13. Among the models assumptions are (i) nonparasitoid-induced density-dependent mortalities act after all parasitism is accounted for, and healthy and parasitized hosts suffer equally [for theoretical exceptions to the latter, see C. Bernstein, *Oikos* **47**, 176 (1986)]; (ii) there is a 1:1 sex ratio for both host and parasitoid species [for theoretical exceptions, see M. P. Hassell, J. K. Waage, R. M. May, *J. Anim. Ecol.* **52**, 889 (1983)]; (iii) in any given generation of the host, a constant proportion of the host population is not encountered by searching parasitoids (*5, 7, 10*); (iv) the parasitoids do not search for hosts in the proportional (for example, structural) refuge [S. B. Vinson, in *Semiochemicals: Their Role in Pest Control*, D. A. Nordlund, R. L. Jones, W. J. Lewis, Eds. (Wiley, New York, 1981), pp. 51–77; J. H. Lawton, in *Insect Parasitoids*, J. K. Waage and D. Greathead, Eds. (Academic Press, London, 1986), pp. 265–287]; (v) attacks on hosts outside of the proportional refuge are distributed negative binomially (*6, 7*); and (vi) outside of the proportional refuge, the distributions of parasitism among parasitoid species are independent of one another [for theoretical exceptions, see N. Kakehashi, Y. Suzuki, Y. Iwasa, *J. Appl. Ecol.* **21**, 115 (1984)]. Certainly for some real systems, one or more of these assumptions will be oversimplifications.
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18. Justification for the ranges and relationships of parameter values employed in this study can be found, for example, in (*7, 17*) and, for spatial heterogeneity, in M. P. Hassell and S. W. Pacala [*Philos. Trans. R. Soc. London Ser. B* **330**, 203 (1990)]. The ranges of parameter values explored in our study are (parameter [minimum, maximum]): $F[1, 10]$, $h[1, Q]$, $b[1, Q]$, $a[0.01, 1]$, $\eta[0, 40]$, $k[0.1, 10]$, $m[0, 50]$, $n[0, 50]$, $N_0[1, Q]$, $S_{j,0}[1, Q]$ (for all j), and sample size of host population [10, 10,000] (parameter Q acts as a scaling factor relative to other parameters).
19. The measure of diversity is standardized based on the propensity to sample parasitoid species in a fixed unit area of habitat, rather than on the sole basis of percentage parasitism. One of the shortcomings of this index is that it omits the quantification of those assemblages in which the host is too rare to meet the minimum size requirements of the sample (see Fig. 2B for an alternative measure of diversity, based on the number of parasitoid individuals per unit area). Even if the host is common enough to permit a standardized sample, then the diversity measure may still omit the rarest parasitoid species (in terms of relative frequency on the host species considered here). The full complement of parasitoid species can be assessed only if the host population is exhaustively sampled.
20. Only for $\alpha < 1/F$ did we observe cases in which there were either too few hosts to provide a standardized sample or cyclic populations; for $\alpha > 1/F$, changing the initial densities of specialist parasitoids and/or the host had no effect on the final diversity estimate. Cyclic systems generally occurred when specialist parasitoids were prominent in the competitive hierarchy.
21. The details of the shape of the diversity curve, especially for $\alpha < 1/F$, depend on the diversity index employed (see Fig. 2, A and B) and the ability of the parasitoid assemblage to exploit hosts that are not in the proportional refuge. Exploitation potential increases with the number of parasitoid species in the assemblage, their respective abilities to parasitize the host, for example, $\hat{G}_i\{N_t\}$, and smaller host carrying capacities, Q. For example, when the total parasitoid species pool is not sufficiently numerous, the diversity curve flattens (Fig. 2, A and B) such that maximal numbers of parasitoid species are found over a range of intermediate α. As the species pool decreases to still lower levels, eventually variation in diversity will all but disappear except for extremely high levels of refuge ($\alpha \to 1$). In assemblages dominated by generalist species, a sufficiently low exploitation potential can sometimes lead to alternatively stable equilibria for $\alpha < 1/F$, one yielding low diversity and the other high diversity.
22. The general argument that host concealment translates into a refuge from parasitism has been made recently in (*14*). For comparison with the diversity patterns generated by our model, hosts are classified by feeding-biology and ranked by increasing structural refuge [(*23, 26*; B. A. Hawkins and J. H. Lawton, *Nature* **326**, 788 (1987)]. For example, externally feeding folivores, being fully exposed, occupy no structural refuge, whereas rollers have a slight refuge within their shelters but remain susceptible to parasitoids searching for exophytic hosts and often leave their shelters for varying lengths of time to feed or construct new ones. Among endophytically feeding hosts, leaf miners receive some protection by being within plant tissues, but otherwise receive little physical protection from mines; gallers are better protected but provide visual cues to their presence (that is, their galls); and borers are both physically protected and well concealed. Root feeders occupy the most extensive refuge by being underground. It should be emphasized, therefore, that this ranking is a qualitative one and that variation in actual levels of proportional refuge between species within any single feeding class will tend to blur the ranking of the categories represented in Figs. 3 and 4.
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Neotropical Mammals and the Myth of Amazonian Biodiversity

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Data were compiled on the distribution of mammal taxa (883 species, 242 genera, 45 families, and 10 orders) among South America's six major macrohabitats: lowland Amazon forest, western montane forests, Atlantic rain forest, upland semideciduous forest, southern mesophytic forest, and drylands. The drylands are the richest area in numbers of species supported and are more diverse than the other habitats, including the lowland Amazon rain forest, when endemics are considered. An analysis of number of endemic and nonendemic taxa versus size of area found a simple positive linear relationship: the drylands, almost twice as extensive as the Amazon lowlands, support more endemic taxa. Conservation plans that emphasize the wet tropics and fail to consider the drylands as special repositories of mammal diversity will be unable to preserve a significant number of novel taxa.

A GREAT DEAL OF CONTROVERSY HAS been focused on the suggestion that the biosphere is approaching a massive, human-induced extinction episode rivaling or surpassing the megaextinctions chronicled in the fossil record (*1*). There is evidence that Neotropical ecosystems, especially the lowland Amazon rain forest, contain an unusually rich array of species, whether vertebrates, invertebrates, or plants are considered (*2, 3*). Because tropical countries are primarily developing nations, efforts to preserve species have assumed importance in the international political arena (*4*); issues of environmental integrity have influenced government policies concerning economic development throughout the world.

Biologists have used the biodiversity issue to rally support for increased funding for research in the wet tropics (*5*), yet there are problems associated with arousing public concern with visions of doomed species. For one thing, data on which such negative scenarios are based may be incorrect (*6, 7*). Additionally, if species are disappearing at a rate below what has been suggested, the public could perceive biologists as alarmists, unnecessarily predicting a mass extinction—one that neither seems demonstrable with hard data nor ever seems to arrive.

In the literature dealing with the potential loss of diversity, at least one important question has yet to be posed: Is the tropical rain forest uncommonly diverse? Few investigators have examined organismal diversity in South America's deserts, grasslands, or scrublands (*8*). I report that when numbers of species and higher taxa of mammals are compared between the Amazon lowlands

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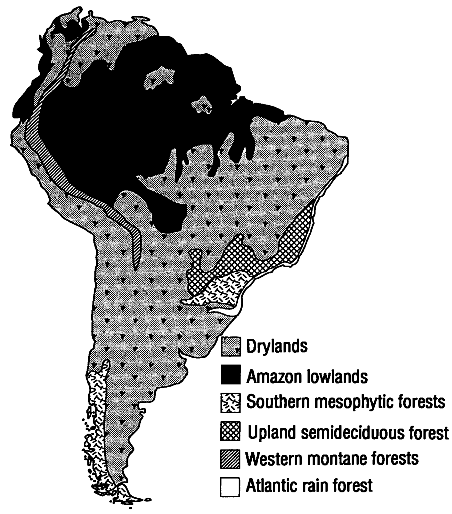

Fig. 1. Map of the six major macrohabitats of South America (*21*).

and the continent's drylands, the Amazon supports fewer taxa at all levels and fewer endemic taxa. Drylands are often considered areas of low diversity, but for mammals they are the most species-rich area on the continent.

One important hypothesis to explain elevated species richness in the Amazon forest postulates the evolution of the biota in Pleistocene refugia (*9*). Purportedly, sets of closely related species and subspecies evolved after their previously continuous geographic ranges were fractured as a result of widespread habitat disruptions related to Pleistocene glaciations. The resultant isolates underwent speciation through a classic geographic isolation mechanism. Other causes of elevated species richness have been proposed (*10*), but whatever the mechanism of species multiplication, these areas contain many closely related species.

Species are made up of individuals that are themselves carriers of genetic information being transferred through time (*11*). The potential loss of genetic information from tropical habitats has been invoked as a tragic consequence of extinction (*12*). However, the community that contains the most species may not contain the greatest amount of unique genetic information (*13*). The argument that some sets of species are more valuable than others is most easily understood with a simple example. Assume that one could save only four of ten species scheduled for extinction. What would be the most effective conservation strategy to employ in choosing which to preserve? Suppose that all ten species were mammals—four rodents, two rabbits, two monkeys, and two bats. Other things being equal, most biologists would choose one species within each higher taxonomic category. Why should this be so?

Although viable hybrids that develop between some plant species may offer unique genetic combinations, when considering animals one attempts to maximize the genetic distance between the species selected for preservation (*13*). For example, mitochondrial DNA divergence between two subspecies of the endangered black rhinoceros (*Diceros bicornis*) was found to be only 0.29%; conservation biologists recommended that they be combined into a single breeding population (*14*). The variety of genetic information stored in species representing four different orders of mammals (rodent, rabbit, monkey, and bat) is greater than that contained in four species from a single order (that is, four rodents). Closely related species may share 95% or more of their nuclear DNA sequences, implying a great similarity in overall genetic information (*15*). Choosing two such species would increase by a miniscule amount the quantity of genetic information that is protected. In contrast, species in different higher taxa imply a much greater genetic distance between them (*15, 16*). By deciding to preserve distantly related taxa, we ensure that genetic diversity, not merely species number, is maximized. This concept is referred to by Pielou (*17*) as hierarchical diversity; she noted (*17*, p. 303), "Suppose we were comparing two communities and that both had the same number of species in the same relative proportions. . . . [I]f in one community all the species belonged to a different genus, it would be reasonable to regard the latter community as the more diverse of the two." When considering Neotropical diversity, the hierarchical diversity of macrohabitats should be considered before continentwide conservation plans are formulated.

I divided South America into six major macrohabitats (Fig. 1): (i) Amazonian lowlands, including the Colombian Chocó, the Pacific lowland rain forest, and all other lowland wet and dry forest below 1500 m (5.34 million km^2, 30% of the continental land area); (ii) western montane tropical and subtropical forests above 1500 m and below the páramo, extending in a narrow band from central Venezuela southward along the eastern Andean and pre-Andean ranges to northwestern Argentina (0.58 million km^2, 3.2%); (iii) Atlantic rain forest of southeastern Brazil, a narrow strip (0.19 million km^2, 1.0%) confined to the east-facing slopes of the coastal ranges; (iv) upland semideciduous forest of Brazil, Argentina, Uruguay, and Paraguay (0.72 million km^2, 4.0%); (v) southern mesophytic forests of southern Brazil, Uruguay, and Argentina (0.78 million km^2, 4.4%); and (vi) drylands, the largest macrohabitat (10.2 million km^2, 57.3%), including the llanos of Venezuela and Colombia, the cerrado grasslands and caatinga scrublands of Brazil, the chacoan thorn forest, the Argentine pampas, the páramo and puna of the high Andes, and the lowland deserts of Argentina, Chile, and Peru.

Mammal species were assigned to one or more macrohabitats. I examined distribution patterns of species and higher taxa among the macrohabitats, noting endemicity to a macrohabitat. There are several possible sources of error in these analyses. Species distributions and habitat preferences of mammals, although better understood than most other South American organisms, are imperfectly known in many cases. By using broadly defined macrohabitats, I hoped to compensate for this type of error. Thus, for example, the dry and wet tropical forests were combined into the lowland Amazon forest category. Taxonomic problems can also influence these analyses. In some cases, although familial determinations are stable, generic rankings are unclear. However, recent taxonomic research helped clarify some particularly vexing problems. Additionally, the patterns are so prevalent that it would take a great deal of taxonomic reclassification or a significant change in the habitat preferences of many taxa to alter them. The

Table 1. Taxonomic diversity and endemism between Amazonian lowland rain forests and all other South American macrohabitats. Endemics are indicated in parentheses.

Taxonomic category	Taxa per macrohabitat			
	Lowland Amazon rain forest (no.)	All other macrohabitats combined (no.)	Amazon taxa shared with other macrohabitats (%)	Taxa shared between non-Amazon and Amazon macrohabitats (%)
Orders	9 (0)	10 (0)	100.0	90.0
Families	36 (1)	42 (3)	94.4	78.6
Genera	151 (10)	227 (65)	95.4*	59.9
Species	434 (138)	732 (336)	68.2*	38.7†

*Eight genera and 13 species are shared with regions outside South America. †Two hundred eighty-three lowland Amazon species are shared with other habitats.

Table 2. Taxonomic diversity and endemism among major macrohabitats. Endemics are indicated in parentheses.

Taxonomic category	Taxa per macrohabitat					
	Lowland Amazon rain forest (no.)	Western montane forests (no.)	Atlantic rain forest (no.)	Upland semideciduous forest (no.)	Drylands (no.)	Southern mesophytic forest (no.)
Orders	9 (0)	10 (0)	9 (0)	9 (0)	10 (0)	6 (0)
Families	36 (1)	31 (0)	31 (0)	32 (0)	39 (2)	22 (1)
Genera	151 (10)	128 (7)	102 (2)	106 (0)	183 (44)	58 (4)
Species	434 (138)	332 (87)	170 (19)	192 (5)	509 (211)	94 (14)

Table 3. Mammalian faunas for combined woodlands macrohabitats. Endemic taxa are in parentheses.

Taxonomic category	Taxa in combined macrohabitats	
	Lowland Amazon rain forest plus western montane forests (no.)	Atlantic rain forest plus upland semi-deciduous forest (no.)
Families	38 (2)	33 (0)
Genera	170 (34)	116 (10)
Species	557 (341)	225 (38)

data analyses yield surprising results (Table 1).

The Amazon lowlands support fewer than 60% (434/732) of the number of species found in all other macrohabitats. Moreover, 68% of the species found in the Amazon lowlands are also distributed in other habitats. If one compares endemic species, there are almost 2.5 (336/138) times as many endemics found in other macrohabitats as in the lowland Amazon rain forest. This pattern is even more pronounced at higher taxonomic categories.

Almost all lowland Amazon rain forest genera (95.4%) also occur in other South American (or Central American) macrohabitats. By contrast, fewer than 60% of the genera occurring in non-Amazonian habitats are also found in the lowland rain forest, and 6.5 (65/10) times as many endemic genera are restricted to non-Amazonian habitats. Essentially all families found in the Amazon are also distributed among the other macrohabitats. Although only one family (the monotypic Callimiconidae) is restricted to the lowland Amazon forest, two marsupial (Caenolestidae and Microbiotheriidae) and five rodent (Myocastoridae, Chinchillidae, Ctenomyidae, Octodontidae, and Abrocomidae) families are endemic to other macrohabitats.

An analysis by macrohabitat is also revealing (Table 2). In comparing the Amazon lowlands and the drylands, the Amazon supports fewer species, fewer endemic species, fewer genera, fewer endemic genera, fewer families, and fewer endemic families.

The lowland Amazon rain forest is not the only tropical rain forest in South America. There are extensive montane wet forests in the west and the Atlantic rain forest in the east. Although it might seem logical to combine all rain forests to obtain an estimate of a "rain forest fauna," an analysis revealed minimal species overlap between the lowland Amazon forest and the Atlantic rain forest. Indeed, not a single species is restricted to the combined area. In effect, there is no mammalian rain forest fauna when restriction to rain forest habitats is the determining factor.

Two forests could be combined: the lowland Amazon forest and the western montane forests. When these two areas are merged, the composite fauna contains 557 species, 170 genera, and 38 families. Moreover, in addition to the endemic taxa shown in Table 2, the combined area yields one additional endemic family (endemic to the two macrohabitats considered as a unit), 17 additional endemic genera, and 75 additional endemic species. This area supports a massive tropical and subtropical forest fauna, with species occurring from lowland wet forests to high, cool, Andean cloud forests and extending from eastern South America to Colombia, then southward to Argentina. Only when this aggregate area is considered does a forest fauna compare favorably with that of the drylands (compare Tables 2 and 3). The forests of southeastern Brazil do not fare as well in combination. Even when joined with the upland semideciduous forest, the Atlantic rain forest is basically a depauperate habitat compared to the drylands (Table 3).

The six macrohabitats differ greatly in size, varying by more than two orders of magnitude. Because area has been considered to play an important role in the conservation of biodiversity (*18*), I performed a regression analysis on the numbers of species and genera occurring within each macrohabitat against the area of the macrohabitats. Data were examined for possible linear, semilog, and log-log relationships; results of all analyses were comparable, but the best fit is given by a linear model.

I found (Fig. 2A) a statistically significant relation for all species versus area and for all genera versus area. When endemic and nonendemic taxa were considered separately, the results (Fig. 2B) showed a greater level of significance for endemic species versus area and for endemic genera versus area.

The results clearly show that the size of the area and the number of taxa it supports are related and that the relation is mainly the result of the endemic taxa. Drylands support more endemic genera and species than other habitats because they are larger. As area increases, the number of endemic species increases more rapidly than does the number of endemic genera (that is, the slope for species is steeper than that for genera). This

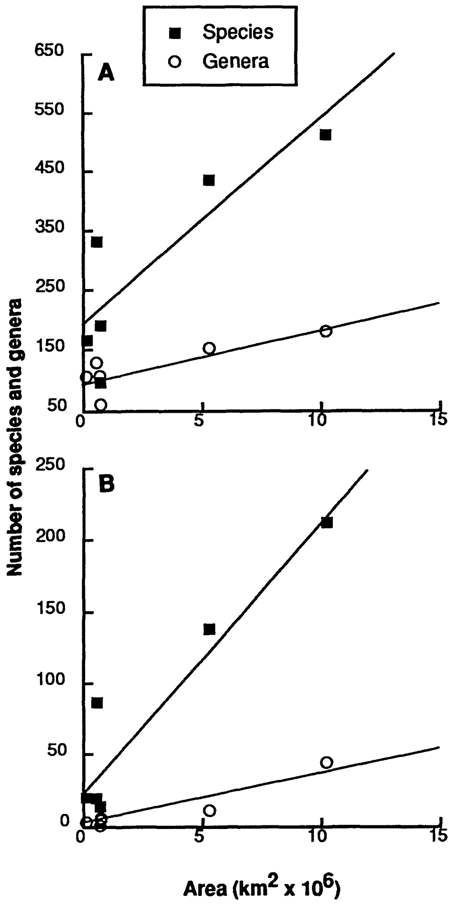

Fig. 2. Regression plots of taxonomic diversity (total number of species and genera) within the major macrohabitats of continental South America versus area. (**A**) Total number of species and genera per macrohabitat versus area: species versus area (slope = 34.598, R^2 = 0.73, $P \leq 0.05$); genera versus area (slope = 8.96, R^2 = 0.70, $P \leq 0.05$). (**B**) Number of endemic species and genera in each macrohabitat versus area: endemic species versus area (slope = 19.109, R^2 = 0.86, $P \leq 0.01$); endemic genera versus area (slope = 3.830, R^2 = 0.88, $P \leq 0.01$).

is not surprising; genera are more widespread than species, having a geographical distribution that is the sum of the geographic ranges of the component species.

The nonendemics include a broad array of eurytopic taxa, such as bats and carnivores, that range widely throughout all macrohabitats. These are core taxa that will be preserved regardless of which macrohabitats are conserved. Endemics, however, are more common in the more extensive macrohabitats, the Amazon lowlands and, especially, the drylands. These data make it clear that, as far as mammal species richness is concerneds, the tropical rain forest enjoys no special advantage. Its diversity comes from the same processes that prevail in other places (*19*).

On the basis of these findings, if one could choose only a single macrohabitat in which to preserve the greatest amount of mammalian biodiversity in South America, one would work in the largely continuous deserts, scrublands, and grasslands. This is exactly the converse of the funding, research, and conservation strategies that have been employed to date. The emphasis on developing additional lowland rain forest parks and reserves may be misguided as far as mammals are concerned; a greater amount of mammalian diversity would be preserved by increasing the number of protected areas in the drylands. Unfortunately, scientists and the ubiquitous popular media have paid scant attention to the need to preserve deserts, grasslands, or scrublands. These dry areas are very likely far more highly threatened than the largely inaccessible rain forests of the lowland tropics (*7*, *8*, *20*).

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Molecular Characterization of Helix-Loop-Helix Peptides

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A class of regulators of eukaryotic gene expression contains a conserved amino acid sequence responsible for protein oligomerization and binding to DNA. This structure consists of an arginine- and lysine-rich basic region followed by a helix-loop-helix motif, which together mediate specific binding to DNA. Peptides were prepared that span this motif in the MyoD protein; in solution, they formed α-helical dimers and tetramers. They bound to DNA as dimers and their α-helical content increased on binding. Parallel and antiparallel four-helix models of the DNA-bound dimer were constructed. Peptides containing disulfide bonds were engineered to test the correctness of the two models. A disulfide that is compatible with the parallel model promotes specific interaction with DNA, whereas a disulfide compatible with the antiparallel model abolishes specific binding. Electron paramagnetic resonance (EPR) measurements of nitroxide-labeled peptides provided intersubunit distance measurements that also supported the parallel model.

INTERACTIONS BETWEEN DIFFERENT members of the "helix-loop-helix" class of transcription factors play a key role in cell cycle progression and developmental gene regulation (*1*). This motif (*2*, *3*) contains a dimerization domain consisting of a conserved amino acid sequence that is predicted to form two amphiphilic α helices connected by a more variable loop. Immediately NH_2-terminal to this sequence is an approximately 15-residue basic region; together these two units form the b-HLH motif (basic region, helix-loop-helix), capable of binding specifically to DNA. Although the name "helix-loop-helix" implies a known three-dimensional structure, the structure of this motif has not yet been determined. Therefore, we studied the conformational properties of MyoD_{rec}, a bacterially expressed peptide spanning residues 102 to 166 of MyoD (*4*).

The ultraviolet (UV) circular dichroism (CD) spectrum of MyoD_{rec} depends on concentration; the protein undergoes a transition from random coil (or aperiodic structure) to primarily α-helix in the micromolar range. The concentration dependence of the ellipticity at 222 nm $[(\theta)_{222}$, a measure of

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