 3. The Americas*. World Wide Fund for Nature and IUCN, Cambridge, United Kingdom.

Appendix 1. Extent and percentage of remaining primary habitat and total number of and percent endemism for birds, mammals, reptiles, amphibians, and plants in each of 25 hotspots (Myers et al. 2000).

Hotspot	Remaining habitat		Birds		Mammals		Reptiles		Amphibians		Plants	
	km ²	percent	total	endemic	total	endemic	total	endemic	total	endemic	total	endemic
(1) Tropical Andes	314,500	25.0	1,666	40.6	414	16.4	479	45.5	830	72.8	45,000	44.4
(2) Mesoamerica	231,000	20.0	1,193	21.0	521	40.3	685	57.1	460	66.7	24,000	20.8
(3) Caribbean	29,840	11.3	668	22.2	164	29.9	497	84.1	189	86.8	12,000	58.3
(4) Brazil's Atlantic Forest	91,930	7.5	620	29.2	261	28.0	200	30.0	280	90.4	20,000	40.0
(5) Chocó-Darién-Western Ecuador	63,000	24.2	830	10.2	235	25.5	210	30.0	350	60.0	9,000	25.0
(6) Brazil's Cerrado	356,630	20.0	837	3.5	161	11.8	120	20.0	150	30.0	10,000	44.0
(7) Central Chile	90,000	30.0	198	2.0	56	16.1	55	61.8	26	53.9	3,429	46.8
(8) California Floristic Province	80,000	24.7	341	2.4	145	20.7	161	26.2	37	46.0	4,426	48.0
(9) Madagascar	59,038	9.9	359	55.4	112	75.0	327	92.1	189	98.9	12,000	80.9
(10) Eastern Arc and Coastal Forests of Tanzania-Kenya	2,000	6.7	585	3.8	183	8.7	188	26.6	63	52.4	4,000	37.5
(11) West African Forests	126,500	10.0	514	17.5	551	8.2	139	33.1	116	76.7	9,000	25.0
(12) Cape Floristic Province	18,000	24.3	288	2.1	127	7.1	109	17.4	38	50.0	8,200	69.3
(13) Succulent Karoo	30,000	26.8	269	0.4	78	5.1	115	31.3	10	40.0	4,849	40.0
(14) Mediterranean Basin	110,000	4.7	345	13.6	184	25.0	179	61.5	62	51.6	25,000	52.0
(15) Caucasus	50,000	10.0	389	0.7	152	21.1	76	27.6	15	20.0	6,300	25.4
(16) Sundaland	125,000	7.8	815	17.1	328	35.1	431	62.2	226	79.2	25,000	60.0
(17) Wallacea	52,020	15.0	697	44.8	201	61.2	188	64.9	56	62.5	10,000	15.0
(18) Philippines	9,023	3.0	556	32.9	201	55.2	252	63.1	84	77.4	7,620	76.5
(19) Indo-Burma	100,000	4.9	1,170	12.0	329	22.2	484	41.5	202	56.4	13,500	51.9
(20) Southcentral China	64,000	8.0	686	5.2	300	0.25	70	22.9	85	60.0	12,000	29.2
(21) Western Ghats-Sri Lanka	12,450	6.8	528	7.6	140	27.1	259	62.2	146	79.5	4,780	45.6
(22) Southwest Australia	33,336	10.8	181	10.5	54	13.0	191	26.2	30	80.0	5,469	79.2
(23) New Caledonia	5,200	28.0	116	19.0	9	66.7	65	86.2	0	—	3,332	76.6
(24) New Zealand	59,400	22.0	149	45.6	3	100.0	61	100.0	4	100.0	2,300	81.1
(25) Polynesia-Micronesia	10,024	21.8	254	68.5	16	56.2	69	53.6	3	100.0	6,557	50.8

Appendix 2. Assumptions made regarding inclusion of geographical units used in the 1997 IUCN Red List of Threatened Plants (Walter & Gillett 1998) within hotspot boundaries (Myers et al. 2000).*

Hotspot

- (1) Tropical Andes
Colombia (Norte de Santander, Antioquia (except Río Magdalena), Santander, Boyacá, Cundinamarca, Caldas, Risaralda, Huila, Tolima), Peru (San Martín, Pasco), Bolivia (La Paz, Cochabamba)
- (2) Mesoamerica
Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Mexico (Chiapas, Tabasco, Colima, Veracruz, Oaxaca, Campeche, Yucatán, Quintana Roo), Panama (Chiriquí, Central Cordillera, Cocle)
- (3) Caribbean
all states and islands (not Trinidad and Tobago)
- (4) Brazil's Atlantic Forest
Brazil (Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Argentina (Misiones)
- (5) Chocó-Darién-Western Ecuador
Panama (Darién), Colombia (Chocó), Ecuador (Esmeraldas, Pichincha, Manabí, Guayas, Los Ríos, Canar, El Oro), Peru (Tumbes, Piura, La Libertad)
- (6) Brazil's Cerrado
Brazil (Goiás, Federal District, Tocantins)
- (7) Central Chile
all of Chile, except Juan Fernández islands
- (8) California Floristic Province
U.S.A. (California)
- (9) Madagascar
Madagascar, Seychelles, Reunión, Comoros
- (10) Eastern Arc and Coastal Forests of Tanzania-Kenya
Kenya and Tanzania (places identified as in hotspot including Taita Hills, Shimba, Pare, Usambara, Nguru, Uluguru, Ukaguru, Rubeho, Udzungwe, Mahenge, Matengo, Zanzibar, Tanga, Kilwa, Lindi, Iringa, Mikangani, Njombe, Morogoro, Mafia Island)
- (11) West African Forests
Sierra Leone, Liberia, Ghana, Cote d'Ivoire, Nigeria, Cameroon, Equatorial Guinea (Fernando Po Island only)
- (14) Mediterranean Basin
Greece, Italy, Morocco, Portugal (including Madeira, excluding Azores), Israel, Lebanon, Spain (southern states, Canary Islands), France (southern departements)
- (15) Caucasus
Georgia, Armenia, Azerbaijan, Russia (Dagestan, Chechenia, Ingushetia, Northern Osetia, Kabardino-Balkaria, Karachai-Cherkesia, Adigea)
- (16) Sundaland
Malaysia, Indonesia (Sumatra, Java, Kalimantan), Singapore, India (Nicobar Islands)
- (17) Wallacea
Indonesia (except Sumatra, Java, Kalimantan, Bali, Irian Jaya)
- (18) Philippines
all Philippines
- (19) Indo-Burma
Myanmar, Laos, Thailand, Cambodia, Vietnam, Bhutan, China (Hainan Island), India (Andaman Islands, Chitagong, Khaysa Hills, Meghalaya, Brahmaputra, Eastern Himalaya, Nagaland, Manipur)
- (20) Southcentral China
China (Sichuan)
- (21) Western Ghats-Sri Lanka
Sri Lanka, India (Kerala, Tamil Nadu [Tirunelveli, Coimbatore, Palani, Niligiri Hills], Maharashtra [Ratnagiri, Pune, Satara])
- (22) Southwest Australia
Australia (all of Western Australia)
- (23) New Caledonia
all New Caledonia
- (24) New Zealand
all of New Zealand
- (25) Polynesia-Micronesia
all islands in region, including Hawaii, Fiji, Pitcairn Island

*Geographic units are only those mentioned by Walter and Gillett (1998). Data for the Cape Floristic Province and the Succulent Karoo are from Hilton-Taylor (1996).