Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots

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Abstract: *Global warming is a key threat to biodiversity, but few researchers have assessed the magnitude of this threat at the global scale. We used major vegetation types (biomes) as proxies for natural habitats and, based on projected future biome distributions under doubled-CO_2 climates, calculated changes in habitat areas and associated extinctions of endemic plant and vertebrate species in biodiversity hotspots. Because of numerous uncertainties in this approach, we undertook a sensitivity analysis of multiple factors that included (1) two global vegetation models, (2) different numbers of biome classes in our biome classification schemes, (3) different assumptions about whether species distributions were biome specific or not, and (4) different migration capabilities. Extinctions were calculated using both species-area and endemic-area relationships. In addition, average required migration rates were calculated for each hotspot assuming a doubled-CO_2 climate in 100 years. Projected percent extinctions ranged from <1 to 43% of the endemic biota (average 11.6%), with biome specificity having the greatest influence on the estimates, followed by the global vegetation model and then by migration and biome classification assumptions. Bootstrap comparisons indicated that effects on hotpots as a group were not significantly different from effects on random same-biome collections of grid cells with respect to biome change or migration rates; in some scenarios, however, hotspots exhibited relatively high biome change and low migration rates. Especially vulnerable hotspots were the Cape Floristic Region, Caribbean, Indo-Burma, Mediterranean Basin, Southwest Australia, and Tropical Andes, where plant extinctions per hotspot sometimes exceeded 2000 species. Under the assumption that projected habitat changes were attained in 100 years, estimated global-warming-induced rates of species extinctions in tropical hotspots in some cases exceeded those due to deforestation, supporting suggestions that global warming is one of the most serious threats to the planet's biodiversity.*

Key Words: biomes, climate change, general circulation models, global vegetation models, migration, species extinctions

Calentamiento Global y Extinciones de Especies Endémicas en Sitios de Importancia para la Biodiversidad

Resumen: *El calentamiento global es una amenaza clave para la biodiversidad, pero pocos investigadores han evaluado la magnitud de esta amenaza a escala global. Utilizamos los principales tipos de vegetación (biomas) como hábitats naturales y, con base en la proyección de la distribución futura de los biomas en condiciones de climas con el doble de CO_2, calculamos los cambios en la superficie de los hábitats y las extinciones de especies de plantas y animales endémicas en sitios de importancia para la biodiversidad. Debido a numerosas incertidumbres en este método, realizamos un análisis de sensibilidad de factores múltiples que incluyó (1) dos modelos de vegetación global; (2) diferentes números de clases de biomas en nuestros esquemas*

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de clasificación de biomas; (3) suposiciones diferentes sobre si la distribución de especies era específica de un bioma o no y (4) diferentes capacidades de migración. Las extinciones fueron calculadas utilizando tanto relaciones especies- como endémico-área. Adicionalmente, se calcularon tasas promedio de migración requeridas para cada sitio de importancia para la biodiversidad asumiendo un clima con el doble de CO_2 en 100 años. Las extinciones proyectadas variaron entre <1 a 43% de la biota endémica (promedio 11.6%), la especificidad de l bioma tuvo la mayor influencia sobre las estimaciones, seguida por el modelo de vegetación global y luego por las suposiciones de migración y clasificación de los biomas. Las comparaciones bootstrap indicaron que los efectos sobre los sitios de importancia para la biodiversidad como grupo no fueron significativamente diferentes de los efectos sobre colecciones de celdas aleatorias del mismo bioma con respecto al cambio de bioma o de tasas de migración; sin embargo, en algunos escenarios los sitios de importancia para la biodiversidad mostraron cambio de bioma relativamente alto y tasas de migración relativamente bajas. Los sitios de importancia para la biodiversidad especialmente vulnerables fueron la Región Florística del Cabo, Caribe, Indo-Burma, Cuenca del Mediterráneo, Suroeste de Australia y los Andes Tropicales, donde las extinciones de plantas por sitio algunas veces excedieron 2000 especies. Bajo la suposición de que los cambios de hábitat proyectados se obtuvieron en 100 años, las tasas estimadas de extinción inducida por calentamiento global en sitios de importancia para la biodiversidad tropicales en algunos casos excedieron a las inducidas por la deforestación, lo que soporta las sugerencias de que el calentamiento global es una de las amenazas más serias a la biodiversidad del planeta.

Palabras Clave: biomas, cambio climático, extinciones de especies, migración, modelos generales de circulación, modelos de vegetación global

Introduction

Global warming represents perhaps the most pervasive of the various threats to the planet's biodiversity, given its potential to affect even areas far from human habitation. Despite this and recent reports outlining the extensive biological changes that are ongoing because of the warming (Parmesan & Yohe 2003; Root et al. 2003), few efforts have been made to assess the potential effects of greenhouse warming on terrestrial biodiversity at a global scale (Kappelle et al. 1999; Noss 2001). A recent exception is Thomas et al. (2004), who used a climate-envelope modeling approach to look at the potential future distributions of 1103 species in six regions. Their work suggests that restricted-range endemic species may be especially vulnerable, which is notable given recent efforts to prioritize conservation at the global scale by identifying biodiversity hotspots that are of particular value based on their high species richness and endemism (e.g., Mittermeier et al. 1998; Myers et al. 2000; see also Olson & Dinerstein 1998). Extensive impacts due to global warming within these high-value ecosystems would constitute a key threat to the planet's biodiversity. Indeed, threats to these ecosystems would presumably constitute the unnatural adaptation of ecosystems that is to be avoided under the United Nations Framework Convention on Climate Change (Article 2).

We build on a previous effort to assess terrestrial biodiversity threats at the global scale (Malcolm et al. 2002) and focus on the vulnerability of 25 global biodiversity hotspots: areas that are home to a disproportionate number of the world's species (some 44% of the world's plants and 35% of its vertebrates in just 1.4% of the land area) and have suffered considerable habitat loss (none have retained >30% of their natural habitat) (Mittermeier et al. 1998; Myers et al. 2000). Brooks et al. (2002) used species-area relationships to estimate extinctions from these hotspots under recent anthropogenic habitat loss. We capitalized on efforts to project the equilibrium distributions of major vegetation types (biomes) under the climate associated with a doubling of CO_2 concentrations (e.g., VEMAP Members 1995; Neilson et al. 1998) and, based on changes in the areas and distributions of the major vegetation types within the hotspots, used species-area relationships to project numbers of extinctions of endemic plant and vertebrate species from the hotspots.

Enquist (2002) investigated projected biome changes in Costa Rica and found that several biomes with the highest numbers of endemic species are especially vulnerable to global warming and experience the largest reductions in area or disappear completely under some climate-change scenarios. This approach, which uses vegetation types as proxies for habitats, is highly relevant to attempts to assess biodiversity impacts. Biomes describe major habitat types that often share many species. Equally important, mapping of biomes uses derived climate variables that are relevant to a wide range of organisms and hence, at least in a heuristic sense, can be thought of as proxies for species climate envelopes (Malcolm et al. 2002). Midgeley et al. (2002) note that a biome approach may be especially valuable in areas where species distributions are poorly known and argue for increased efforts to test the performance of biome-level approaches against species-level approaches.

We used vegetation distributions from 14 combinations of general circulation models (GCMs) and global vegetation models (GVMs) to project habitat changes and associated extinctions. Because of several major uncertainties in this approach, we also undertook sensitivity analyses in which we varied key factors that we expected to affect our estimates: the GVM used (which make different assumptions about sensitivities to key climatic drivers), abilities of species to tolerate habitat/climatic changes, the extent to which species were restricted to particular biome types, capabilities of species to migrate to keep up with the change, and use of endemic-area relationships rather than species-area relationships (Kinzig & Harte 2000). In addition, because of the uniqueness of the hotspots from a biodiversity perspective, we tested whether they appeared to be especially vulnerable to global warming when judged against random collections of grid cells from the Earth's terrestrial surface that had the same total area and biome composition.

Methods

Climate and Vegetation Models

Biomes were modeled using GVMs under recent ($1\times CO_2$) and projected future ($2\times CO_2$) climatic conditions, the latter as modeled by GCMs. One area of uncertainty was variation among the models. We reasoned that if a broad suite of models gave similar results, then, at least with respect to current understanding of climate and vegetation modeling, our projections would be robust. Therefore we used a suite of 14 combinations of two GVMs and seven GCMs developed by Neilson et al. (1998). Rather than presenting results for all 14 model combinations here, we instead present average results for the two GVMs. Previous analyses showed that by far the major source of variation among the 14 model combinations with respect to future migration rates and habitat change was the GVM used (Malcolm et al. 2002; J.R.M., unpublished data). Therefore, we were able to span most of the range of variation among the 14 scenarios just by using means for the 2 GVMs.

These models provided biome distributions at a global resolution of 0.5° latitude/longitude under recent and GCM-based $2\times CO_2$ climates (Malcolm et al. [2002] used this same set of models to examine projected migration rates under global warming; see also Neilson et al. [1998]). The vegetation models were MAPSS (Neilson 1995) and BIOME3 (Haxeltine & Prentice 1996), which predict potential vegetation on well-drained upland sites under average seasonal climate conditions. The MAPSS and BIOME2 (a precursor to BIOME3) produced generally similar results for the coterminous United States; compared with BIOME2, however, the modeled vegetation in MAPSS was consistently more sensitive to water stress, producing drier future outcomes, and had a larger benefit from the direct physiological effects of increased CO_2, particularly the ability of plants to use water more efficiently (VEMAP Members 1995).

The GCMs included both older-generation models that used simple mixed-layer oceans (GISS, GFDL-R30, OSU, and UKMO) and newer-generation transient models that used coupled atmospheric-ocean dynamics and, in one case, the cooling effect of atmospheric aerosols (MPI-T106, HADCM2GHG, and HADGCM2SUL). The coarse grids of the GCMs were interpolated to 0.5° latitude and longitude grids and climate-change scenarios were created by applying ratios or differences between $1\times CO_2$ and $2\times CO_2$ simulations to a baseline ($1\times CO_2$) monthly climate data set (Leemans & Cramer 1991). Both vegetation models were run under HADCM2GHG and HADGCM2SUL, whereas only BIOME3 was run under MPI-T106 and only MAPSS was run under the GFDL-R30, GISS, OSU, and UKMO. The net effect was six GCM scenarios for BIOME3 and eight for MAPSS. For the newer GCMs, GVMs were run both with and without direct CO_2 effects, whereas in keeping with the VEMAP analyses, for the older GCMs, GVMs were run only with direct CO_2 effects (see Neilson et al. [1998] for additional details).

Habitat Loss

A second area of uncertainty was the method used to estimate habitat loss. Brooks et al. (2002) equate habitat loss with loss of primary habitat (following Myers et al. [2000]); as they note, however, some anthropogenic habitats may still serve as suitable habitat for hotspot endemics. The situation is even more complicated when considering climate change. First, climate-induced habitat changes may sometimes be more subtle than those brought about by common human disturbances such as land-use conversion and fragmentation. Second, and even more problematic, is the possibility that as climates shift, habitats may disappear from some areas but reappear in novel locations. Thus, one must consider not only the breadth of habitat conditions that a species can tolerate but also the possibility that species and their habitats may migrate to novel locations. Accordingly, we estimated habitat loss under four scenarios of species tolerances and two scenarios of migration capabilities. In all scenarios we did not consider the possibility that species would shift to areas outside the current boundary of a hotspot. This was a reasonable assumption given that significant biogeographic barriers (such as oceans and topographic variation) are likely to prevent such movement for most hotspots.

We varied species tolerances with two methods. First, we followed Malcolm et al. (2002) and varied the number of biome types in the biome classification scheme. If a species is assumed to inhabit a single biome type or biome climate envelopes are used as generic species climate envelopes (Malcolm et al. 2002), then schemes with fewer biome types imply broader habitat and climatic tolerances. The net effect of a broad classification scheme compared with a finer one is less habitat change

Table 1. Sensitivity analysis of numbers of extinctions of endemic plant and vertebrate species from 25 biodiversity hotspots under scenarios of global warming as calculated using species-area relationships (SAR) and endemic-area relationships (EAR).[a]

Migration scenario	*Biome definition*	*Biome specificity*	*Global vegetation model*	*Plants (133,149 endemics)*[b]		*Vertebrates (9,645 endemics)*[b]	
				EAR	*SAR*	*EAR*	*SAR*
Perfect	broad	broad	BIOME3	231 (<1)	2,660 (2)	17 (<1)	197 (2)
			MAPSS	2,415 (2)	5,502 (4)	106 (1)	342 (4)
		narrow	BIOME3	8,931 (7)	9,903 (7)	609 (6)	678 (7)
			MAPSS	20,361 (15)	21,208 (16)	1,500 (16)	1,566 (16)
	narrow	broad	BIOME3	1,070 (1)	4,512 (3)	73 (1)	327 (3)
			MAPSS	5,308 (4)	8,300 (6)	273 (3)	513 (5)
		narrow	BIOME3	13,620 (10)	14,375 (11)	1,008 (10)	1,060 (11)
			MAPSS	34,273 (26)	34,734 (26)	2,251 (23)	2,288 (24)
Zero	broad	broad	BIOME3	1,278 (1)	4,354 (3)	91 (1)	316 (3)
			MAPSS	6,395 (5)	8,790 (7)	354 (4)	551 (6)
		narrow	BIOME3	15,680 (12)	17,192 (13)	1,053 (11)	1,162 (12)
			MAPSS	30,668 (23)	31,700 (24)	2,150 (22)	2,232 (23)
	narrow	broad	BIOME3	5,121 (4)	7,854 (6)	357 (4)	560 (6)
			MAPSS	14,724 (11)	15,559 (12)	934 (10)	1,017 (11)
		narrow	BIOME3	24,733 (19)	26,110 (20)	1,814 (19)	1,908 (20)
			MAPSS	56,120 (42)	56,606 (43)	3,788 (39)	3,829 (40)

[a] *Extinctions are shown for two migration scenarios, two biome breadth definitions, two levels of biome specificity, and two global vegetation models.*

[b] *Percent loss of endemic species in parentheses.*

for a given amount of climate change (and hence lower extinction rates). In the coarse classification scheme, we assigned the planet's terrestrial surface to 10 biome types (Malcolm et al. 2002, their Table 1). In this scheme, for example, the ecologically closest biome to the Tropical Broadleaf Forest biome was Savanna/Woodland. In a finer scheme, we used the original classification systems of the GVMs themselves (18 biome types for BIOME3 and 45 for MAPSS) (Malcolm et al. 2002, their Table 1). In this scheme, for example, in BIOME3 the ecologically closest biome to the Tropical Rain Forest biome was Tropical Seasonal Forest (which itself was distinguished from the Tropical Deciduous Forest).

Second, we varied habitat specificity by either (1) using biomes as proxies for the overall climate envelope of a hotspot or (2) assuming that species distributions were biome specific. For the first approach, habitat loss was equated with a loss in area of any of the original set of biomes of the hotspot. Specifically, we calculated the area of each biome type in the hotspot under $1\times CO_2$ conditions and, for those biomes that showed a reduction in area between the 1× and $2\times CO_2$ climates, summed the areas lost. For example, if a hotspot originally was 50% Tropical Broadleaf Forest and 50% Savanna/Woodland but under future conditions became 90% Savanna/Woodland and 10% Arid Lands, then habitat loss was assumed to have been 50% (i.e., the lost area of Tropical Broadleaf Forest). Thus, species loss based on a standard species-area equation with an exponent (z) of 0.15 would be $100\% \times (1 - 0.50^{0.15}) = 9.9\%$ (see below).

For the second approach we assumed that species were restricted to certain biomes and calculated habitat loss and associated extinctions for each biome separately. Unfortunately we did not have information on the distributions of species within the hotspots and hence did not know the numbers of species per biome type. Instead we assumed that the number of species per biome followed expectations based on species-area relationships. Specifically, if a hotspot was comprised of biomes a, b, and c in proportions p_a, p_b, and p_c, then the proportion of species restricted to a was estimated as $p_a{}^z/(p_a{}^z + p_b{}^z + p_c{}^z)$. In the above example, Savanna/Woodland and Tropical Broadleaf Forest each would be expected to have one-half the species (because of their equal area); hence overall species loss due to the complete loss of Tropical Broadleaf Forest would be 50% (because of the total loss of the Tropical Broadleaf Forest biome).

To vary migration capabilities we calculated habitat loss in two ways depending on the spatial configuration of the loss. In a "perfect migration" scenario, we assumed species would be perfectly able to track biome shifts within the hotspot, including shifts to novel locations (i.e., locations where the biome did not occur under the $1\times CO_2$ climate). Thus, in calculating projected habitat loss, all that mattered was the area of a biome under recent and future conditions. Whether or not the two spatial distributions overlapped was immaterial. In contrast, in a "zero migration" scenario species were assumed to be unable to migrate to novel locations. Thus if a grid cell changed its biome type between recent and future conditions then the habitat of that cell was assumed to have been lost.

Because of the potential importance of migration in determining responses to climate change, in addition to the two migration scenarios we calculated required migration rates for each of the hotspots following Malcolm et al. (2002). Migration distance was calculated as the straight-line distance between a grid cell of future biome type x and its nearest same-biome-type grid cell in the baseline climate (the "crow-fly" distances of Malcolm et al. 2002). These distances were converted to migration rates by dividing by 100 years, which is a conservative estimate of the time period to a $2 \times CO_2$ climate based on an Intergovernmental Panel on Climate Change midrange emission scenario, "medium" climate sensitivity (2.5° C), and sulfate aerosol cooling (Houghton et al. 1996). These migration rates were averaged across the grid cells in a hotspot.

We compared each hotspot with a series of random collections of grid cells that under $1 \times CO_2$ conditions had the same number of grid cells and the same biome-type composition. The grid cells in each random collection were chosen at random from areas outside the hotspot, without replacement. We used 10,000 such random collections to test whether habitat change and average migration rates differed between the hotspot and the random population.

Species Extinctions

In addition to the standard species-area relationship we also calculated species loss using the more conservative endemic-area relationship developed by Kinzig and Harte (2000; see also Harte & Kinzig 1997). Kinzig and Harte (2000) note that predictions from species-area relationships in some cases overestimate the number of extinctions and propose that immediate extinctions might be expected only for species endemic to the area of destroyed habitat. To derive a more realistic relationship under this possibility, endemic-area relationships takes into account the number of species expected to be confined to smaller patches within the total area of habitat loss. If habitat loss exceeds 50%, endemic-area estimates and species-area estimates are the same (Kinzig & Harte 2000).

Following Kinzig and Harte (2000), under species-area relationships the loss of a fraction ϕ_A of the habitat A_0 of a hotspot will lead to the extinction of a fraction f of the original S_0 species, as given by

$$f_{\text{lost}-\text{SAR}} = 1 - (1 - \phi_A)^z,$$

where z is the species-area exponent and SAR is the species-area relationship. Under the endemic-areas relationship (EAR), the predicted fraction lost is

$$f_{\text{lost}-\text{EAR}} = \phi_A^{z'},$$

where

$$z' = -\ln(1 - 1/2^z)/\ln(2).$$

We sought to examine the potential effects of climate change in isolation from other anthropogenic change; hence instead of a z value typical of fragmented habitats (e.g., $z = 0.25$, Brooks et al. 2002) we used a conservative value more typical of continental situations ($z = 0.15$).

Results

Projected extinctions varied markedly depending on assumptions about migration capabilities, species tolerances, and biome specificities and the GVM used (Table 1). Lowest extinction risk was observed under perfect migration, a broad biome definition, non-biome-specific ranges, and BIOME3. In this case, <1–2% of the hotspot endemic fauna faced extinction (i.e., 100s to 1000s of plant and vertebrate species). Highest extinction risk was observed under zero migration, narrow habitat/climate tolerances, biome-specific ranges, and MAPSS. In this case, 39–43% of hotspot endemics were projected to become extinct (i.e., >50,000 plant and vertebrate species).

Among the four sensitivity factors, biome specificity had the greatest influence on the estimates, followed by the GVM and then by migration and biome-breadth assumptions. For example, a four-way analysis of variance on the species-area-based plant extinctions in Table 1 indicated that 57% of the explained variance was attributable to biome specificity ($p = 0.0002$; 3.7-fold change in means), 22% to the GVM ($p = 0.005$; 2.1-fold change in means), 11% to the migration scenario ($p = 0.03$; 1.7-fold change in means), and 11% to biome breadth ($p = 0.03$; 1.7-fold change in means). Corresponding figures for species-area-based vertebrate extinctions were 60% ($p = 0.0001$; 3.9-fold change in means), 19% ($p = 0.007$; 2.0-fold change in means), 11% ($p = 0.03$; 1.7-fold change in means), and 10% ($p = 0.03$; 1.6-fold change in means).

As expected, endemic-area-based estimates were small compared with species-area-based estimates when the total amount of habitat was low. When habitat loss approached or exceeded 50% in the most extreme scenarios, however, endemic-area-based estimates and species-area-based estimates converged. Averaged across all four sensitivity factors, endemic-area-based extinctions were approximately 90% of species-area-based extinctions (average endemic-area-based estimates and species-area-based estimates, respectively, were 15,058 and 16,835 plant species and 1,024 and 1,159 vertebrate species).

Only a few hotspots showed climate-change-related habitat loss that was markedly different from that of sets of random grid cells (Table 2; calculated for non-biome-specificity only). Two hotspots that showed consistently less habitat loss than random collections were Central Chile and, to a lesser extent, Wallacea. Other hotspots that tended to show low amounts of change relative to random sets included the California Floristic Province and New Zealand. In contrast, Tropical Andes, Southwest Australia, Guinean Forests of West Africa, and the Cape Floristic Region often showed significantly more habitat loss

Table 2. Percent habitat loss from 25 biodiversity hotspots under various scenarios of global warming (two migration scenarios, two biome breadth definitions, and two global vegetation models [BIOME3 and MAPSS]) assuming broad biome specificity.

Hotspot	*Number of grid cells*[a]	*Perfect migration*[b]				*Zero migration*[b]			
		broad biome definition		*narrow biome definition*		*broad biome definition*		*narrow biome definition*	
		BIOME3	*MAPSS*	*BIOME3*	*MAPSS*	*BIOME3*	*MAPSS*	*BIOME3*	*MAPSS*
Atlantic Forest	519	19	26	24	26	22	32	29	36
California Floristic Province	145	(15)	(18)	(16)	(42)	27	(30)	(30)	(64)
Cape Floristic Region	30	(15)	57**	27	72*	(17)	67*	41	81
Caribbean	93	19	39	(19)	51	24	47	(26)	75
Caucasus	240	(21)	(14)	(24)	30	37	43	(46)	63
Central Chile	110	(14)	(10)***	(15)	(29)**	(17)	(18)**	(19)*	(40)***
Brazilian Cerrado	619	(12)	30	40	42	(13)	30	47	60
Choco-Darien-Western Ecuador	82	13	(12)	19	(18)	22	(17)	30	(29)
Eastern Arc Mountains & Coastal Forest	63	(11)	(9)	(31)	57	(12)	(10)	(38)	60
Indo-Burma	789	(12)	31	29	37	17	35	39	57
Madagascar & Indian Ocean Island	213	11	(16)	25	27	17	(26)	40	50
Mediterranean Basin	936	(12)	(22)	(18)**	(32)	(23)	43	36	(59)
Mesoamerica	391	16	(17)	28	31	22	(28)	40	54
New Caledonia	7	(<1)	(<1)	(<1)	75	(0)	(0)	(0)	75
New Zealand	120	(15)	(27)	(15)	(27)	(18)	(34)	(18)	52
Philippines	111	3	22	(6)	23	(3)	23	(8)	32
Polynesia & Micronesia	11	14	(23)	(18)	(43)	14	(30)	24	64
Mountains of South Central China	210	25	(21)***	(25)	46	(43)	(49)	(44)	72
Succulent Karoo	38	15	38*	(18)	51	19	46	25	76
Sundaland	507	(1)	(4)	5	(5)	(2)	(4)	6	(6)
Southwest Australia	120	(14)	67***	30	72***	(17)	74***	40	89***
Tropical Andes	461	17	(21)	24	(22)	36***	50**	52***	63***
Guinean Forests of West Africa	288	9	29***	(13)	31	10	31**	20	44**
Wallacea	120	(2)	(8)	(9)	(15)	(2)	(8)*	(10)	(18)
Western Ghats & Sri Lanka	86	13	(15)	(18)	(32)	17	(19)	(25)	(47)

[a] *Grid-cell dimensions were 0.5° latitude by 0.5° longitude.*

[b] *Parentheses indicate whether or not mean biome change was greater than (no parentheses) or less than (parentheses) bootstrap-based global expectations. Mean significance levels comparing the observed and bootstrap means:* $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

than expected. Other hotspots that tended to show relatively large amounts of habitat loss were the Atlantic Forest, Indo-Burma, and Succulent Karoo. For most of the sensitivity analyses there was little evidence that the hotspots as a group showed either more or less change than expected as judged against the random sets (i.e., $p > 0.05$, two-tailed binomial test). The exception was the scenario with the highest numbers of projected extinctions (i.e., zero migration, narrow biome definition, and the MAPSS GVM), where 18 hotspots showed more change than expected and only 7 showed less change ($p = 0.03$, two-tailed binomial test).

Migration rates varied considerably among the hotspots, from rates reminiscent of average postglacial migration rates (100–200 m/year) to rates well in excess of 1000 m/year (Table 3). In agreement with Malcolm et al. (2002), narrower biome definitions resulted in higher required migration rates than did broader ones, as did use of the MAPSS model in comparison to BIOME3. Hotspots that showed unusually low rates relative to random expectations were the Mountains of South Central China, Caucasus, and Tropical Andes and, to a lesser extent, Central Chile, Sundaland, Western Ghats and Sri Lanka, and the California Floristic Province. Those with relatively high rates included two island hotspots (Caribbean and Polynesia and Micronesia) and Southwest Australia. Hotspots with relatively low migration rates outnumbered those with high migration rates, although significantly so only for the scenario that used broad biome definitions and the BIOME3 model (19 of 25 hotspots had rates less than expected, binomial test, $p = 0.009$).

To identify hotspots that appeared to be especially vulnerable to climate change, we ranked them with respect to average percent species-area-based species loss and endemic-area-based species loss across the four sensitivity factors and average migration rates in Table 3. Hotspots that were among the top eight in either ranking were judged to be especially vulnerable (Table 4). The California Floristic Province, Cape Floristic Region, Polynesia and Micronesia, and Southwest Australia were among the top eight in both rankings. With the exception of New Caledonia, all of the vulnerable hotspots showed SAR-based extinctions of >100 plant species in one or more scenarios, and several showed extinctions of >100 species across all scenarios (Cape Floristic Region, Caribbean, Indo-Burma, Mediterranean Basin,

Table 3. Mean required migration rates (meters per year) in 25 biodiversity hotspots under scenarios of global warming based on two biome breadth definitions and two global vegetation models (BIOME3 and MAPSS).

	Broad biome definition^{a,b}		*Narrow biome definition*^{a,b}	
Hotspot	*BIOME3*	*MAPSS*	*BIOME3*	*MAPSS*
Atlantic Forest	309	(315)	(455)	(356)
California Floristic Province	(175)*	(267)	(667)	2,398
Cape Floristic Region	(206)	852	1,004	(2,224)
Caribbean	263	1,452*	(545)	2,117*
Caucasus	(254)***	(340)**	(352)***	(1,680)
Central Chile	(193)*	(265)*	(414)	(1,078)
Brazilian Cerrado	(231)	471	(914)	880
Choco-Darien-Western Ecuador	174	(140)	(273)	(325)
Eastern Arc Mountains & Coastal Forest	(228)	(408)	(542)	1,516
Indo-Burma	230	463	1,228	(681)
Madagascar & Indian Ocean Island	(144)	(264)	(952)	(532)
Mediterranean Basin	(294)	647	(645)	2,509
Mesoamerica	257	445	(527)	944
New Caledonia	(0)	(0)	(0)	11,119
New Zealand	(188)	1,460	(188)	2,562
Philippines	(59)	255	736	(365)
Polynesia & Micronesia	(104)	12,959	6,332	15,660***
Mountains of South Central China	(339)***	(484)***	(349)***	(929)
Succulent Karoo	(242)	(317)	(499)	(1,036)
Sundaland	(57)	(105)*	216	(124)**
Southwest Australia	1,915***	1,157**	2,399***	2,731
Tropical Andes	(276)***	(409)*	(514)	(690)*
Guinean Forests of West Africa	(68)	(265)	1,008	(386)
Wallacea	(60)	263	1,806	842
Western Ghats & Sri Lanka	(118)	(195)	(348)*	(610)

[a] *Parentheses indicate whether or not mean biome change was greater than (no parentheses) or less than (parentheses) bootstrap-based global expectations.*

[b] *Mean significance levels comparing the observed and bootstrap means:* $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Mountains of South Central China, and Tropical Andes; Table 4). In one or more scenarios, several hotspots showed species-area-based extinctions of >2000 plant species (Cape Floristic Region, Caribbean, Indo-Burma, Mediterranean Basin, Southwest Australia, and Tropical Andes). Hotspots that showed relatively large numbers of species-area-based vertebrate extinctions (consistently 10 or more) were the Caribbean (21–377 species), Indo-Burma (10–214), and Tropical Andes (42–737 species) (Table 4).

Discussion

Our results highlight the potential seriousness of the impacts of global warming on biodiversity hotspots. At the high end, projected extinctions in hotspots under doubled-CO_2 climates were 39–43% of the biota, representing the potential loss of some 56,000 endemic plant species and 3,700 endemic vertebrate species. Individual hotpots in some cases showed extinctions of more than 3,000 plant species (Cape Floristic Region, Caribbean, Mediterranean Basin, Tropical Andes) and, in three cases, of more than 200 vertebrate species (Caribbean, Indo-Burma, and Tropical Andes). Our bootstrap comparisons generally provided little evidence that the hotspots as a group had higher than average vulnerability to global warming, although they sometimes showed relatively high amounts of habitat change and relatively low required migration rates (presumably because of their often mountainous nature). Although it is encouraging on the one hand that these species-rich regions did not appear to be unusually vulnerable to climate change compared with other areas, on the other hand it suggests that these high extinction rates can be extended to non-hotspot areas with similar collections of biome types (mostly tropical and subtropical in this case) and where species have similarly restricted geographic ranges.

We recognize that species, not habitats, will respond to climate change and that species responses are likely to be individualistic. Where wholesale changes in vegetation structure occur, however, as indicated by changes in plant functional types in a GVM, species can be expected to suffer range losses. Such range losses can be expected to result in decreased numbers of species in the hotspots, including global extinctions in the case of endemic species.

To put these extinction rates in the context of other threats to biodiversity, it is of interest to compare them

Table 4. Projected species-area-based percent extinctions of endemic species in 12 hotspots judged to be especially vulnerable to global warming.[a]

		Perfect migration				*Zero migration*			
		broad biome definition		*narrow biome definition*		*broad biome definition*		*narrow biome definition*	
Hotspot[b]	*Global vegetation model*	*broad specificity*	*narrow specificity*	*broad specificity*	*narrow specificity*	*broad specificity*	*narrow specificity*	*broad specificity*	*narrow specificity*
California Floristic Province	BIOME3	2.4	30.9	2.5	27.8	4.5	46.4	5.2	41.9
(2125; 71)	MAPSS	3.0	4.0	7.8	40.9	5.3	6.0	14.4	53.5
Cape Floristic Region	BIOME3	2.4	2.3	4.5	5.8	2.7	2.8	7.5	8.0
(5682; 53)	MAPSS	11.8	28.6	17.4	52.4	15.4	43.9	21.9	68.0
Caribbean	BIOME3	3.1	2.7	3.1	2.8	4.0	3.6	4.4	3.8
(7000; 779)	MAPSS	7.2	12.1	10.0	15.5	9.0	25.3	19.0	48.5
Indo-Burma	BIOME3	1.9	17.8	5.1	18.8	2.7	27.1	7.2	31.2
(7000; 528)	MAPSS	5.5	23.8	6.7	29.6	6.2	33.6	11.9	40.5
Mediterranean Basin	BIOME3	1.9	10.6	2.9	9.7	3.9	16.4	6.4	24.5
(13,000; 235)	MAPSS	3.7	4.4	5.6	26.6	8.1	9.9	12.4	44.3
New Caledonia	BIOME3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(2551; 84)	MAPSS	0.0	0.0	18.8	75.0	0.0	0.0	18.8	75.0
New Zealand	BIOME3	2.5	5.3	2.5	5.3	2.8	5.5	2.8	5.5
(1865; 136)	MAPSS	4.6	24.8	4.6	29.1	6.1	40.7	10.4	38.7
Polynesia & Micronesia	BIOME3	2.2	16.6	3.0	17.7	2.2	16.6	4.1	27.8
(3334; 223)	MAPSS	3.8	42.9	8.1	55.3	5.1	43.8	14.1	58.2
Mountains of South Central China	BIOME3	4.3	3.1	4.3	12.1	8.0	8.9	8.2	28.9
(3500; 178)	MAPSS	3.5	27.3	8.8	21.6	9.5	54.6	17.3	43.5
Succulent Karoo	BIOME3	2.4	19.1	3.0	22.5	3.2	27.9	4.1	30.2
(1940; 45)	MAPSS	7.0	30.1	10.1	46.7	8.8	34.4	19.3	70.6
Southwest Australia	BIOME3	2.3	9.8	5.3	18.4	2.8	10.1	7.3	22.6
(4331; 100)	MAPSS	15.2	32.2	17.2	38.7	18.1	41.8	28.2	66.1
Tropical Andes	BIOME3	2.7	10.6	4.0	13.9	6.4	31.0	10.5	32.2
(20,000; 1567)	MAPSS	3.5	13.0	3.7	13.9	9.8	29.7	13.8	47.0

[a] *Percentages are shown for two migration scenarios, two biome breadth definitions, two levels of biome specificity, and two global vegetation models (BIOME3 and MAPSS).*

[b] *Numbers of endemic plant and vertebrate species, respectively, are shown in parentheses below hotspot names.*

with rates of habitat loss due to deforestation, which is generally recognized as one of the most serious threats to the planet's biodiversity. Brooks et al. (2002) estimate annual rates of deforestation for 13 tropical forest hotspots. From their data we used a species-area exponent of 0.15 to calculate annual percent species loss and compared these estimates with our estimates for the same hotspots, but divided by 100 years (a relatively conservative estimate of the time it will take to reach a doubled-CO_2 climate [Houghton et al. 2001]). The deforestation-based average was 0.24%, which was more than twice as great as our overall SAR-based average of 0.11%. Under certain scenarios, however, the estimates associated with climate change exceeded those associated with deforestation. For example, under zero migration, narrow habitat/climate tolerances, and biome-specific ranges, our average was 0.26%. Achard et al. (2002) estimated annual deforestation in the humid tropical forest at 0.52%, which gives annual percent species loss of 0.08%, which is below our overall average.

Climate models based on the upper range of emission scenarios indicate that a doubled-CO_2 climate could occur in as little at 50 years (Houghton et al. 2001), which would double our estimates and make our overall average similar to that based on deforestation. These calculations rely on many assumptions; nevertheless they suggest that global warming ranks among the most serious threats to the planet's biodiversity and, under some scenarios, may rival or exceed that due to deforestation. For areas currently experiencing low rates of habitat loss, global warming presumably ranks as the most serious threat to biodiversity. Thomas et al. (2004) similarly argue that global warming ranks alongside other main threats to biodiversity and moreover suggest that it is likely to be the greatest threat in many if not most regions.

Perhaps equally important, however, is the considerable range of extinction estimates that we obtained, which highlights the numerous uncertainties involved in trying to estimate global warming-induced extinctions for a given emissions scenario. Our estimates varied approximately 40-fold, from >40% of endemic taxa at the high end to approximately 1% at the low end. The four factors we investigated—species migration capabilities, the GVM used, the breadth of biome definitions, and whether or not species distributions were specific to certain biomes—all strongly affected the estimates, although the last had the greatest influence. Variation among endemic-area-based estimates was even stronger than among species-area-based estimates, which is not surprising given the exponential relationship between these two estimates at habitat losses of less than 50% (Kinzig & Harte 2000). Additional factors that we did not investigate include the possibility of higher species-area exponents even in the absence of anthropogenic fragmentation, for example, through increased fragmentation in mountainous areas as species distributions become increasingly restricted to higher elevations and fragmented by topography and through losses of coastal habitats to sea level rise (e.g., Harris & Cropper 1992).

Thomas et al. (2004) similarly observed that migration scenarios were important in influencing extinctions (see also Peterson et al. 2002), observing a 2.0-fold increase in species-area-based extinction rates when comparing zero against perfect variation, which is similar to the 1.7-fold increase we observed. Unfortunately, species migration capabilities remain poorly understood (Pitekla et al. 1997; Clark 1998; Malcolm et al. 2002). The rapid rates of migration considered here will presumably be exacerbated by the considerable habitat loss that has occurred in the hotspots (Myers et al. 2000) and the associated reduced population sizes and opportunities for dispersal (e.g., Schwartz 1992; Dyer 1995; Collingham et al. 1996).

Although the importance of migration rates in affecting extinction rates was expected, more surprising was the importance of the GVM used. Differences between the GVMs reflect both differences of opinion regarding sensitivities to key climatic drivers and problems associated with classifying ecosystem types (e.g., the difficulties of superimposing a simplified 10-biome classification system onto the more detailed GVM-specific classification systems) (VEMAP Members 1995; Neilson et al. 1998). These differences highlight some of the problems involved in using a biome approach to estimate habitat loss. By using biomes to estimate species loss, one is assuming that either (1) species tend to be restricted to certain major vegetation types and climate-induced shifts in vegetation types will result in shifts in species ranges or (2) species typically show climate tolerances similar in breadth to the range of climatic conditions within biomes and the climatic drivers of biome change are similarly important in driving species responses. Under this last assumption, biome climate envelopes are used as proxies for species envelopes (Malcolm et al. 2002). Both assumptions are clearly approximate and ultimately require information on species distributions (and responses) to be tested. Presumably, habitat tolerances and climatic drivers will vary among taxonomic groups and among regions, making the use of biomes potentially problematic. For example, given the average increase in geographic range size with latitude (Rapport's rule), it might make sense to vary both the amount of detail in biome definitions (Malcolm et al. 2002) and species-area exponents (Arita & Rodriguez 2002) as a function of latitude.

Of particular interest in this regard is a comparison of our results with those from two recent studies that used species-level modeling to estimate extinction rates (in one case in 1 of the 25 hotspots). Thomas et al. (2004) compiled results from several climate envelope studies that examined range shifts of 1103 species in six regions, and Midgley et al. (2002) examined climate envelope-based range shifts of 330 Proteaceae species in the Fynbos biome. Unfortunately, both groups used climate-change projections for 2050, whereas we used doubled-CO_2 climates, making direct comparisons difficult. When we compared percent extinctions estimated by Thomas et al. (2004) under their most extreme climate scenario (which most closely approximated our doubled-CO_2 climates) and recalculated their extinction percentages with our z exponent (0.15) instead of theirs (0.25), their recalculated estimates of 13–21% under perfect migration and 25–36% under zero migration were at the high end of our estimates, which ranged from 2 to 26% under perfect migration and 3 to 43% under zero migration. Midgley et al. (2002) report complete range dislocations for 33% of 330 Proteaceae species endemic to the Fynbos by 2050, which based on a z value of 0.15 is the same as the our zero-migration estimate for the Cape Floristic region averaged across all the scenarios (i.e., 21%).

Although these comparisons suggest that our lower-end estimates may underestimate potential extinctions, one must keep in mind that the species-level climate-envelope approach itself may be problematic (e.g., Loehle & LeBlanc 1996; Pearson & Dawson 2003). Perhaps most seriously, species may have broader climatic tolerances than their observed ranges would indicate. Different assumptions about species habitat/climatic tolerances were most important in affecting our extinction estimates, which highlights the value of understanding the factors that control species distributions. In essence, the climate envelope approach is modeling realized rather than fundamental niches and relies on only climate to model both climate effects and species interactions. Several authors have highlighted the dangers of such an approach (e.g., Loehle & LeBlanc 1996; Davis 1998*a*, 1998*b*; Pearson & Dawson 2003). Thus we believe that statements about the accuracy of the biome- and species-level approaches are premature until the accuracy of both approaches is better evaluated. Of key importance in this regard are empirical studies that test the climate envelope approach, for example, by comparing observed distributional shifts against those modeled using the climate-envelope approach.

Our estimates of global-warming-induced extinctions based on changes in major vegetation types in some of the world's most species-rich ecosystems suggest that climate change poses a serious threat to global biodiversity. We project the eventual loss of thousands, perhaps tens of thousands, of hotspot endemic plant and vertebrate species under a climate associated with a doubling of CO_2 concentrations. Other significant anthropogenic impacts in the hotspots can be expected to exacerbate this vulnerability to climate change. Although some hotspots appear to be unusually vulnerable to global warming because of both large amounts of projected vegetation change and reduced likelihoods that species will be able to migrate to accompany the changes, high rates of habitat loss also were observed in areas that are not hotspots, indicating the global nature of the threat posed to biodiversity by climate change. Our analyses also revealed numerous uncertainties in predicting biological responses to climate change. Empirical studies that test climate-envelope approaches and examine biome-level habitat associations should prove particularly valuable in reducing this uncertainty.

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