CHAPTER 9. AMPHIBIANS OF THE NEOTROPICAL REALM

Cochranella vozmedianoi *(Data Deficient) is a poorly known species endemic to Cerro El Humo, in the Península de Paria, in northern Venezuela. It is a glass frog from the Family Centrolenidae that inhabits tropical humid forests, along streams. It lays its eggs on the upper side of leaves overhanging streams. The larvae fall into the stream below after hatching. © Juan Manuel Guayasamin*

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THE GEOGRAPHIC AND HUMAN CONTEXT

The Neotropical Realm includes all of mainland South America, much of Mesoamerica (except parts of northern Mexico), all of the Caribbean islands, and extreme southern Texas and Florida in the United States.

South America has a long history of geographic isolation that began when this continent separated from other Southern Hemisphere land masses 40-30 Ma. The Andes, one of the largest mountain ranges on earth and reaching 6,962m at Acongagua in Argentina, began to uplift 80-65Ma as South America drifted west from Africa. The other prominent mountainous areas on the continent are the Tepuis of the Guianan Shield, and the highlands of south-eastern Brazil. The complex patterns of wet and dry habitats on the continent are the result of an array of factors, including the climatic effects of cold ocean currents interacting with these mountain ranges, orographic barriers to winds carrying humidity within the continent, and the constant shifting of the intertropical convergence zone, among others.

The geological history of Mesoamerica is very complex and still not completely understood. The land north of the Isthmus of Tehuantepec in southern Mexico is historically part of the North American continent, with the highest point at Pico de Orizaba at 5,610m asl. The land south of the Isthmus to the southern Nicaragua lowlands is a mosaic of plates that have rearranged themselves and alternately been submerged and exposed by the sea several times during the last 65 million years. The region encompassed by Panama, Costa Rica, and southern Nicaragua formed over the last three to ten million years through a combination of volcanic activity and uplift. The result is a jumble of mountain ranges interrupted by valleys and lowlands, with the highest point being Volcán Tajumulco at 4,220m asl in Guatemala. The closing of these different blocks of land in present-day Nicaragua during the Pliocene (5.3 - 1.8 Ma) has had a marked impact on the distribution of amphibians today.

The geological history of the Caribbean also remains under intense study, but most geologists now agree that the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) are geological cousins of the plates that make up northern Central America. Some 100 Ma, these islands were lined up more or less between North and South America in approximately the location of present day Central America. Over the last 70 million years, these islands have drifted east to their current positions. The trailing edge of this parade of islands has fused to North America and now makes up northern Central America. Some of the Greater Antilles may have had temporary land connections with North and/or South America as they drifted eastward. The Lesser Antilles formed in a completely different manner. As the Caribbean Plate carrying the Greater Antilles moved eastward, the America Plate subducted beneath it, creating an island arc known today as the Lesser Antilles.

The region is enormously varied ecologically. Equatorial South America is dominated by the lowland rainforest of the Amazon Basin. South of this the habitats become progressively drier and less suitable for amphibians, with the exception of the now extensively cleared Atlantic Forest of southern and eastern Brazil, eastern Paraguay, and north-eastern Argentina, and the temperate forests of Chile. There are important wetland areas in the Llanos of Venezuela and Colombia, and the Pantanal of Brazil, Paraguay and Bolivia. The topographically varied Andean region includes all varieties of habitats, from some of the wettest lowland rainforest in the Pacific lowlands of Colombia to the Atacama Desert in northern Chile (the driest place on earth), and from cold temperate habitats in the extreme south of the continent to high mountain paramos in the tropics. In Mesoamerica there is a very complex patchwork of natural habitats, with humid mountain slopes rising above both dry (generally on the Pacific side) and wet (Caribbean side) lowland habitats. The Caribbean islands are also a complex mosaic of habitats, with low-lying islands tending to be semi-arid, and wetter environments occurring where trade winds encounter the higher Caribbean mountains giving rise to a variety of moist tropical forest types.

On average, the Neotropics have a relatively low human population density (approximately 27 people per square kilometre in 2005), only 22% of which lives in rural areas, and a population growth rate (1.4% per annum) that is decreasing. However, some Caribbean islands are among the most densely populated places on Earth. Historically, South America has been subject to relatively low levels of anthropogenic disturbance, but human impact has been higher in northern Mesoamerica and on the Caribbean islands. The low impact in much of the region is related to low human population densities. The gross income per capita was around US$3,500 in the region in 2004. However, 33% of the region's Gross Domestic Product is concentrated in Mexico and a further 30% in Brazil, where the human impacts on natural ecosystems and biodiversity have been much more severe. Economic growth rates in the region have been modest (2.7% in 2003).

The human impact on ecosystems is very variable through the region. Natural habitats have been particularly severely damaged on many of the Caribbean islands (and especially in Haiti), and in the northern part of Mesoamerica (from central Mexico, south to Guatemala, Honduras and El Salvador). There has also been extensive habitat loss through much of the Andes, and especially in the Atlantic Forests and Cerrado of central, southern and eastern Brazil, and in the native southern temperate forests of Chile. The forests of the Amazon Basin and Guianan Shield are still largely intact, although there is much clearance currently taking place along the southern edge of the forest zone in Brazil. Habitat loss in the region has been driven largely by expanding subsistence agriculture to support growing human populations, and also by commercial agriculture and logging.

GLOBAL CONSERVATION STATUS

A total of 2,916 amphibian species (49% of the world's total) are recorded from the Neotropical Realm, of which 1,145 (39%) are considered to be globally threatened (Figure 1). This is significantly more than the global average of 33%[1]. As is the case globally, the percentage of threatened species is expected to increase as the status of DD species is clarified, as new species (some of which are likely to be rare, and/or have small ranges) are discovered, and as the taxonomic status of many species complexes is resolved.

Figure 1. *Summary of Red List categories for amphibians in the Neotropical Realm.*

Red List Category	Number of species
Extinct (EX)	7
Extinct in the Wild (EW)	0
Critically Endangered (CR)	358
Endangered (EN)	456
Vulnerable (VU)	324
Near Threatened (NT)	140
Least Concern (LC)	956
Data Deficient (DD)	675
Total Number of Species	**2,916**

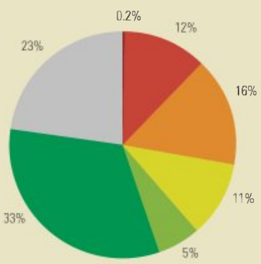

Table 1. *The Critically Endangered (Possibly Extinct) amphibian species in the Neotropical Realm (*denotes species that also occur in the Nearctic Region). A full list of CR(PE) species can be found in Appendix IX.*

ANURA
Bufonidae
Andinophryne colomai
Atelopus arthuri
Atelopus balios
Atelopus carbonerensis
Atelopus chiriquiensis
Atelopus chrysocorallus
Atelopus coynei
Atelopus famelicus
Atelopus guanujo
Atelopus halihelos
Atelopus lozanoi
Atelopus lynchi
Atelopus mindoensis
Atelopus muisca
Atelopus nanay
Atelopus oxyrhynchus
Atelopus pachydermus
Atelopus peruensis
Atelopus pinangoi
Atelopus planispina
Atelopus sorianoi
Atelopus senex
Atelopus sernai
Bufo fastidiosus
Bufo fluviaticus
Bufo holdridgei
Melanophryniscus macrogranulosus[2]
Rhamphophryne rostrata
Centrolenidae
Centrolene ballux
Centrolene heloderma
Hyalinobatrachium crybetes
Dendrobatidae
Aromobates nocturnes
Colostethus dunni
Colostethus edwardsi
Colostethus jacobuspetersi
Colostethus ruizi
Colostethus vertebralis
Dendrobates abditus
Mannophryne neblina
Hylidae
Aplastodiscus fluminеus
Bromeliohyla dendroscarta
Bokermannohyla claresignata
Bokermannohyla izecksohni
Charadrahyla altipotens
Charadrahyla trux
Ecnomiohyla echinata
Hyla bocourti
Hyla chlorostea
Hypsiboas cymbalum
Isthmohyla calypsa
Isthmohyla debilis
Isthmohyla graceae
Isthmohyla rivularis
Isthmohyla tica
Megastomatohyla pellita
Plectrohyla calvicollina
Plectrohyla celata
Plectrohyla cembra
Plectrohyla cyanomma
Plectrohyla ephemera
Plectrohyla hazelae
Plectrohyla siopela
Plectrohyla thorectes
Scinax heyeri
Leptodactylidae
Craugastor anciano
Craugastor andi
Craugastor angelicus
Craugastor coffeus
Craugastor cruzi
Craugastor escoces
Craugastor fecundus
Craugastor fleischmanni
Craugastor guerreroensis
Craugastor merendonensis
Craugastor omoaensis
Craugastor polymniae
Craugastor saltuarius
Craugastor stadelmani
Craugastor trachydermus
Crossodactylus trachystomus
Cryptobatrachus nicefori
Cycloramphus ohausi
Eleutherodactylus bernali
Eleutherodactylus emleni
Eleutherodactylus eneidae
Eleutherodactylus glanduliferoides
Eleutherodactylus jasperi
Eleutherodactylus karlschmidti
Eleutherodactylus olanchano
Eleutherodactylus orcutti
Eleutherodactylus schmidti
Eleutherodactylus semipalmatus
Eleutherodactylus zongoensis
Gastrotheca lauzuricae
Holoaden bradei
Odontophrynus moratoi
Paratelmatobius lutzii
Paratelmatobius mantiqueira
Phrynopus spectabilis
Telmatobius cirrhacelis
Telmatobius niger
Telmatobius vellardi
Ranidae
Rana omiltemana
Rana pueblae
*Rana tlaloci**
Rhinodermatidae
Rhinoderma rufum
CAUDATA
Plethodontidae
Bolitoglossa jacksoni
Bradytriton silus
*Chiropterotriton magnipes**
Ixalotriton parva
Oedipina paucidentata
Pseudoeurycea aquatica
Pseudoeurycea naucampatepetl
Pseudoeurycea nigromaculata
Pseudoeurycea praecellens
Thorius infernalis
Thorius magnipes
Thorius narismagnus
Thorius narisovalis

The Neotropical Realm contains 60% (1,145) of all globally threatened amphibians. The region accounts for a massive 79% of CR species, 59% of the EN species, and 48% of the VU species in the world. In other words, unlike the case elsewhere, threatened Neotropical amphibians are more likely to be in a higher category of threat (CR or EN), when compared with the global distribution of threatened species amongst categories. This tendency for threatened species to be in CR and EN is probably explained in part by the effects of habitat loss on species with very small ranges, in particular in the Andes, Mesoamerica, and the Caribbean islands, and also the very severe impact of enigmatic declines that are probably due to the synergistic effects of the pathogenic chytrid fungus and climate change, especially through the higher elevations of the region.

There have been seven recorded recent extinctions of amphibians in the Neotropical Realm (21% of the global total): *Atelopus ignescens* (the Jambato Toad from Ecuador); *Atelopus longirostris* (Ecuador); *Atelopus vogli* (Venezuela); *Bufo periglenes* (the famous Golden Toad from Monteverde, Costa Rica); *Phrynomedusa fimbriata* (southern Brazil); *Craugastor chrysozetetes* (Honduras); and *Craugastor milesi* (Honduras). With the exception of the Golden Toad, all of these were stream-associated species that occurred at middle to high elevations (above 700m asl) – the typical ecological profile of species that have experienced rapid declines (Lips *et al.* 2003; Ron *et al.* 2003; Burrowes *et al.* 2004; Stuart *et al.* 2004; La Marca *et al.* 2005). Some additional undescribed species are possibly extinct, especially in the genus *Atelopus* (see Pounds *et al.* [2006] for details).

In addition, 121 Critically Endangered species in the Neotropics are considered possibly extinct. This represents 93% of the 130 possibly extinct species in the world, thus dramatically highlighting the extinction crisis that has unfolded with the Neotropical amphibians. Most of the Critically Endangered (Possibly Extinct) species (listed in Table 1) share the same ecological characteristics as those that have gone extinct. Of the 121 possibly extinct species, 22 are harlequin toads in the genus *Atelopus* (representing 29% of the described species in the genus), which have experienced catastrophic declines, especially in southern Mesoamerica, and in the Andes south at least to Peru (La Marca *et al.* 2005; Pounds *et al.* 2006; and see Essay 9.1). Four genera concentrated in Mesoamerica also have large proportions of possibly extinct species: *Isthmohyla* (36%), *Plectrohyla* (20%), *Craugastor* (14%) and *Thorius* (17%) (see, for example, Lips *et al.* [2004, 2006] and Mendelson *et al.* [2004]). In each of these cases, further work is likely to show that the percentage of possibly extinct species has been underestimated. Another genus for which the percentage of possibly extinct species might have been underestimated is *Cycloramphus* from southern Brazil (see Eterovick *et al.* [2005] and Heyer *et al.* [1988] for more details). The genus *Telmatobius*, which occurs in the Andes from Ecuador southwards, is also subject to extensive disappearances, but much of this information is only just now becoming available, and for the most part is not yet included in these results (De la Riva 2005; and see Essay 9.2). Possibly extinct species range very widely in the Neotropics, generally in mountainous regions from southern Mexico (for example, *Plectrohyla cyanomma*) south to Chile (for example, *Rhinoderma rufum*). A number of recent declines and possible extinctions in Colombia have come to light since the GAA data were collected (F. Castro pers. obs.).

The percentage of DD species is very similar to the global average of 23%. As mentioned above, many of these DD species are likely to be threatened, but many others could be LC, especially those that occur in poorly surveyed low-lying areas, such as in parts of the Amazon basin, and the Cerrado of Brazil.

SPECIES RICHNESS AND ENDEMISM

Species Richness and Endemism Across Taxa

Of the 2,916 native amphibian species in the Neotropical Realm, 2,808 (or 96%) are endemic to the Neotropics (Table 2). All three orders of amphibians are represented in the Neotropical Realm. The overwhelming majority of Neotropical amphibians (89%) are frogs and toads (Anura), 97% of which are endemic. All species of Neotropical caecilians (Gymnophiona), and 91% of Neotropical salamanders (Caudata), are endemic. Only 392 species (13%) are members of families that are endemic to the region, but this low percentage is really a reflection of the fact that the very large family Leptodactylidae (accounting for 42% of Neotropical amphibian species) marginally occurs in the Nearctic Region.

The Strawberry Poison Frog Dendrobates pumilio *(Least Concern) is a poison frog from the Family Dendrobatidae, a Family famous for the stunning coloration of its species. This species lives on the floor of lowland rainforest in Nicaragua, Costa Rica and Panama. The females lay egg clutches on the forest floor, and carry the larvae, after hatching, to water-filled bromeliads, where they complete their development. © Piotr Naskrecki*

The Burrowing Toad Rhinophrynus dorsalis *(Least Concern) is the only member of the Family Rhinophrynidae. It is a lowland species ranging from southern Texas to Costa Rica. It can be found in forest, thorn scrub, savannah, and cultivated areas with friable soils. It is usually subterranean, except after heavy rains, when it emerges to breed explosively in temporary pools. © Paddy Ryan*

Under current climatic conditions, there is less isolation between the Neotropical and Nearctic Regions than there is between the Afrotropical and Palaearctic Regions, and there are points of contact between the two faunas along the Caribbean coast of Mexico, and Florida (although the transvolcanic belt in central Mexico does form a barrier to faunal dispersal). The result of this indistinct boundary is to reduce the level of endemism of each region. The families Leptodactylidae and Rhinophrynidae are nearly endemic to the Neotropics, and Scaphiopodidae, Ambystomatidae, Amphiumidae and Sirenidae are almost endemic to the Nearctic. Salamandridae is also a northern element that is only marginally present in the Neotropics. Of the 20 families that are native to the region, six are endemic. Amphibian family-level diversity is higher than in any other biogeographic realm, but endemism is lower than in the Afrotropics (where there are nine endemic families) because of the relative lack of isolation. From the perspective of amphibian biogeography, the region is almost defined by the distribution of the Neotropical frogs (family Leptodactylidae), which are present through nearly all of Mexico, Central America, South America, and the Caribbean islands. Summaries of the amphibian fauna of the Neotropics are provided by Campbell (1999a), Duellman (1999) and Hedges (1999).

There are 189 genera occurring in the region (41% of the global total), of which 157 are also endemic. These endemic genera represent over one-third (34%) of the 460 amphibian genera worldwide. The Neotropics, therefore, account for a larger proportion of the overall diversity of amphibians at the species level than at the generic level. The most species-rich genus in the region is *Eleutherodactylus* (607 species, and 715 if the genus *Craugastor* is included within it, *contra* Crawford and Smith [2005]). At the opposite end of the spectrum, there are 46 monotypic genera endemic to the Neotropical Realm, which equates to just over one-third (33%) of the 126 monotypic genera of amphibians worldwide. Interestingly, nine of these monotypic genera are in the family Microhylidae, which is not particularly diverse in the region. The 32 non-endemic genera in the Neotropics include 13 genera from Hylidae, four from Plethodontidae, three from Leptodactylidae, two each from Microhylidae, Scaphiopodidae and Sirenidae, and one each from Bufonidae, Ranidae, Rhinophrynidae, Ambystomatidae, Amphiumidae and Salamandridae. These non-endemics include the widespread genera *Bufo* and *Rana*.

Of the 20 amphibian families that occur in the Neotropics (42% of the global total), six are endemic to the region: Allophrynidae, Brachycephalidae, Centrolenidae, Dendrobatidae, Rhinodermatidae, and Rhinatrematidae.[3] The characteristics of these families are provided in Chapter 1.

Among the non-endemic families, the majority of Neotropical species are in Bufonidae, Hylidae, Leptodactylidae and Microhylidae. Of the Neotropical Bufonidae, 121 species (47% of those occurring in the region) are within the widespread genus *Bufo*. There are 77

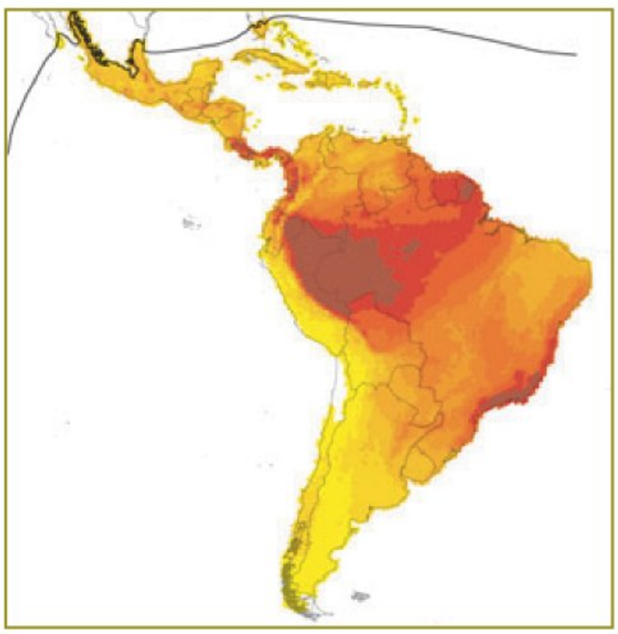

Figure 2. *The species richness of amphibians in the Neotropical Realm, with darker colours corresponding to regions of higher richness. Colour scale based on 10 quantile classes; maximum richness equals 144 species.*

Table 2. *The number of Neotropical amphibians in each taxonomic Family present in the region.*

Family	Native species (endemics to region)	Percentage of species in region that are endemic	Percentage of species in family that are endemic to region	Native genera (endemics to region)	Percentage of genera in region that are endemic	Percentage of genera in family that are endemic to region
Anura						
Allophrynidae	1 (1)	100	100	1 (1)	100	100
Brachycephalidae	8 (8)	100	100	1 (1)	100	100
Bufonidae	256 (240)	94	50	13 (12)	92	35
Centrolenidae	138 (138)	100	100	3 (3)	100	100
Dendrobatidae	234 (234)	100	100	9 (9)	100	100
Hylidae	610 (585)	96	73	46 (33)	72	67
Leptodactylidae	1,235 (1,215)	98	98	55 (52)	95	95
Microhylidae	56 (52)	93	12	19 (17)	89	25
Pipidae	7 (7)	100	23	1 (1)	100	14
Ranidae	34 (17)	50	3	1 (0)	0	0
Rhinodermatidae	2 (2)	100	100	1 (1)	100	100
Rhinophrynidae	1 (0)	0	0	1 (0)	0	0
Scaphiopodidae	3 (0)	0	0	2 (0)	0	0
TOTAL ANURA	**2,585 (2,499)**	**97**	**48**	**153 (130)**	**85**	**36**
Caudata						
Ambystomatidae	15 (9)	60	30	1 (0)	0	0
Amphiumidae	1 (0)	0	0	1 (0)	0	0
Plethodontidae	221 (210)	95	58	14 (10)	71	34
Salamandridae	2 (0)	0	0	1 (0)	0	0
Sirenidae	2 (0)	0	0	2 (0)	0	0
TOTAL CAUDATA	**241 (219)**	**91**	**41**	**19 (10)**	**53**	**16**
Gymnophiona						
Caeciliidae	81 (81)	100	72	15 (15)	100	58
Rhinatrematidae	9 (9)	100	100	2 (2)	100	100
TOTAL GYMNOPHIONA	**90 (90)**	**100**	**52**	**17 (17)**	**100**	**52**
TOTAL ALL AMPHIBIANS	**2,916 (2,808)**	**96**	**47**	**189 (157)**	**83**	**34**

Family	EX	CR	EN	VU	NT	LC	DD	Total number of species	Number Threatened or Extinct	% Threatened or Extinct
Anura										
Allophrynidae	0	0	0	0	0	1	0	1	0	0
Brachycephalidae	0	0	0	1	1	1	5	8	1	13
Bufonidae	4	73	29	30	10	77	33	256	136	53
Centrolenidae	0	6	16	29	10	28	49	138	51	37
Dendrobatidae	0	20	29	16	14	58	97	234	65	28
Hylidae	1	65	58	35	24	312	115	610	159	26
Leptodactylidae	2	145	246	172	61	350	259	1,235	565	46
Microhylidae	0	0	2	5	2	37	10	56	7	13
Pipidae	0	0	1	0	0	6	0	7	1	14
Ranidae	0	5	2	7	4	14	2	34	14	41
Rhinodermatidae	0	1	0	1	0	0	0	2	2	100
Rhinophrynidae	0	0	0	0	0	1	0	1	0	0
Scaphiopodidae	0	0	0	0	0	3	0	3	0	0
TOTAL ANURA	**7**	**315**	**383**	**296**	**126**	**888**	**570**	**2,585**	**1,001**	**39**
Caudata										
Ambystomatidae	0	8	2	0	0	3	2	15	10	67
Amphiumidae	0	0	0	0	0	1	0	1	0	0
Plethodontidae	0	35	70	28	14	28	46	221	133	60
Salamandridae	0	0	1	0	0	1	0	2	1	50
Sirenidae	0	0	0	0	0	2	0	2	0	0
TOTAL CAUDATA	**0**	**43**	**73**	**28**	**14**	**35**	**48**	**240**	**144**	**60**
Gymnophiona										
Caeciliidae	0	0	0	0	0	29	52	81	0	0
Rhinatrematidae	0	0	0	0	0	4	5	9	0	0
TOTAL GYMNOPHIONA	**0**	**0**	**0**	**0**	**0**	**33**	**57**	**90**	**0**	**0**
TOTAL ALL AMPHIBIANS	**7**	**358**	**456**	**324**	**140**	**956**	**675**	**2,915**	**1,145**	**39**

Table 3. *The number of species within each IUCN Red List Category in each Family and Order in the Neotropical Realm. Introduced species are not included.*

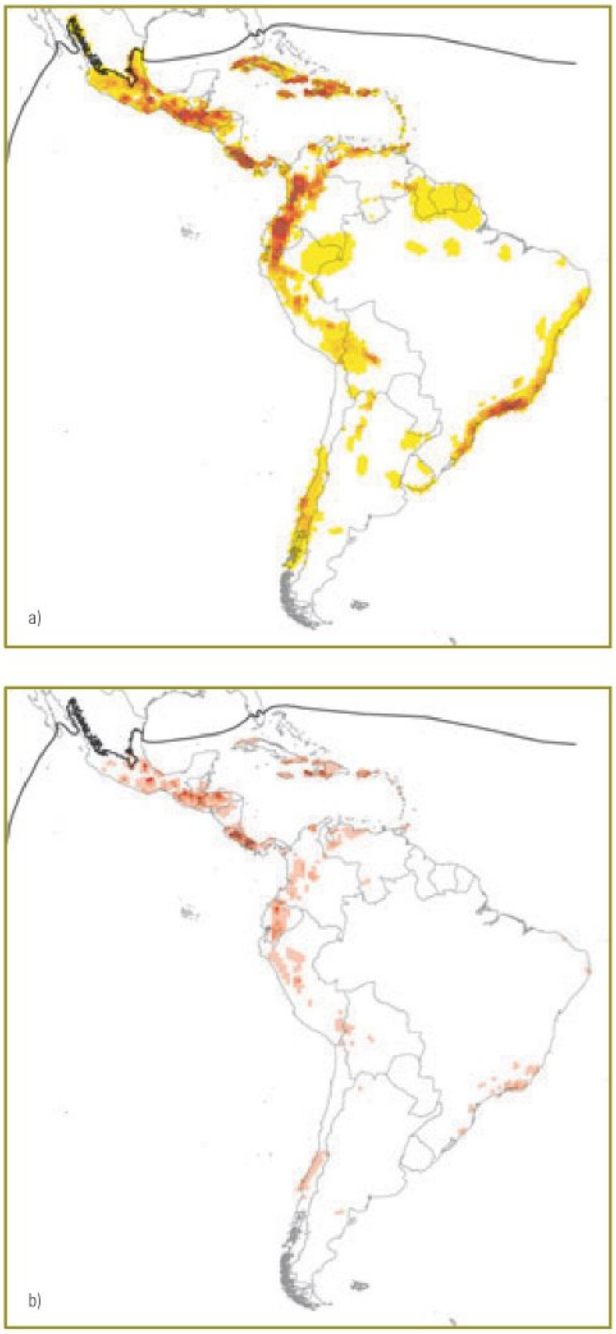

Figure 3. *a) The richness of threatened amphibians in the Neotropical Realm, with darker colours corresponding to regions of higher richness. Colour scale based on 10 quantile classes; maximum richness equals 42 species.* ***b)*** *The richness of CR amphibians in the Neotropical Realm. Colour scale based on five quantile classes; maximum richness equals 18 species.*

species in *Atelopus*, 19 in *Melanophryniscus*, and 10 in *Rhamphopryne*, but the remaining nine genera have small numbers of species. Most of the Neotropical species breed by larval development, but breeding (where it is known) is by direct development in *Metaphryniscus*, *Oreophrynella* and *Osornophryne* and unknown in *Andinophryne*, *Crepidophryne*, *Rhamphopryne* and *Truebella*. The family is widely distributed through most of the Neotropics, with highest species richness in the equatorial regions.

Hylidae is overwhelmingly a Neotropical family, the main radiation outside the region occurring in Australia and New Guinea. At the species level, 73% of the family (585 species) is endemic to the Neotropics, where it occurs widely through most of the region (excluding Chile), with especially high species richness in Brazil (over 300 species, with very high diversity in the Atlantic Forest). There are over 160 species in Mesoamerica. Two subfamilies, Phyllomedusinae and Hylinae, occur in the Neotropics (and see Essay 1.5). The genera have recently been extensively revised (Faivovich *et al.* 2005), and under this new arrangement, the genera *Dendropsophus*, *Scinax*, *Hypsiboas*, *Plectrohyla*, *Hyloscirtus*, *Phyllomedusa*, *Hyla* and *Bokermannohyla* all have more than 20 species. The Neotropical hylids are associated with many different habitats, but species richness is highest in forests, and all known breeding is by larval development.

The family Leptodactylidae, which is almost endemic to the Neotropics, is by far the largest family of amphibians worldwide. It ranges widely throughout the region, with the highest species richness in the tropical Andes from Venezuela and Colombia south to Bolivia (over 550 species), with significant diversity in Brazil (nearly 300 species), Mesoamerica (*c.* 160 species), the Caribbean islands (*c.* 160 species) and the Southern Cone (*c.* 130 species). The family includes the largest genus of vertebrates, *Eleutherodactylus* (607 species) with the following genera including more than 20 species: *Craugastor*, *Leptodactylus*, *Gastrotheca*, *Telmatobius*, *Physalaemus*, *Phrynopus*, *Cycloramphus*, and *Hylodes*. The family includes species that breed by direct development and larval development. Although these frogs occur in many habitats, species richness is highest in forests.[4]

The Neotropical Microhylidae species are widely distributed within the region, from Mexico south to central Argentina, but not on the Caribbean islands (except Trinidad). With the exception of *Chiasmocleis* (19 species), all genera are small. Most species occur at low elevations, with highest species richness in the equatorial regions. In the Neotropics, all species breed by larval development, and many are subterranean when not breeding.

The Neotropical Ranidae species (all of which are in the widespread genus *Rana*) are all larval developers, and occur predominantly in Mesoamerica, with three species reaching South America, and none on the Caribbean islands (except Trinidad). Of the remaining families, the highly aquatic Pipidae, with a single genus in the region, *Pipa*, ranges from Panama south to Bolivia. Scaphiopodidae, Amphiumidae, Salamandridae and Sirenidae are Nearctic taxa that only marginally occur in the northern Neotropics. Ambystomatidae (mole salamanders) is also a Nearctic element, but there is an important radiation of species in central Mexico, including the famous Axolotl *Ambystoma mexicanum* (CR). Ambystomatidae breed by larval development, and some retain their aquatic larval features throughout their life cycles.

Most Neotropical salamanders are in the large family Plethodontidae (lungless salamanders). This family has its highest species richness in the Nearctic, but there are *c.* 110 species in Mexico, *c.* 40 in Guatemala, *c.* 25 in Honduras, *c.* 40 in Costa Rica, *c.* 25 in Panama, but only 28 in the whole of South America (12 of these being endemic to Colombia). The largest Neotropical genus is *Bolitoglossa* (91 species), with *Pseudoeurycea*, *Oedipina* and *Thorius* each having more than 20 species. Lungless salamanders occur as far south as Bolivia. With the possible (but even then unlikely) exception of a single species (*Pseudoeurycea aquatica*), all Neotropical species breed by direct development, and almost all are associated with forest habitats (and see Essay 9.3).

The caecilian family Caeciliidae is very poorly known in the Neotropics, as in other parts of the world. A total of 81 species (in 15 genera) is recorded from the region, comprising 72% of the family at the species level. Species richness is highest in the Amazon Basin, with only 16 species in Mesoamerica (as far north as southern Mexico), and four species reaching northern Argentina. The species exhibit a wide variety of reproductive modes, from larval and direct development, to live-bearing. The majority are subterranean species in the forest floor, but certain species (in the genera *Atretochoana*, *Potomotyphlus* and *Typhlonectes*) are aquatic, sometimes referred to as "rubber eels".

Not surprisingly, the larger families – Bufonidae, Centrolenidae, Dendrobatidae, Hylidae, Leptodactylidae and Plethodontidae – have the largest absolute numbers of globally threatened species (Table 3). The percentage of threatened species ranges greatly between the families, from zero for the Allophrynidae, Rhinophrynidae, Scaphiopodidae, Amphiumidae, Sirenidae, Caeciliidae, and Rhinatrematidae, to 100% for the endemic Rhinodermatidae of Chile and Argentina. The zero percentages of threatened species in the caecilian families is probably because these species are so poorly known (with >50% of species Data Deficient in both the Caeciliidae and Rhinatrematidae). The percentages of threatened species are also very high in the salamander families Ambystomatidae (67% - reflecting the serious conservation problems on the Mexican plateau) and Plethodontidae (60% - reflecting the poor state of forest conservation in the pine-oak regions of Mexico, Guatemala, and Honduras). The percentage levels of threat are also high (>30%) in the Bufonidae (53% - reflecting, in part, the devastating declines in the genus *Atelopus*), Leptodactylidae (46% - with several genera, including *Craugastor*, *Eleutherodactylus* and *Telmatobius* showing high levels of threat), Ranidae (41%), and Centrolenidae (37%).

Some of the larger families have more species in the Endangered category than in Critically Endangered or Vulnerable (e.g., Dendrobatidae, Leptodactylidae, Plethodontidae). However, Centrolenidae show a similar pattern to birds and mammals (Baillie *et al.* 2004), with least in Critically Endangered and most in Vulnerable. Conversely, Bufonidae and Hylidae have most in Critically Endangered and least in Vulnerable, showing how severely impacted these families have been by recent dramatic declines (indeed, 55% of threatened Neotropical Bufonidae are Critically Endangered). Among the smaller families, there is also a high percentage of Critically Endangered species in Rhinodermatidae and Ambystomatidae.

Geographic Patterns of Species Richness and Endemism

A map of overall species richness of amphibians in the Neotropical Realm (Figure 2), shows that species richness is highest in the tropical regions, notably Costa Rica and Panama, the Pacific lowlands of western Colombia and north-western Ecuador, the Guianan Shield, the Atlantic Forest of southern Brazil, and in particular in the Amazon Basin (especially in the west). Species richness is lowest in more temperate regions (Mexico, Argentina and Chile), on the Caribbean islands, and especially in arid regions, such as northern Mexico and northern Chile (there being no amphibians at all in most of the Atacama Desert region). The higher taxon diversity is particularly low in the Caribbean islands, where there are just four families and five genera (compared with 15 families and 67 genera in Mesoamerica). The vast majority (88%) of the Caribbean's amphibian species belong to just one genus, *Eleutherodactylus*. No salamanders or caecilians occur on these islands.

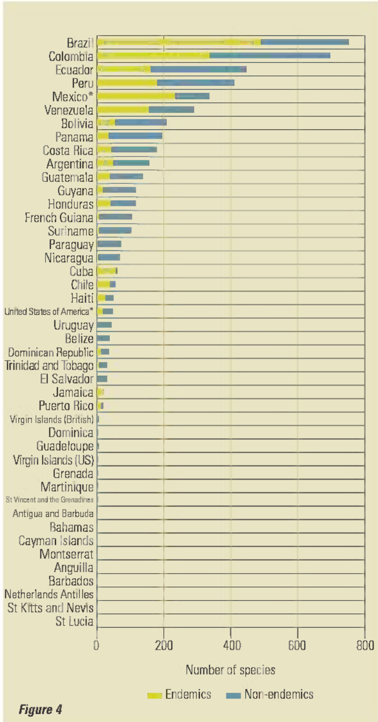

Figure 4

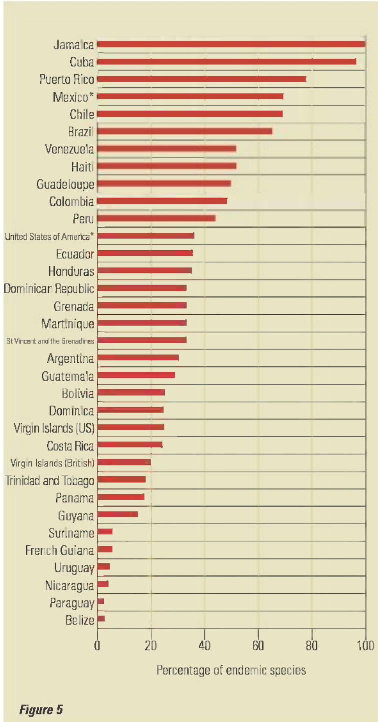

Figure 5

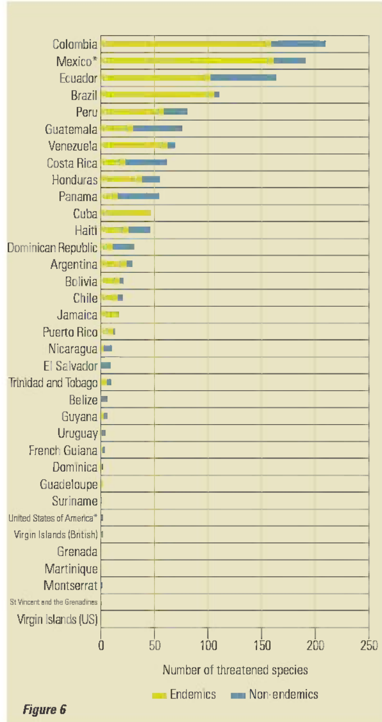

Figure 6

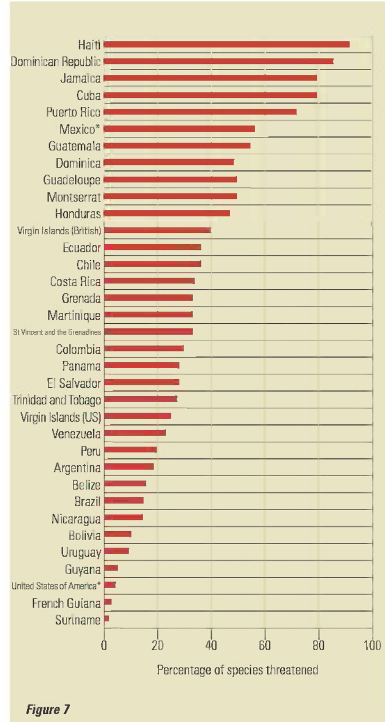

Figure 7

As with other parts of the tropics, Figure 2 probably does not reflect genuine patterns of amphibian species richness everywhere in the region, due to uneven survey effort. In particular, species richness is probably under-sampled in the Guianan Shield, in the Venezuelan, Colombian and Bolivian Amazon, in the Peruvian and Bolivian Andes, and in the Cerrado of Brazil. However, sampling appears to be less uneven than in the Old World tropics (similar maps for the Afrotropical, Indomalayan and Australasian Realms make much less overall biogeographic sense). New species continue to be discovered at a rapid rate almost everywhere in the Neotropics, but nevertheless the overall patterns of species richness are probably reasonably clear.

Over 85% of the threatened amphibian species in the Neotropics occur in the region from southern Mexico to Ecuador and northern Venezuela, and on the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico) (see Figure 3a). This region represents by far the greatest concentration of threatened amphibian species anywhere in the world. Within this region there are peaks of threatened species in montane areas in southern Mexico, Guatemala, Honduras, Costa Rica, western Panama, Cuba, Hispaniola, Jamaica, Puerto Rico, and the Andes of Venezuela, Colombia and Ecuador. Outside this region, the largest concentration of threatened amphibian species in the Neotropics is in the Atlantic Forests of southern Brazil. There are lesser concentrations in the Peruvian and Bolivian Andes, and in the austral forest zone of Chile. It is possible that, due to the poor state of knowledge, the levels of threat have been under-estimated in the Peruvian and Bolivian Andes; further, with very recently recorded declines in *Telmatobius* species (De la Riva 2005), and probably in other species too, not yet included in our data, it is likely that a new concentration of threatened species will soon be identified in the Andes running from Peru south to Bolivia, Chile, and Argentina. These concentrations of threatened species correlate with those for other taxa (Baillie *et al.* 2004). These geographic concentrations reflect the topographically diverse (usually montane) parts of the region where amphibians have naturally small ranges, and where habitat destruction is ongoing (and in central and southern Peru is in part a reflection of the over-harvesting of some frogs (e.g., in the genus *Telmatobius*) for human consumption). However, these are also the places where rapid population declines and disappearances have been noted due to chytridiomycosis and climate change (Heyer *et al.* 1988; La Marca and Reinthaler 1991; Young *et al.* 2001; Lips *et al.* 2003, 2004, 2006; Ron *et al.* 2003; Burrowes *et al.* 2004; Mendelson *et al.* 2004; De la Riva 2005; Eterovick *et al.* 2005; La Marca *et al.* 2005; Pounds *et al.* 2006).

The concentrations of Critically Endangered species (Figure 3b) broadly match those of threatened species as a whole. The greatest concentrations of these most severely threatened species are in southern Mexico (in particular Veracruz and Oaxaca), Guatemala, Honduras, Costa Rica, western Panama, the Ecuadorian Andes, and Haiti (especially the Massif de la Hotte and Massif de la Selle). Lesser concentrations of Critically Endangered species are found in the Andes of Venezuela, Colombia, Peru, southern Brazil, central Chile, Puerto Rico, Dominican Republic, Jamaica, and eastern Cuba (although recent data from the Colombian Andes suggest that the next update of the GAA might reveal this region to be a major concentration of Critically Endangered species (F. Castro pers. obs.).

Species Richness and Endemism within Countries

Amphibians occur naturally in every mainland country in Mesoamerica and South America, and on all but the smallest Caribbean islands (Figure 4). However, only one extant species occurs naturally in St. Lucia, St. Kitts and Nevis, the Netherlands Antilles, Barbados and Anguilla, and only two on Antigua and Barbuda, the Bahamas, the Cayman Islands and Montserrat. There are no indigenous amphibians on the Galapagos Islands.

The two countries with the largest number of species in the Neotropical Realm are Brazil (751 species; and see Essay 9.4) and Colombia (697 species; see Essay 9.5). There is also very high species richness in Ecuador (447 species), Peru (411), Mexico (336), Venezuela (298) and Bolivia (209). Brazil, Colombia, Ecuador, Peru, and Mexico are the top five countries in the world in terms of amphibian species richness. Another eight Neotropical countries have more than 100 species (Panama – 195, Costa Rica – 179, Argentina – 157, Guatemala – 138, Guyana – 118, Honduras – 116, French Guiana – 104, Suriname – 103).

These figures are, of course, a reflection of current knowledge, and as mentioned earlier, certain regions and countries have been better studied than others. In certain places, the existing knowledge has been well summarized in review literature, and in books, including: Mexico (Flores-Villela 1993; Flores-Villela *et al.* 1995; Calderon Mandujano *et al.* 2005); Yucatán (Campbell 1999b; Lee 1996, 2000); Guatemala (Lee 2000, Campbell 1999b, 2001); Belize (Campbell 1999b, Lee 2000); Honduras (McCranie and Wilson 2002; McCranie *et al.* 2006); El Salvador (Köhler *et al.* 2005); Nicaragua (Köhler 2001); Costa Rica (Savage 2002; Guyer and Donnelly 2005); Panama (Ibáñez *et al.* 1999, 2000); Colombia (Ruiz-Carranza *et al.* 1996); Venezuela (La Marca 1992, 1997; Barrio Amorós 2004); Ecuador (Coloma 2005); Peru (Lehr 2002); Bolivia (De la Riva *et al.* 2000, Köhler 2000); Argentina (Cei 1980, 1987; Lavilla *et al.* 2000; Lavilla and Cei 2001); Chile (Veloso and Navarro 1988; Formas 1995); Brazil (Sociedade Brasileira de Herpetologia 2004); the Guianas (Hoogmoed 1979); the Guianas (Señaris and MacCulloch 2005); French Guiana (Lescure and Marty 2000); the Caribbean islands (Crother 1999; Schwartz and Henderson 1988; Powell and Henderson 1999); the Lesser Antilles (Malhotra and Thorpe 1999); Guadeloupe (Breuil 2002); Netherlands Antilles (Powell *et al.* 2005; van Buurt 2005); and Trinidad and Tobago (Murphy 1997). There have also been some important reviews of particular taxonomic groups, for example on the Hylidae of Mesoamerica (Duellman 2001), on the western Ecuadorian *Eleutherodactylus* (Lynch and Duellman 1997), and Neotropical plethodontid salamanders (Wake and Lynch 1976; Wake 2003).

Brazil has more endemic species (489) than any other country in the Neotropics (Figure 4), or in the world, followed by Colombia (337), Mexico (234), Peru (181), Ecuador (159), and Venezuela (155). More than 50 endemic species are also known from Cuba and Bolivia. In terms of percentage of the fauna being endemic, the highest endemism is on the Greater Antilles (Figure 5), with Jamaica at 100%, Cuba at 97% and Puerto Rico at 78%. Although the percentage endemism in Haiti and the Dominican Republic is lower, for the island of Hispaniola as a whole it is 100%. On the mainland the highest percentage endemism is found in Mexico (70%), Chile (69%), and Brazil (65%), with levels over 40% in Venezuela, Haiti, Guadeloupe, Colombia, and Peru (Figure 5).

Threatened species occur in 35 of the 44 countries in which there are native amphibians (Figure 6). In fact, threatened species are concentrated in relatively few countries. Colombia has more threatened amphibian species than any other country in the Neotropics (209), followed by Mexico (190), Ecuador (163) and Brazil (110). A further 12 countries have 20 or more threatened species: Peru, Guatemala, Venezuela, Costa Rica, Panama, Honduras, Cuba, Haiti, Dominican Republic, Argentina, Bolivia and Chile. The percentage of threatened amphibian species is highest in the Greater Antilles (Figure 7), with Haiti at a staggering 92%, the Dominican Republic at 86%, Jamaica at 81%, Cuba at 80% and Puerto Rico at 72%. Overall, the percentage threat levels for amphibians on the Caribbean islands are worse than anywhere else in the world, and is a reflection of the very poor state of habitat conservation, coupled with chytridiomycosis in some places (see Essay 9.6) (of course, in these relatively species-poor countries, even a limited number of threatened species can result in a high percentage of species at risk of extinction). The highest percentage of threatened species on the mainland is in Mexico (57%), closely followed by Guatemala (55%), with a further 12 countries having levels greater than 30%: Guadeloupe, Dominica,

Figure 4. *The number of amphibians present in and endemic to each Neotropical country. *denotes countries not entirely within the Neotropical Realm, hence only the species whose ranges fall within the region are included.*

Figure 5. *Percentage of species endemic to each Neotropical country. *denotes countries not entirely within the Neotropical Realm, hence only the species whose ranges fall within the region are included.*

Figure 6. *The number of threatened amphibians present in and endemic to each Neotropical country. Countries with no threatened species are not included in the diagram. *denotes countries not entirely within the Neotropical Realm, hence only the species whose ranges fall within the region are included.*

Figure 7. *Percentage of native species that are threatened. Countries with no threatened species are not included in the diagram. *denotes countries not entirely within the Neotropical Realm, hence only the species whose ranges fall within the region are included.*

Rhinatrema bivittatum *(Least Concern) is a caecilian from the small Family Rhinatrematidae, occurring in Brazil, Guyana, Suriname and French Guiana. It is a subterranean species in lowland rainforest, and is presumed to breed in streams by larval development, like other members of its Family. © Peter Stafford*

The Upland Coqui Eleutherodactylus portoricensis *(Endangered) is one of more than 600 species in the genus Eleutherodactylus in the Family Leptodactylidae. It occurs in mesic, upland broadleaf forests, and calls from bushes and tree trunks, and has not been recorded outside forest habitat. The eggs are laid in bromeliads, and these develop directly without a free-living larval stage. © Alejandro Sanchez*

Montserrat, Honduras, British Virgin Islands, Ecuador, Chile, Costa Rica, St Vincent and the Grenadines, Martinique, Grenada, and Colombia (Figure 7). Overall, percentage threat levels are high in the Neotropics compared with the rest of the world, but the overall levels of threat do appear to be lower in the Guianan Shield and Amazonian Brazil.

Assessments of the conservation status of Neotropical amphibians at national level are still at an early stage, but there have been assessments in El Salvador (Greenbaum and Komar 2005), Panama (Young *et al.* 1999), Venezuela (Rodríguez and Rojas-Suárez 1995), Brazil (Ministério do Meio Ambiente 2003), Argentina (Lavilla *et al.* 2000), Chile (Glade 1993) and Bolivia (Reichle 2006). An official Mexican red list of amphibians is in preparation (the draft is on http://www.semarnat.gob.mx/leyesynormas/Normas%20Oficiales%20Mexicanas%20vigentes/NOM-ECOL-059-2001.pdf. Hedges (2006) provided an overview of the conservation of Caribbean amphibians.

Some countries have particularly high proportions of Critically Endangered species. The most extreme example is Haiti, where 31 species are CR, 10 are EN and five are VU (out of a total amphibian fauna of 50 species). In the neighbouring Dominican Republic, the situation is marginally less severe (10 CR, 16 EN, 5 VU out of 36 species), though still very serious. Puerto Rico has 7 CR, 5 EN and 1 VU out of a fauna of 18 species. On the mainland, things are particularly bad in Honduras (30 CR, 24 EN, 19 VU out of 116 species), and also very disturbing in Chile (9 CR, 4 EN, 7 VU out of 55), Mexico (69 CR, 80 EN, 41 VU out of 335), Guatemala (27 CR, 30 EN, 19 VU out of 140), and Costa Rica (19 CR, 22 EN, 20 VU out of 179).

In general, the levels of threat are worse in Mesoamerica than South America, because habitat loss has in general been more severe in the former, and also chytridiomycosis has been especially severe in this region (and see Essay 9.7). The situation is also serious and deteriorating in the Andean countries, where there is also significant habitat loss, and chytridiomycosis is currently spreading (De la Riva 2005; La Marca *et al.* 2005). However, because most of the Andean countries also have large, intact Amazonian amphibian faunas, the percentage of threatened species is not usually as high as in some of the Mesoamerican countries. The percentage of threatened species in Peru and Bolivia is almost certainly underestimated due to paucity in knowledge.

HABITAT AND ECOLOGY

Habitat Preferences

Most Neotropical amphibians (85%) occur in forests, and only just over 20% can survive in secondary terrestrial habitats (Table 4; Figure 8). Compared with Afrotropical species, for example, Neotropical amphibians appear to be less able to survive in disturbed areas. They also appear to make more use of flowing water habitats than still, open freshwater habitats, or marshes and swamps. This is presumably a reflection of the great diversity of stream-associated species in the Andes and Mesoamerica. Forest-dwelling amphibians are more likely to be threatened than those occurring in any other terrestrial habitats, with over 40% of them being globally threatened. A similar percentage of amphibians associated with flowing water (generally streams) is threatened. Forest-associated amphibians that live along streams are particularly likely to be threatened, a combination that has also been associated with rapid declines worldwide (Stuart *et al.* 2004).

The percentage of threatened species varies considerably between different types of forest. In montane tropical forest, over 50% of known species are threatened, compared with just over 30% in lowland tropical forest. These figures probably reflect smaller range sizes of montane species, the lack of effective habitat conservation measures in many mountainous parts of the region, and the high incidence of chytridiomycosis in montane areas (Lips *et al.* 2003; Burrowes *et al.* 2004). Amphibians occurring in savannahs, marshes and swamps, still open freshwater habitats, and secondary terrestrial habitats are much less likely to be threatened than those occurring in other habitats (Table 4; Figure 8).

Reproductive Modes

Of those species where reproduction is known or reasonably inferred, larval development is the most common reproductive mode in the Neotropics (59% of species), compared with 38% for direct development and 1% live-bearing (this compares with the global picture of 68% larval development, 30% direct development, and 1% live-bearing) (Table 5). The Neotropical amphibians clearly have a larger proportion of direct-developing species than the global average, and this is largely because of the enormous genus *Eleutherodactylus* (607 species), all but one of which (the possibly extinct *Eleutherodactylus jasperi* from Puerto Rico) are believed to be direct developers, but also because of other large genera such as *Craugastor* and *Phrynopus*. In addition, all but one of the 221 Neotropical plethodontid salamanders are believed to be direct developers. Although live-bearing is uncommon, the Neotropics account for 39% of the world's known live-bearing amphibians (all but one of these live-bearing species are caecilians, with the exception of the aforementioned *E. jasperi*).

In the Neotropics, the percentage of globally threatened direct-developing amphibians is much higher than for larval-developing species. This is probably because direct-developing species have smaller ranges on average, and are therefore more seriously impacted by habitat loss. This result is interesting because chytridiomycosis appears to have its greatest impact on stream-associated, usually larval-developing species (Lips *et al.* 2003) (though it should be noted that some stream-associated species, such as the species in the *Craugastor rugulosus* group, are direct-developers, and have been severely impacted by chytridiomycosis). The low percentage of threatened live-bearing species in the Neotropics could be a reflection of the high number of Data Deficient caecilians.

Habitat type	Number of species in each habitat	% of all species occurring in the habitat	Threatened or Extinct species	% of species occurring in habitat that are Threatened or Extinct
Forest	2,478	85	1,029	42
All tropical forest	2,407	83	1,007	42
Lowland tropical forest	1,405	48	427	30
Montane tropical forest	1,494	51	773	52
Savannah	200	7	6	3
Grassland	429	15	120	28
Shrubland	343	12	73	21
Secondary terrestrial habitats	621	21	110	18
Flowing freshwater	1,133	39	505	45
Marsh/swamp	168	6	23	14
Still open freshwater	746	26	116	16
Arid and semi-arid habitats	25	1	5	21

Table 4. *The habitat preferences of amphibians in the Neotropical Realm.*

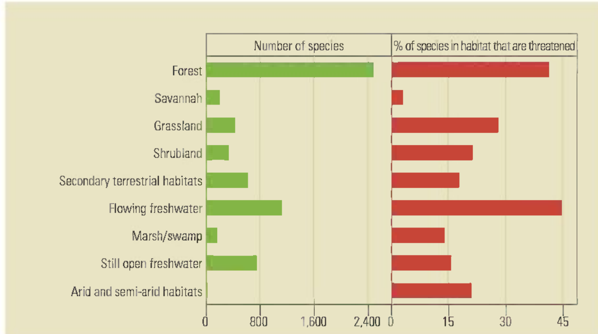

Figure 8. *The habitat preferences of Neotropical amphibians. The plot on the left-hand side shows the number of species in the region in each habitat type. On the right-hand side, the percentage of these species which are threatened is given.*

Reproductive mode	All species	Threatened or Extinct species	% Threatened or Extinct
Direct development	1,105	584	53
Larval development	1,719	555	32
Live-bearing	24	1	4
Not known	68	5	7

Table 5. *Neotropical amphibians categorized by reproductive mode.*

MAJOR THREATS

Habitat loss is overwhelmingly the major threat to amphibians in the Neotropics (Table 6; Figure 9), affecting nearly 90% of the threatened species. The two other most commonly recorded threats are pollution and disease (both affecting nearly 30% of threatened species). With the exception of fire (17%), all other threats are of minor importance. Over-utilization appears to be a minor threat in the region as a whole (at least, based on current knowledge), but it can have a serious impact on some species (e.g., on the genus *Telmatobius* in Peru, and probably elsewhere).

In terms of the types of habitat loss that are impacting amphibians in the Neotropics, the impacts of expanding croplands (affecting just over 70% of threatened species) and vegetation removal (mainly logging) (64%) are the most severe, but urbanization / industrial development and livestock grazing are each affecting more than 40% of threatened species. However, the importance of different types of habitat loss varies within the region. For example, removal of vegetation for charcoal production is a major mechanism of habitat loss in the Greater Antilles, especially in Haiti (Hedges 2006).

The distribution of chytridiomycosis in the Neotropics is only gradually becoming clear. Ron (2005) documented confirmed records of the disease widely in Mesoamerica (southern Mexico, Guatemala, Costa Rica, Panama), the Caribbean (Dominican Republic, Puerto Rico), and north-western South America (Ecuador, Venezuela). More recently the

Threat type	Threatened species	% Threatened Species
Habitat loss	1,007	89
Agriculture – Crops	806	71
Agriculture – Tree plantations	143	13
Agriculture – Livestock	478	42
Timber and other vegetation removal	728	64
Urbanization and industrial development	538	47
Invasive species	81	7
Utilization	34	3
Accidental mortality	3	0.3
Pollution	336	29
Natural disasters	73	6
Disease	324	28
Human disturbance	101	9
Changes in native species dynamics (excluding disease)	1	0.1
Fire	197	17

Table 6. *The major threats to globally threatened amphibians in the Neotropical Realm. Only present threats to species are tallied.*

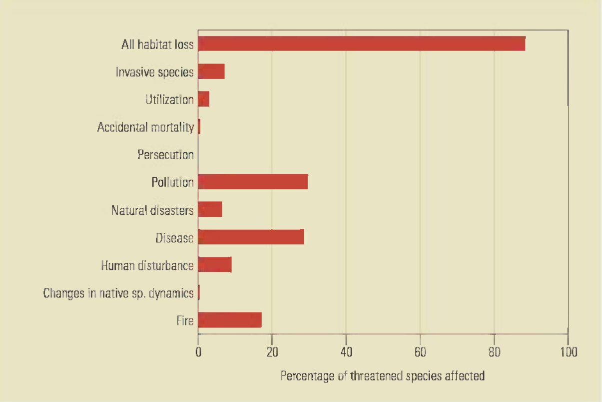

Figure 9. *The major threats impacting threatened amphibians in the Neotropical Realm.*

Purpose	Subsistence	Sub-national/ National	Regional/ International	Number of species
Food – human	41 (20)	16 (7)	5 (1)	44 (21)
Food – animal	1 (0)	1 (1)	0	2 (1)
Medicine – human and veterinary	15 (12*)	5 (2)	4 (1)	19 (13*)
Poisons	5 (0)	0	2 (0)	7 (0)
Wearing apparel, accessories	1 (0)	0	0	1 (0)
Handicrafts, curios, etc.	2 (0)	1 (0)	1 (0)	2 (0)
Pets, display animals	10 (2)	29 (8)	125 (38*)	132 (38*)
Research	0	6 (1)	6 (1)	11 (1)
Specimen collecting	0	0	1 (1)	1 (1)

Table 7. *The purposes for which amphibians are used in the Neotropical Realm. The numbers in brackets are the number of species within the total that are threatened species. *One of the species in the brackets is actually now listed as Extinct.*

disease has been recorded more widely in the continent, for example in southern Peru (Seimon *et al.* 2005), southern Brazil (Carnaval *et al.* 2005) and the Pampas region of Argentina (Herrera *et al.* 2005). The earliest records of the fungus in the region date from the early 1980s, and coincide roughly with the onset of amphibian declines (Carnaval *et al.* 2006; Lips *et al.* 2006).

A total of 181 species are recorded as being used for some or other purpose in the region (61 of which are threatened (though not necessarily by use) and one now considered Extinct). The most common reason for harvesting Neotropical amphibians is for the international pet trade, followed by local human consumption (Table 7). Well-known examples of utilization in the region include the pet trade in colourful, poisonous frogs in the genera *Dendrobates*, *Epipedobates* and *Phyllobates*, and the horned frogs (in the genus *Ceratophrys*), and harvesting *Telmatobius* frogs for local human consumption in parts of the Andes. Much of the harvesting of amphibians in the region is not considered to constitute a major threat to the species, but there are exceptions (for example, in the case of several species of *Telmatobius*). Of the 180 extant species being harvested, utilization is considered to be a major threat for 71 (of which only 34 are threatened species for which harvesting is believed to be contributing to deterioration in their status).

POPULATION STATUS AND TRENDS

Estimates of Population Trends

A summary of the inferred population trends of Neotropical amphibians is presented in Table 8. In the absence of more rigorous population monitoring studies, these trends are largely inferred from trends in the state of the habitats on which the species depend (though in some cases, dramatic population declines have been noted). Species with decreasing populations are typically forest-dependent species that can tolerate little disturbance to their habitats. The overall trends of Neotropical amphibians are very similar to the global results.

The Titicaca Water Frog Telmatobius culeus *(Critically Endangered) in the Family Leptodactylidae is endemic to Lake Titicaca in Peru and Bolivia. It is a wholly aquatic species, breeding in shallow waters close to the shoreline. It was previously common, but has declined massively due to the over-harvesting of adults, the presumed predation of larvae by introduced trout, water extraction from the lake, and domestic and agricultural water pollution. © Mikael Lundberg*

Population Trend	Number of species	% of species
Decreasing	1313	45
Stable	725	25
Increasing	15	0.5
Unknown	856	29

Table 8. *The population trends for all extant Neotropical amphibians.*

Family	Number of species in "rapid decline"	Percentage of species in family in "rapid decline"	Number of species in "enigmatic decline"	Percentage of species in family in "enigmatic decline"
Bufonidae	89	35	76	30
Centrolenidae	4	3	4	3
Dendrobatidae	17	7	11	5
Hylidae	53	9	39	6
Leptodactylidae	110	9	53	4
Ranidae	6	18	4	12
Rhinodermatidae	1	50	1	50
Ambystomatidae	5	36	0	0
Plethodontidae	20	9	6	3

Table 9. *The number of species in "rapid decline" and "enigmatic decline" in the Neotropical Realm by Family.*

"Rapidly declining" species

The Neotropics are home not only to nearly 50% of the world's amphibian species, but to nearly two-thirds (65%; 305 species) of the world's "rapidly declining" species (Stuart *et al.* 2004) (a full list of all "rapidly declining" species is provided in Appendix IV and includes their occurrence within each of the regions). The Neotropics are the global epicentre for amphibians in catastrophic decline. Twelve of these 305 species are in decline due to over-exploitation, 99 due to reduced habitat, and 194 due to so-called "enigmatic declines", which are currently attributed to chytridiomycosis and climate change (Lips *et al.* 2006; Pounds *et al.* 2006).

The "rapidly declining" species show a distinct taxonomic pattern (Table 9). Among the larger families, Bufonidae show by far the highest percentage of species in serious decline, and in particular in "enigmatic decline". Most of this very serious situation can be accounted for by the genus *Atelopus* (73 species in "rapid decline", 72 in "enigmatic decline"). There are many species in serious decline in Hylidae and Leptodactylidae, but percentage wise these families are much less seriously affected than Bufonidae. However, some genera seem to be particularly affected, notably *Isthmohyla* (6 out of 14 species in serious decline), *Plectrohyla* (21 out of 41), *Craugastor* (22 out of 108), *Telmatobius* (14 out of 52), and *Thoropa* (3 out of 6). The 43 species of *Eleutherodactylus* (especially from the Caribbean islands) in rapid decline should be seen in the context of a genus of 610 species. Some small families have high percentages of species in serious decline, most notably Rhinodermatidae and Ambystomatidae. The two species in the Rhinodermatidae, in particular, require comment. One of them, Darwin's Frog *Rhinoderma darwinii* (VU) is currently in "enigmatic decline". The other, *Rhinoderma rufum* (CR), also has declined enigmatically and was last seen in 1978; however, it is not recorded as a "rapidly declining" species, as its population crashed prior to 1980, the year from which "rapid declines" have been measured (Stuart *et al.* 2004).

The "rapid declines" in the Neotropics are concentrated in particular regions, most especially in Mesoamerica (from central Mexico south to Panama, as typified by the genera *Isthmohyla*, *Plectrohyla* and *Craugastor*) and the Andes (as typified by *Atelopus* and

Flectonotus pygmaeus *(Least Concern), in the Family Leptodactylidae, occurs in Venezuela and Colombia. It is a species of pre-montane humid forests, and is particularly associated with bromeliads. The eggs are carried on the back of the female in a pouch, and the larvae are deposited in bromeliad axils. © Francisco José López-López*

Bolitoglossa pesrubra *(Endangered) is a lungless salamander from the Family Plethodonitidae, and is restricted to the Cordillera de Talamanca in Costa Rica. It still occurs in many places within its range, but has drastically declined in some sites where it was formerly abundant, while appearing to be stable in others. © Twan Leenders*

Telmatobius). There have also been many declines in the Greater Antilles, for the most part in the genus *Eleutherodactylus*. In addition, there are some smaller foci of "rapid declines" in Chile (especially in *Alsodes* and *Rhinoderma*) and the Brazilian Atlantic Forest (where declines are still poorly documented, but involve several genera, including *Cycloramphus* and *Thoropa* (Heyer *et al.* 1988; Eterovick *et al.* 2005). The growing evidence suggests that the Neotropics is in the process of losing most of its montane, stream-associated amphibian fauna in the space of just a few decades.

KEY FINDINGS

- A total of 2,916 species are recorded from the Neotropical Realm, of which 1,145 (39%) are considered threatened.
- At the species level, 2,808 amphibians (96% of those present) are endemic to the Neotropics - roughly half of all recognized amphibians worldwide; of the 20 families found in the region, six are endemic, and of 189 amphibian genera occurring, 157 are endemic.
- The percentage of threatened species is very high in the families Rhinodermatidae (100%), Ambystomatidae (67%), Plethodontidae (60%), Bufonidae (53%), Salamandridae (50%), Leptodactylidae (46%) and Ranidae (41%), reflecting both habitat loss and declines most likely related to chytridiomycosis and climate change.
- Geographic concentrations of threatened species occur in the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico); Mesoamerica (Central America south to Panama); the tropical Andes (especially in Colombia and Ecuador, but also increasingly in Peru and Bolivia); the Venezuelan highlands; central Chile; and the Atlantic Forests of southern Brazil.
- Brazil has the largest number of species in the Neotropical Realm (751 species), and has more endemics than any other country (489). Thirteen other countries have more than 100 species (Colombia, Ecuador, Peru, Venezuela, Bolivia, Panama, Costa Rica, Argentina, Guatemala, Guyana, Honduras, French Guiana, and Suriname), with the first five of these countries having more than 50 endemics.
- Colombia has the largest number of threatened species (209), followed by Mexico (190), Ecuador (163), and Brazil (110). Peru, Guatemala, Venezuela, Costa Rica, Panama, Honduras, Cuba, Haiti, Dominican Republic, Argentina, Bolivia, and Chile each have 20 or more globally threatened species.
- Among species occurring in tropical forests, 52% of species in montane tropical forest are threatened, compared with 30% in lowland tropical forest, probably reflecting smaller range sizes of montane species, the lack of effective habitat conservation in many montane regions, higher human population densities in mountainous areas, the widespread incidence of chytridiomycosis, and the increased vulnerability of montane species to the impacts of climate change. Further, 45% of Neotropical amphibians associated with flowing water (most of which are montane) are threatened.
- Habitat loss, primarily due to expanding croplands, vegetation removal (mainly logging), urbanization/industrial development, and livestock grazing, is affecting almost 90% of the threatened species in the region. Disease (usually chytridiomycosis) and pollution are both impacting nearly 30% of globally threatened species.
- A massive 65% of the 470 globally "rapidly declining" species occur within the region; these are concentrated in Mesoamerica, the Andes and the Greater Antilles where habitat loss and chytridiomycosis have been especially severe. A total of 63% of the "rapid declines" in the Neotropics are classified as "enigmatic declines" (probably due to chytridiomycosis and climate change).
- Seven amphibian extinctions have been recorded from the Neotropics, and a further 121 species are possibly extinct (again concentrated in Mesoamerica, the Andes, and the Greater Antilles).

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The Suriname Toad Pipa pipa *(Least Concern) occurs widely in the Amazon Basin and the Guianan Shield, and is an aquatic species that lives in slow-flowing watercourses and pools in tropical rainforest. The fertilized eggs are placed by the male on the female's back, where they become embedded in the skin, and develop directly without a free-living larval stage. © Manfred Beier*

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The Pumpkin Toadlet Brachycephalus ephippium *(Least Concern) is a member of the small Family Brachycephalidae from the Atlantic Forests of southern and eastern Brazil. It is a common species in leaf-litter on the floor of primary and secondary forest. The egg clutches are deposited on the forest floor, and these develop directly without a free-living larval stage. © Juarez Silva*

Endnotes

1 P<0.01 (binomial test)

2 This species was assessed as Vulnerable at the GAA workshop in Brazil and this is the official category as listed on the Red List website. It is listed here as Critically Endangered which is the category determined by the GAA coordinating team.

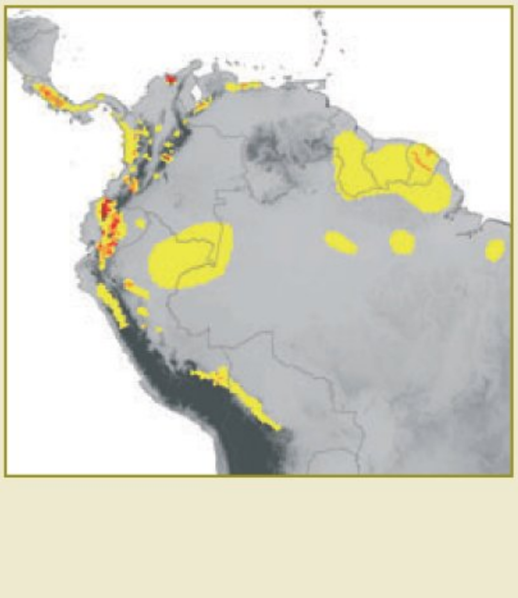
3 Frost *et al.*'s (2006) and Grant *et al.*'s (2006) proposed taxonomic changes result in 26 families in the Neotropics, of which 13 are endemic: Amphignathodontidae; Aromobatidae; Batrachophrynidae; Brachycephalidae; Centrolenidae; Ceratophryidae; Cryptobatrachidae; Cycloramphidae; Dendrobatidae; Hemiphractidae; Hylodidae; Leiuperidae; and Rhinatrematidae. However, in this section we follow the former taxonomic arrangement of families based on Frost (2004).

4 Frost *et al.* (2006) and Grant *et al.* (2006) split the Leptodactylidae into nine families (also comprising the current Brachycephalidae and Rhinodermatidae). Three small genera (collectively comprising just six species), *Batrachophrynus*, *Caudiverbera* and *Telmatobufo*, from southern Chile and north into southern Andean Peru and Bolivia are separated to form a new family Batrachophrynidae. The genus *Hemiphractus* (six species) from Panama to the upper Amazon Basin forms a new family Hemiphractidae. The genera *Adelophryne, Atopophrynus, Barycholos, Dischidodactylus, Craugastor, Eleutherodactylus, Euparkerella, Geobatrachus, Holoaden, Ischnocnema, Phrynopus, Phyllonastes* and *Phyzelaphryne* are transferred to the existing family Brachycephalidae, creating a new grouping of nearly 800 species covering almost the same geographic range as the former Leptodactylidae. The genera *Cryptobatrachus* and *Stefania* are transferred to the new family Cryptobatrachidae (21 species) endemic to northern South America. The genera *Flectonotus* and *Gastrotheca* are transferred to the new family Amphignathodontidae (nearly 60 species), ranging from Costa Rica south to Argentina. The genera *Atelognathus, Batrachyla, Ceratophrys, Insuetophrynus, Lepidobatrachus,* and *Telmatobius* are transferred to the new family Ceratophryidae (*c.* 80 species) ranging from Colombia south to Chile and Argentina. The genera *Alsodes, Crossodactylodes, Crossodactylus, Cycloramphus, Eupsophus, Hylodes, Hylorina, Limnomedusa, Macrogenioglottus, Megaelosia, Odontophrynus, Proceratophrys, Thoropa,* and *Zachaenus* are transferred to the new family Cycloramphidae (together with *Rhinoderma* from Rhinodermatidae), with c. 130 species, in southern tropical and temperate South America. The genera *Edalorhina, Engystomops, Eupemphix, Physalaemus, Pleurodema, Pseudopaludicola,* and *Sumuncuria* are transferred to Leiuperidae (75 species) ranging from southern Mexico throughout Central and South America south to central Chile and central Argentina. With these changes, the family Leptodactylidae is reduced to including the genera *Hydrolaetare, Leptodactylus* (including the subgenus *Lithodytes* for the former genera *Adenomera* and *Lithodytes*), *Paratelmatobius* and *Scythrophrys*, comprising *c.* 90 species through much of the Neotropics and southern Nearctic, including on some Caribbean islands.

ESSAY 9.1. THE EXTRAORDINARY CASE OF THE NEOTROPICAL HARLEQUIN FROGS *(ATELOPUS)*: MASS EXTINCTION WITHIN A GENUS

Atelopus sorianoi *(Critically Endangered) has the most restricted geographic range of any Venezuelan* Atelopus *species, being known from a single stream in an isolated cloud forest in the Cordillera de Mérida. The last record of the species was in 1990. © Pascual Soriani*

Figure 1. *Richness map of species in the genus Atelopus, with dark red colours corresponding to regions of higher richness. Maximum richness equals four species.*



The harlequin frogs (genus *Atelopus*) are small, colourful "jewels" distributed in the humid forests and paramos of Central and South America. The genus is the largest in the family Bufonidae, with about 80 described species distributed from Costa Rica south to Bolivia and eastward through the Amazon basin into the Guianas (Figure 1). Despite interest by scientists in these species, their conservative morphology and variable coloration have often obscured their taxonomy. Many species have highly variable colour patterns, and different species frequently have similar colour patterns. Recent genetic studies reveal both unappreciated genetic diversity among populations, but also great variation within a given taxon. More than 30 previously unrecognized species are currently in the process of being described or being elevated to the species level.

Most *Atelopus* species are associated with streams, although many occur part time of the year in terrestrial habitats (Lötters 1996). They range from sea level to approximately 4,800m elevation, but the majority live in highlands at 1,500-3,000m. Some species, such as *A. varius* (CR), *A. chiriquiensis* (CR), *A. carbonerensis* (CR), and the now Extinct *A. ignescens* and *A. vogli*, have been characterized as locally abundant, with hundreds of animals seen in a few hundred meters, often during annual breeding events (La Marca and Reinthaler 1991; Manzanilla and La Marca 2004; Pounds and Crump 1994; Ron *et al.* 2003). Local endemism is common in the genus, making species particularly vulnerable to extinction. At least 26 species are known from only one site (per Ricketts *et al.* 2005).

Sadly, these beautiful and once common diurnal amphibians are now vanishing. A recent study based on 113 *Atelopus* species (i.e., including also undescribed forms and a few just recently named), revealed that 37% of these species have undergone significant declines, and only 10 species have what are believed to be stable populations (La Marca *et al.* 2005). The majority of the declining species have disappeared in the last two decades only, and many, such as *Atelopus sorianoi* (CR) are feared extinct; at least 30 species have been missing from all known localities for at least eight years. All species restricted to elevations of above 1000m have declined and 75 percent have disappeared. At least three *Atelopus* species are considered as Extinct according to the IUCN Red List Categories and Criteria, namely *Atelopus ignescens* and *A. longirostris* from Ecuador, and *A. vogli* from Venezuela (Lötters *et al.* 2004). To put things in perspective, harlequin frogs represent about 15% of the 442 Critically Endangered (CR) amphibian species on the IUCN Red List.

The first red flag that something was amiss came many years ago (La Marca and Reinthaler 1991). Several potential causes were then discussed trying to explain the observed declines, but today the most commonly cited cause is the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*, which strikes even in undisturbed montane habitats. Habitat loss may explain a few of the disappearances. However, it is not considered to be a major cause in the case of the *Atelopus* species, since almost 20% of the harlequin frogs have disappeared from protected areas. Other potential causes of declines, such as introduced species, trade, and pollution may partly explain a few cases, too, but are unlikely to have affected the majority of the species. Synergistic combinations of factors are expected to affect some harlequin frogs, as illustrated by the case of *Atelopus zeteki* (CR), believed to be nearly extinct in the wild due to the combined effects of habitat change, illegal collecting, and fungal disease (Mendelson *et al.* 2006).

A recent finding suggests that large-scale warming of our planet is correlated with mass extinction in *Atelopus* (Pounds *et al.* 2006). The warming trend, estimated at about 0.18ºC per decade, has been to the benefit of the fungal pathogen. The rise in temperatures has most probably increased the amount of evaporation in the tropical montane environments inhabited by harlequin frogs, which in turn has been translated into increased cloud formation. Increased cloud cover in turn leads to a decrease in incoming solar radiation, thus reducing daytime temperatures, and by night may result in a green-house effect that impedes natural heat loss from the ground, with resulting warmer night-time temperatures. These cooler days and warmer nights brings the pathogenic fungus to near optimum thermal conditions, believed to be between17 and 25ºC, thereby encouraging its growth, reproduction and propagation. The theory gains support since most of the species have disappeared in the altitudinal band between 1,000 and 2,400m elevation, while recent "re-appearances" have occurred either in low-elevation (humid lowland forests) or high-elevation (paramo) habitats (Lötters *et al.* 2005). Both extremes in temperature conditions for the fungal pathogen may act as "thermal refuges" for the few surviving *Atelopus* populations.

Unfortunately, the problem of declines and extinctions in *Atelopus* is not likely to diminish in the foreseeable future. Under a scenario of double CO_2 concentrations within the next century (Malcolm *et al.* 2006), the rate of amphibian extinctions is expected to increase in many regions, including the Tropical Andes, where most harlequin frogs are known to occur. *Atelopus* may actually be a good indicator of what is happening to other less conspicuous species that could experience similar declines. The loss of these important links in the trophic web has unforeseeable consequences (Ranvestel *et al.* 2004). Furthermore, the resulting impoverished biodiversity may also represent a loss in potential advances in biomedicine and biotechnology (Mendelson *et al.* 2006).

Currently, there is no known effective protection against *Batrachochytrium dendrobatidis* in the wild. Therefore, one of the most tempting alternatives to cope with the *Atelopus* declines is to initiate captive-breeding programmes (see Essay 11.5). The success with the Panamanian Golden Frog, *Atelopus zeteki* (Zippel 2002), which is now available in breeding colonies in numerous zoos, is promising in this regard. Nevertheless, comprehensive captive-breeding programs for all *Atelopus* species threatened with extinction appear to be impossible due to the many species involved.

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ESSAY 9.2. CONSERVATION STATUS OF THE ANDEAN FROGS OF THE GENERA *TELMATOBIUS* AND *BATRACHOPHRYNUS*

The frogs of the genera *Telmatobius* and *Batrachophrynus* constitute a remarkable group of endemic Andean anurans that occur from central Ecuador in the north, to northern Chile and Argentina in the south (Figure 1). The most recent classification of *Telmatobius* (Lavilla 2005) includes 56 species, with Peru harbouring the highest diversity (23 species), followed by Bolivia (15 species), Argentina (14 species), Chile (9 species; the description of an additional species was in press at the time of writing this report) and Ecuador (3 species). *Batrachophrynus* includes two species (endemic to central Peru), and while we treat it as distinct in the current essay, recent studies have indicated that *Batrachophynus* is not a valid genus and should rather be included in *Telmatobius* (Aguilar and Pacheco 2005; Córdova and Descailleaux 2005; Sinsch *et al.* 2005).

The genus *Telmatobius* is mostly aquatic, occupying a wide, albeit montane, altitudinal range (1,300-5,000m asl), and inhabiting habitats as diverse as cloud forests to humid paramos and dry puna. Many species have co-existed with humans for centuries, and, undoubtedly, habitat destruction, mining, agricultural practices and livestock (especially camelids) have influenced the distribution and local abundance of some taxa (De la Riva 2005). Several species are captured either for food or because of certain putative medicinal or magical properties; other potential threats include water pollution and the introduction of trout for fishing. Particularly concerning is the case of the giant Lake Titicaca Frog (*Telmatobius culeus*, CR) and the even larger Lake Junin Frog (*B. macrostomus*, EN), both of which have been affected by over-fishing and other problems. Although some protection measures have been implemented (such as captive breeding), they have proved to be mostly unsuccessful (Pérez 2005).

Since *Telmatobius* and *Batrachophrynus* frogs inhabit montane areas and are stream- or lake-breeders, their biology and ecology render them particularly susceptible to chytrid infection. Indeed, there is growing evidence that chytridiomycosis is having a direct impact on populations of these frogs. Reports of serious population declines in *Telmatobius* first came from Ecuador, and a recent summary of the conservation status of Ecuadorian *Telmatobius* yields conclusive evidence of a catastrophic decline of the three species endemic to that country (Merino-Viteri *et al.* 2005). Specimens found in the 1980s and 1990s had malformations and symptoms of diseases, including chytridiomycosis. Despite intensive surveys for living animals in recent years (including 2005), the last living *Telmatobius* specimen seen in Ecuador was a tadpole of *T. niger* (CR) with severe epidermal damages, collected on 1 December 1994; *T. vellardi* (CR) was last seen in 1987, and *T. cirrhacelis* (CR) in 1981. The three Ecuadorian *Telmatobius* are now likely extinct.

While the situation in Ecuador has been thoroughly investigated, there is almost no published information for other range countries. In Perú, Lehr (2005) stated that these frogs are threatened due to agricultural practices, water pollution, and commercial utilization. Seimon *et al.* (2005) reported a case of chytridiomycosis affecting *T. marmoratus* (VU), collected in July 2002 in the department of Cusco, although without reference to population declines. This species has the broadest distribution of any *Telmatobius*, and occurs in the Altiplano and Puna highlands above the tree line. Healthy specimens were found in the department of Puno in southern Peru during recent fieldwork (February 2006; De la Riva, unpubl.), and although it is plausible that some populations of this widespread species are extinct or have declined due to chytridiomycosis, the presence of larvae and adults in many sites indicates that, overall, the species is not severely threatened. However, this situation could change in the future if climate change facilitates a shift to favorable conditions for chytrid in previously unsuitable zones.

Unfortunately, more alarming data, albeit preliminary, concern species from the humid paramos and upper cloud forest regions of Peru. In 1999-2001, *Telmatobius* were largely extirpated from the department of Cajamarca, where farmers frequently encountered dead animals (R. Schulte, in. litt.). Recent fieldwork (February 2006) by a team of five herpetologists surveying nine Andean valleys in the department of Puno and southern Cusco did not yield a single specimen of *Telmatobius*, despite thorough searches in appropriate sites. In several places, local people explained that all "kaylas" frogs (=*Telmatobius*) vanished two years ago.

In Bolivia, the situation seems to be similar. De la Riva (2005) documented a severe decline of a newly described upper cloud forest species, *T. espadai*. Tadpoles of this species were extremely abundant in Río Apaza (Cochabamba) in 1990, but no tadpoles were found in 1994 and 1999, and only a single one in 1998. A recent examination of the oral structures of this individual showed an almost complete destruction of keratinized structures, which is consistent with chytridiomycosis. Another paramo/upper cloud forest species, *T. sanborni*, occurred at least between Pelechuco (La Paz, Bolivia), where it was abundant at least in 2001, and Ollachea (Puno, Peru) (De la Riva 2005). No trace of this species was found during the recent surveys in Peru in February 2006, although it has yet to be searched for in Bolivia. The last records of two other threatened species, *T. sibiricus* (EN) and *T. verrucosus* (VU), are from 2004 (De la Riva 2005).

Chilean species of *Telmatobius* occur in mostly desertic conditions and dry puna, and are subject to the same general threats as other highland species (Formas *et al.* 2005). At present, there is no direct or indirect evidence of chytrid infection in Chilean *Telmatobius*. The available information in Argentina is not promising (Lavilla and Barrionuevo 2005). Early in 2006, S. Barrionuevo (pers. comm.) found evidence of chytrid fungus in individuals of *Telmatobius atacamensis* (CR; a species already threatened by mining activities) in the environs of San Antonio de los Cobres (Salta) and in a population of *Telmatobius pisanoi* (EN) near El Pichao (Tucumán). Another species, *T. laticeps* (EN), fairly common in the past in the area of Tafí del Valle (Tucumán) disappeared from its range in the last few years due to unknown causes; the same might have happened with the forest-dwelling *T. ceiorum* (EN; S. Barrionuevo and M.L. Ponssa, pers. comm.).

In summary, frogs of the genera *Telmatobius* (and *Batrachophynus*) are severely threatened, and at a scale comparable only to the bufonid genus *Atelopus* (see Essay 9.1). In *Telmatobius*, as with *Atelopus*, many species are still to be named, many of those already described are known only from the type locality or nearby, and several extinctions have already taken place. However, there is one important difference: *Telmatobius* has no lowland species, and thus the entire genus faces the very real danger of extinction in the very near future. Unfortunately, the case of *Telmatobius* frogs seems to strongly support Lips *et al.*'s (2006) statement: "…it is no longer correct to speak of global amphibian declines but, more appropriately, of global amphibian extinctions."

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Telmatobius marmoratus *(Vulnerable) has the widest range of any species in the genus, being known from the Andean region of southern Peru, northern and central Bolivia, and northern Chile. © Ignacio de la Riva*

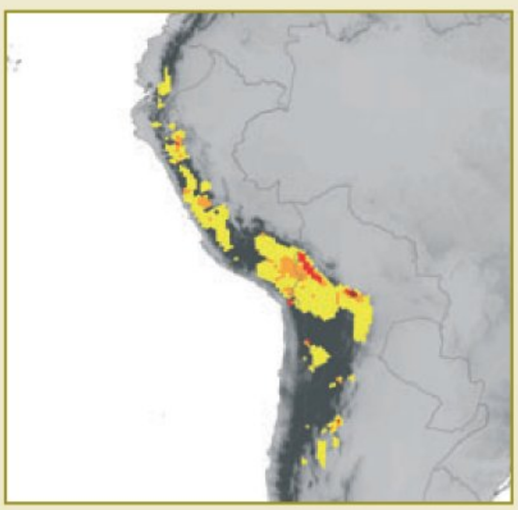

Figure 1. *Richness map of species in the genera* Telmatobius *and* Batrachophrynus, *with dark red colours corresponding to areas of higher richness. Maximum richness equals four species.*

ESSAY 9.3. NEOTROPICAL SALAMANDERS

Living salamanders comprise about 550 species, representing approximately one-tenth of living amphibians. The order Caudata hosts the largest amphibian, the Chinese Giant Salamander (*Andrias davidianus*, CR), in which adults measure 180cm from nose to tip of tail (and see Essay 4.7), as well as one of the smallest, *Thorius arboreus* (EN), one of several species of the genus that achieve sexual maturity at about 15mm in length. Although the number of salamander species is small compared with that of frogs, the diversity of species and life histories, coupled with late 20th century declines and disappearances worldwide, make salamanders an important model for understanding the causes of global change (i.e., climate change, pollution, habitat loss, etc) and their effect on biodiversity.

Salamanders are more commonly representatives of the northern temperate regions. Only a few groups have colonized tropical regions: the Salamandridae in south-eastern Asia and the Plethodontidae in tropical America. The magnitude and extent of these tropical invasions differs greatly. While tropical Asia has been colonized by only a few species, the Neotropics have been the stage for a large-scale radiation encompassing almost 40% of all salamander species.

The main Neotropical salamander radiation is restricted to a single clade, the supergenus *Bolitoglossa* (Parra-Olea *et al.* 2004), which is represented by more than 180 species and 12 genera, and ranges from northern México to Brazil (Figure 1). Bolitoglossine salamanders share fully terrestrial life histories, internal fertilization, direct development within encapsulated eggs, and a highly specialized feeding mechanism. These derived traits have played a major role in the success of bolitoglossines in the tropics (Wake 1987). A second radiation in the Neotropics can be found in the genus *Ambystoma* in the Transvolcanic Axis of central Mexico. Although this radiation has produced relatively few species, it includes several independently evolved paedomorphic lineages. A prime example is the Axolotl (*Ambystoma mexicanum*, CR), which is widely used to illustrate paedomorphosis in vertebrate evolution.

"Cryptic speciation" is common in salamanders. Their morphological evolution is conservative, and different populations often share traits that have arisen through convergence or that have evolved in parallel. Genetic studies are thus often necessary to identify new species. Such studies, coupled with fieldwork, have shown that salamanders in the tropics often exhibit a pattern of local isolation, with extreme genetic differentiation occurring over short distances ("tropicality" syndrome) (García-París *et al.* 2000). Units that have been previously treated as single species often comprise multiple and genetically distinct lineages. Accordingly, the total number of salamander species remains unknown, and new forms are steadily being described. In Mexico, for example, the number of recognized species has risen from 93 to 128 in the past 10 years — a 39% increase (Flores-Villela and Canseco 2004).

Amphibian populations are declining worldwide and Neotropical salamanders are no exception. In several localities where salamanders were seen or collected by the hundreds in the 1970s and 1980s, it is now difficult to find a single individual. Some declines have occurred in seemingly pristine areas, such as Cerro San Felipe in Oaxaca, Mexico, and Reserva de Monte Verde in Costa Rica (Parra-Olea *et al.* 1999). The results of the Global Amphibian Assessment found that out of a total of 226 species in the Neotropics, 36 are Critically Endangered, 74 Endangered, and 28 Vulnerable. An additional 42 were listed as Data Deficient. Habitat loss and water pollution is the major threat to most species of salamanders, and, for some species, over-collecting (e.g., for food), the introduction of exotic species, and urban development are significant threats. Other factors such as climate change, increased UV-B radiation, chemical contamination, and emerging infectious disease are currently being evaluated.

To date, the chytrid fungus *Batrachochytrium dendrobatidis* has been found in four species of plethodontid salamanders (Lips *et al.* 2006) and in four ambystomatid species (G. Parra-Olea, unpubl.), but massive die offs of salamanders have, as yet, not been linked to this pathogen. Climate change and forest fragmentation could have important impacts on salamanders, especially considering the limited dispersal abilities of these animals. Bioclimatic envelope modelling suggests that the terrestrial salamander *Pseudoeurycea leprosa* (VU) in Mexico could lose almost 75% of its range area over the next 50 years because of climate change (Parra-Olea *et al.* 2005). This will be true for all terrestrial salamanders that inhabit pine and/or pine-oak forests, and will be exacerbated for the majority of species with small distributional ranges.

Traditionally, aquatic salamanders of the genus *Ambystoma*, such as the Axolotl and the Achoque, *A. mexicanum*, have played an important role in local communities. The Aztecs considered the Axolotl as the transfiguration of the deity Xolotl, and both species are exploited by local communities as a food source and as a remedy for respiratory infections (see Essay 2.3). The main threats to most *Ambystoma* species include contamination and drying out of their aquatic habitats, the introduction of exotic species, and over-exploitation. For example, the local conditions of Lake Pátzcuaro, to which the Achoque is endemic, have changed following an increase in water temperature, a decrease in the mean depth of the lake, and the introduction of exotic fish (Centrarchidae, Cyprinidae and Cyclidae) and their accompanying parasites (i.e. *Bothriocephalus acheilognathi*) (García *et al.* 1993). Furthermore, between 1987 and 2000 the harvest of the Achoque was approximately 27,592 kg (Huacuz 2002). A management plan has been proposed for the Achoque and a captive-breeding program was started by a group of nuns from the Pátzcuaro convent, with the main objective of sustainably harvesting the species from the wild for the production of cough syrup for the community. However, we still know little about the size of the population, its genetic structure, or its dynamics, so evaluating its chances of survival is difficult.

Given the alarming declines and disappearances that have been witnessed among Neotropical salamanders, examining the various potential threats is urgent, particularly where these threats act in synergy (Pounds *et al.* 2006). Most importantly, we cannot begin to propose adequate management plans for species, unless we know and understand the taxonomic and phylogenetic identity of the species of concern. Resolving taxonomic uncertainties is thus fundamentally important. Studies involving the use of phylogenetics for uncovering cryptic species diversity will help reveal the true diversity of the group, and in turn also help identify unique lineages and hot spots of diversity. Finally, they will identify the affinities of individual populations, thus facilitating appropriate decisions about the translocation or reintroduction of salamanders.

Gabriela Parra-Olea

Figure 1. *Richness map of Neotropical salamander species (n=242) in the genera* Batrachoseps, Bolitoglossa, Chiropterotriton, Cryptotriton, Dendrotriton, Ixalotriton, Nototriton, Nyctanolis, Oedipina, Parvimolge, Pseudoeurycea *and* Thorius. *Dark red colours correspond to higher richness. Colour scale based on five quantile classes. Maximum richness equals 17 species.*

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ESSAY 9.4. BRAZIL: THE WORLD LEADER IN AMPHIBIAN DIVERSITY

More than 8.5 million km^2 in size, Brazil is the fifth largest country in the world and the largest among those in the tropics. It has the largest continental biota on Earth, and inspired the concept of Megadiversity countries (Mittermeier *et al.* 1997). Conservative estimates indicate that Brazil is home to 13% of global biodiversity, and has the richest flora with more than 56,000 species.

Not surprisingly, then, Brazil is also the world leader in amphibian diversity and endemism. The Global Amphibian Assessment records 751 native species, of which around 65% are endemic. However, the rate of description of new species is very high, and according to an updated list of the Brazilian Society of Herpetology (SBH) there are now 794 amphibian species in Brazil. Only Colombia can come close to rivaling Brazil in terms of absolute numbers of amphibians present (see Essay 9.5). Further, even the current number of recognized amphibians is an underestimate, as evidenced by the number of species that have been discovered and described just in recent years. Several areas have never been inventoried and likely would reveal many new species waiting to be described, including large areas in the Cerrado and Amazon, such as southern Pará and Maranhão states, western Bahia state, northern Mato Grosso, and almost all of Tocantins state.

Amphibian diversity is not evenly distributed across the country, and there is a noticeable concentration of species in some regions, for example in the Atlantic Forest (Figure 1). Unfortunately, the Atlantic Forest is also the center of origin for reports of amphibian declines in Brazil (Eterovick *et al.* 2005) (Figure 2). The Atlantic Forest (or *Mata Atlântica*) stretches along Brazil's Atlantic coast from the northern state of Rio Grande do Norte south to Rio Grande do Sul, extending from 4° to 32°S. Long isolated from other major rainforest blocks in South America, the Atlantic Forest has an extremely diverse and unique mix of vegetation and forest types, with elevation varying from the sea level to about 2,900m. Unfortunately, this biome has been largely destroyed, and only about 7% of its original native forest cover remains intact, and it is regarded as a recognized global biodiversity hotspot (Mittermeier *et al.* 2004).

In a recent review of amphibian declines in Brazil, Eterovick *et al.* (2005) found that most species experiencing declines in the Atlantic Forest are recorded at elevations up to 1,000m, some of them associated with streams (*Colostethus olfersioides* VU, *Bokermannohyla langei* DD, *Crossodactylus dispar* DD, *C. gaudichaudii* LC, *Hylodes babax* DD, *Cycloramphus boraceiensis* LC, *C. mirandaribeiroi* DD, *C. semipalmatus* NT, *Hyalinobatrachium uranoscopum* LC), others with cliffs dripping with water for tadpole development (*Cycloramphus duseni* DD, *Thoropa lutzi* EN, *T. petropolitana* VU). The species are either direct developers (*Adelophryne baturitensis* VU), or their mode of reproduction is unknown (*Colostethus carioca* DD, *Cycloramphus eleutherodactylus* DD). A few species are recorded only above 1,500m (*Eleutherodactylus paranaensis* DD, *Cycloramphus granulosus* DD, *Paratelmatobius lutzii* DD).

But declines are not only reported from the Atlantic Forest. The Brazilian Cerrado, another global biodiversity hotspot, makes up one-fifth of the country, and is the most extensive woodland-savannah in South America. The Cerrado receives abundant rainfall between October and April, while the rest of the year is characterized by a pronounced dry season. The Cerrado also contains a rich montane meadow vegetation found at higher portions of some of the mountain ranges in south-eastern Brazil, such as the Serra do Espinhaço. Eterovick *et al.* (2005) reported the first declines of amphibians in the Cerrado, among the species *Crossodactylus bokermanni* (DD) and *Epipedobates flavopictus* (LC). They recorded only a few adult individuals of *Crossodactylus bokermanni*, from the Serra do Cipó in 2001 in the Parque Nacional da Serra do Cipó, and yet the species was known to be common in the same study area in 1971–1974.

The main cause for declines in amphibians in Brazil is undoubtedly habitat destruction, largely as a consequence of deforestation, agricultural expansion, mining, fire, and infrastructure development and urbanization. However, other factors, such as severe winters, pollution and acid rain, and extended dry periods, are all possible causative factors (Eterovick *et al.* 2005). Furthermore, disease may also play an important role. Carnaval *et al.* (2006) conducted histological screenings of 96 preserved specimens of anurans collected at 10 sites in the Atlantic Forest and found chytrid fungus to be widely distributed, having recorded the disease in specimens of *Colostethus olfersioides*, *Bokermannohyla gouveai* DD and *Hypsiboas freicanecae* DD, as well as *Thoropa miliaris* LC and *Crossodactylus caramaschii* LC. More concerningly, the altitudinal range is broad, spanning from less than 100m to about 2,400m (in the Parque Nacional do Itatiaia). The widespread occurrence of chytrid in the Atlantic Forest adds to the challenge of conserving an already threatened biome. More recently, Toledo *et al.* (2006) extended the distribution of the fungus in Brazil ca. 630km southward from the previous southernmost record of Carnaval *et al.* (2006), reaching São Francisco de Paula in the state of Rio Grande do Sul (the southernmost limits of the Atlantic rainforest), and speculated on its distribution in the Cerrado and Pantanal (and see Ron 2005).

The Brazilian politics of conservation include important legal instruments, such as lists of threatened species and the selection of priority areas for conservation in all Brazilian biomes. On the other hand, the country still has much to do to improve its protected areas network, particularly given the noticeable gaps in coverage in the Atlantic Forest. The Cerrado biome deserves special attention because of the scarce knowledge about amphibians and its high rate of habitat loss due to the rapid advance of the agricultural frontier. Brazilian herpetologists have clearly made dramatic strides forward in the last two decades in improving our knowledge on natural history, ecology, and basic life-history of many species, but a great deal remains to be done to better understand the causes of the declines being witnessed among the country's amphibians, and the most appropriate means to mitigate these threats.

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Figure 1. *Richness map of all amphibian species in Brazil, with dark red colours corresponding to regions of higher richness. Colour scale based on 10 quantile classes. Maximum richness equals 139 species.*

Figure 2. *Richness map of all threatened amphibian species in Brazil, with dark red colours corresponding to regions of higher richness. Colour scale based on five quantile classes. Maximum richness equals 24 species.*

ESSAY 9.5. A BRIEF OVERVIEW OF THE AMPHIBIANS OF COLOMBIA

The amphibian fauna of Colombia is among the largest and most diverse on the planet. According to the results of the Global Amphibian Assessment, nearly 700 recognized species of amphibians are known from, or expected to occur in, Colombia, and our current estimate stands at 732. The diversity of amphibians in Colombia is, to a certain degree, the fortuitous consequence of human politics – it is as if Colombia's borders were drawn with the specific intent of maximizing its amphibian diversity. That is, Colombia's amphibian diversity is a function not only of the area of this tropical country, but also its specific location. For example, the two countries with the greatest number of amphibian species are Brazil and Colombia (Ecuador is a distant third, with "only" 449 species). With 752 recognized species listed in the GAA, Brazil has a slightly larger amphibian fauna, but its area is over eight times greater than that of Colombia. Consequently, Brazil has $8.8X10^{-5}$ species per km^2, whereas Colombia has $6.1X10^{-4}$ species per km^2 – a full order of magnitude more.

In occupying the north-western-most portion of South America, Colombia includes the rich amphibian fauna of the rain-soaked Pacific lowlands and adjacent Andean foothills, and this is augmented by capturing many species (e.g., the dendrobatid *Colostethus panamensis*, LC) and lineages (e.g., the brachycephalid genus *Craugastor*) that extend into Colombia from Central America. The eastern borders reach far into Amazonia, and further north the Llanos secure fauna associated with the Orinoco river drainage. Predominantly Venezuelan lineages, such as the aromobatid *Aromobates*, extend into Colombia in the Serranía de Perijá, and the isolated Sierra Nevada de Santa Marta harbors an endemic fauna that includes such enigmatic species as the brachycephalid *Geobatrachus walkeri* (EN).

Nevertheless, although Colombia's regional span contributes greatly to the diversity of amphibians, it is the Andean backbone that is most significant (Lynch *et al.* 1997). Whereas to the south and north-east the Andes form comparatively simple systems, in Colombia they divide into three isolated ranges that radiate from the Nudo de Pasto, and these ranges harbor about two-thirds of Colombian amphibians. Among the Andean species, most occur in the cool, moist cloud forests between 1,200 and 2,500m asl, and many are confined to extremely small areas. Although experimental data are lacking, it is assumed that this isolation is due to the adaptation of species to specific environments and their inability to survive under even mildly different conditions. For example, although two adjacent mountains may share identical environmental conditions, the different environment (e.g., higher temperature and lower precipitation) of the intervening valley would serve as a barrier to dispersion and gene flow (Lynch and Duellman 1997).

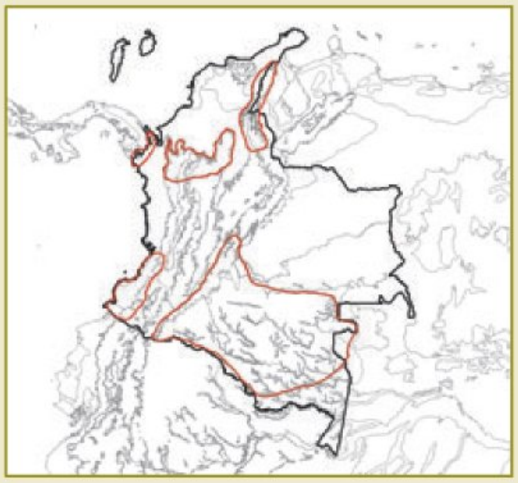
The limited geographic distribution of most Colombian amphibians makes them extremely susceptible to habitat alteration and destruction. This poses a special challenge for Colombian policy makers because humans have targeted precisely the same elevations of the Andes for their development activities. For many Andean species, the removal of a single remaining patch of forest may mean the extinction of the species. For example, *Atopophrynus syntomopus* (CR) is the only species of its genus and is known from a single locality in the Cordillera Central of Antioquia in an area that has been subjected to extreme deforestation. In addition to the habitat alteration that accompanies human development, other actual or potential threats to Colombian amphibians include the introduction of exotic species (including the illicit introduction of the North American Bull frog, *Lithobates catesbeiana*, for commercial purposes), global climate change and increased exposure to ultraviolet radiation, and infectious disease – especially chytridiomycosis, caused by the chytrid fungus *Batrachochytrium dendrobatidis* (Rueda-Almonacid *et al.* 2004).

According to the IUCN Red List, just less than half (47%) of all Colombian amphibian species are classified as Least Concern. Of the remainder, 18% are Endangered or Critically Endangered, and another 18% are Near threatened or Vulnerable. Quantitative data derived from rigorous monitoring studies are lacking for all of those species, but data are so scant for an additional 17% of Colombian species that not even a rough estimate of their status could be made, and they are designated as Data Deficient.

Given the state of knowledge of Colombian amphibians, two areas of research are in urgent need of increased attention. First, taxonomic research – including the exploration of under-sampled areas and the production of revisionary, monographic studies of groups and regions – must be expanded to complete the identification of Colombian amphibians. Although few localities can be considered thoroughly sampled, Acosta-Galvis (2000) highlighted a number of high-priority regions, including mid- to high-elevations of the central

Geobatrachus walkeri *(Endangered) is a frog known only from the north-western and western slopes of the Sierra Nevada de Santa Marta in northern Colombia. © Taran Grant*

Figure 1. *Priority regions for further inventory and survey work in Colombia.*



and northern Cordillera Central and Cordillera Occidental, higher elevations along the length of the Serranía de Perijá, the páramos of the Cordillera Oriental in southern Cundinamarca and Tolima departments, the Serranía del Darién along the Colombo-Panamanian border, the southern Cordillera Occidental and adjacent lowlands in Cauca and Nariño departments, and the Cordillera Oriental and rainforests of Putumayo, Amazonas, Caquetá, Guaviare, Vaupés, and Gauinía departments (Figure 1).

The discovery and identification of previously unknown species in all major groups of Colombian amphibians shows no sign of slowing in the foreseeable future. Indeed, as the expansion of institutional (e.g., natural history collections, molecular laboratories, GIS databases, parallel computing facilities) and human resources (e.g., active scientists and hyperactive students trained in amphibian systematics) continues, we anticipate that the current rate of discovery will continue or increase in the coming years. For example, although it once seemed that the Amazonian fauna was spatially quite uniform (albeit highly diverse), denser sampling, exploration of previously unstudied localities, and analysis of non-traditional data – especially DNA sequences – are revealing much greater complexity, and what were believed to be widespread species are frequently found to involve numerous, even distantly related species of more modest distributions. As our appreciation of the diversity of Colombian species increases, so too does our understanding of their basic biology so crucial to implementing effective conservation strategies to ensure their survival.

A second critical area of research in need of attention is the establishment of long-term, reliably funded studies that monitor natural populations at key localities in both pristine and fragmented, or otherwise developing, areas. Such monitoring programs would allow researchers to track the spread of infectious diseases, understand the response of individual species to differing pressures, and distinguish natural and normal population fluctuations from extreme and abnormal declines, all of which is necessary to design and implement an efficient conservation strategy to ensure the survival of one of the world's most diverse and fascinating amphibian faunas.

Taran Grant, Andrés R. Acosta-Galvis and John D. Lynch

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ESSAY 9.6. THREATENED AMPHIBIANS OF THE WEST INDIES

Eleutherodactylus orientalis *(Critically Endangered) from a small flat top mountain in eastern Cuba called El Yunque de Baracoa. The very small range and declining quality of habitat in the region are causes for concern. Adults are only 11mm long, only one millimetre longer than the smallest frog in the world,* E. iberia, *which also occurs in eastern Cuba. © S. Blair Hedges, Penn State*

The West Indies is a complex assortment of islands and countries located between North and South America. In total land area (224,000km²) it is similar in size to Great Britain and includes three major island groups: a chain of four large and old islands (the Greater Antilles), a relatively flat limestone bank to the north (Bahamas and Turks and Caicos Islands), and a classical volcanic island-arc in the east (the Lesser Antilles). The Greater and Lesser Antilles are located within, or at the border of the Caribbean Sea, but the Bahamas Bank is within the Atlantic Ocean. From the standpoint of biodiversity, the West Indies – sometimes called the "Caribbean Islands" – includes the Cayman and Swan Islands, but usually excludes islands neighboring Central and South America (e.g., Aruba, Curaçao, Trinidad and Tobago, etc.), which have faunas that more closely resemble those on the continents (Figure 1).

The origin of the West Indian fauna has been debated for more than a century, and continues to be an area of active research. Because the Greater Antilles were once connected, as a geological unit, with North and South America in the late Cretaceous (~60–70 million years ago), it has been suggested that the present fauna arose by "vicariance" – in other words, traveled with the islands as they broke away from the continents. But fossil and genetic research has failed to identify more than a few West Indian groups that fit this model, if any. Most, or all, groups probably arrived to the West Indies by flying, swimming, or floating on flotsam (mats of vegetation). The east to west direction of ocean currents means that the source for almost all flotsam in the West Indies is South America (or, more rarely, Africa), and this agrees with the evolutionary affinities of much of the non-flying land fauna (Hedges 2001, 2006).

With its 172 native species, the amphibian fauna of the West Indies is remarkably diverse for such a small land area. Yet it is also peculiar in that all the native amphibians are frogs – there are no salamanders or caecilians – and most (147 species) belong to a single genus of direct-developing leptodactylid frogs, *Eleutherodactylus* (Schwartz and Henderson 1991; Hedges 1999). West Indian amphibians range in adult size, from the smallest frog in the world, *Eleutherodactylus iberia* of eastern Cuba, at 10mm, to the giant ditch frog *Leptodactylus fallax* (the "Mountain Chicken") of the Lesser Antilles, reaching 210mm.

Frogs of the genus *Eleutherodactylus* (see Essay 1.4) lay their eggs on land, bypassing the aquatic tadpole stage, which eventually hatch into miniatures of the adults. One species of *Eleutherodactylus* in Puerto Rico even gives birth to living froglets. Parental care is common among the species, and many guard their eggs during development. The sex of the egg-guarder follows evolutionary lines, with the father having this job in the Puerto Rican group of species, whereas in Jamaica the mother is usually the guarder (Townsend 1996). Individual species are adapted to a great many terrestrial niches, including underground burrows, rock caves, cliffs, salt marshes, waterfalls, bromeliads, tree holes, leaf litter, and vegetation of all types. The term "ecomorph" has been used with West Indian *Eleutherodactylus* to recognize the morphological and ecological convergence in species from different islands and their adaptations to these niches.

Other native amphibians include a modest radiation of toads (11 species, family Bufonidae) and an assortment of tree frogs (nine species, family Hylidae). With eight species, Cuba is the center of diversity for toads, whereas Jamaica and Hispaniola are hot spots of hylid frog diversity, with four species each. There are several species of aquatic ditch frogs (*Leptodactylus*) as well, including the Mountain Chicken that occurs on Montserrat and Dominica. A single species of dendrobatid frog occurs on Martinique. All but a few species of West Indian amphibians are endemic to a single island.

Many species occur in the lowlands, but a peak in species density occurs between 550 and 1,150m elevation, usually corresponding to cloud forest habitat. On average, species body size decreases by about one mm per 100m of increasing elevation, so a lowland species is typically twice as long (~56mm) as one on a mountaintop at 2,500m (Hedges 1999). The number of sympatric (co-occurring) species varies among and within islands, with the highest number recorded being 24 species near the Haitian village of Castillon, in the Massif de la Hotte of Hispaniola.

From a conservation standpoint, the West Indies is one of the hottest biodiversity hotspots (Smith *et al.* 2005). On average humans have destroyed more than 90% of the original native habitat in the West Indies and it is no surprise that these forest-dwelling species have been decimated. Clearing of land is often for subsistence farming, but trees are also sold for building materials or made into charcoal for cooking fuel. Charcoaling is practiced in Jamaica, Cuba, and Hispaniola and is one of the major sources of income in Haiti where the human population has soared to over eight million and where essentially no original forests remain (Hedges and Woods 1993; Young *et al.* 2004).

A recent assessment of the status of West Indian amphibians found that 84% of the species are threatened (Young *et al.* 2004), with 37% listed as Critically Endangered, 36% as Endangered, and 11% as Vulnerable. There is no other region of the world that has such a high proportion of threatened species. Among those 63 species listed as Critically Endangered, eight are considered to be "possibly extinct" because they have not been seen in many years (Hedges 1993, 1999; Young *et al.* 2004). These include the live-bearing species *Eleutherodactylus jasperi* of Puerto Rico, as well as several stream-dwelling species.

Besides the major threat from deforestation, a few species have disappeared from forested areas and the reason for this is unclear. Certainly, no forests in the West Indies are pristine because of introduced flora and fauna that impact the native biota. For example, Old World rats and mongooses can be encountered throughout forested areas high on mountains in the Greater Antilles and these species are known to prey on amphibians. Still, it remains to be established whether introduced predators, climate change, a chytrid fungus, another threat, or rather a combination of these factors is the primary cause for the presumed extinctions of these amphibians (Burrowes *et al.* 2004).

Most countries have made some efforts to control deforestation, such as the designation of national parks and protected areas. These efforts are to be applauded, but unfortunately most have had limited or no success in slowing the destruction of habitat. This is especially true in the countries such as Haiti and the Dominican Republic, where clear-cutting and charcoaling continue within protected areas, mostly because budgets allocated to environmental protection are insufficient. Essentially no original forests remain in Haiti (Hedges and Woods 1993), and therefore many endemic species – including those not found in the Dominican Republic – will likely become extinct in the near future unless something is done soon. Species in other countries may not be far behind.

It is imperative that international agencies, both conservation-based and

Figure 1. *Map of the West Indies (Caribbean Islands).*

Eleutherodactylus glanduliferoides *(Critically Endangered) from the Massif de La Selle of Haiti. This species is only known from a few places on the northern slope of these mountains, just above the densely populated capital city of Port-au-Prince. The region is completely deforested and this species is possibly extinct. © S. Blair Hedges, Penn State* otherwise, step in to help protect the environment in Haiti and elsewhere in the West Indies before it disappears. Salaries for park guards and logistical support (e.g., vehicles, communication equipment, and supplies) for existing parks would provide the most immediate benefit. An accurate knowledge of the amphibian fauna is also a pre-requisite for conservation efforts, as is basic systematic work, which needs to be supported through increased training of local scientists, better education of government officials charged with protecting the environment (e.g., scientists do not pose a threat!), and greater facilitation of work by foreign scientists. Together with prompt and vigorous support directed towards existing protected areas, the real threats facing the amphibian fauna of the West Indies may be reduced – if we are lucky.

S. Blair Hedges

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ESSAY 9.7. SPREAD OF DISEASE IN LATIN AMERICAN AMPHIBIAN POPULATIONS

In 2005–2006, the world watched as avian flu spread across Asia and into Europe. As we write this, Americans are expecting the disease to cross the Atlantic and infect birds in the United States. Fortunately, at least in the case of bird flu, we have an example of a global monitoring system that can track the spread of disease across geopolitical boundaries, as well as a network of health-care providers that are prepared to treat patients infected by the virus. Although many people will be saved, many will still suffer from this emerging infectious disease despite the benefit of advanced warning systems, treatment facilities, and trained personnel. But let us consider a different hypothetical situation. What would happen if:

- Entire populations of humans were dying from an unknown disease in remote regions of the world?
- Few scientists or doctors were aware of the situation?
- Nobody contacted the news media or policy makers?
- We realized that this was an epidemic, but we had no monitoring network or treatment facilities?
- The few personnel trained to detect and potentially treat the disease were distantly located and had neither financial resources nor sufficient infrastructure to offer any help?
- We could prevent deaths in hospitals, but nowhere else?

Where and how could we even begin to offer help? With few data, no dedicated sources of funding, and no infrastructure, the situation would seem impossible. Yet, to do nothing would clearly be unacceptable. In all respects, this is the situation for Latin American amphibians, as population after population succumbs to the frog-killing fungal disease, chytridiomycosis.

The current crisis of global amphibian extinctions is the result of multiple causal factors (Collins and Storfer 2003), but none is more insidious than chytridiomycosis. Considered an emerging infectious disease (Daszak *et al.* 2000), caused by a recently discovered fungal pathogen, *Batrachochytrium dendrobatidis* (*Bd*), chytridiomycosis has been found infecting more than 80 species of amphibians in Latin America and over 150 species worldwide, and more areas and species are predicted to be affected in the future (Ron 2005). The disease has been directly implicated in numerous population declines and extinctions, and is acknowledged to have caused many other such catastrophes that were not observed. Yet, we still lack a complete understanding of *Bd's* basic biology, pathology, epidemiology, and taxonomic/geographic distribution.

A case study from El Copé, Panama (Lips *et al.* 2006) illustrates the devastation that *Bd* can inflict upon diverse tropical amphibian communities that are typical of upland areas in Central and South America. Following a period of eight years of monitoring both amphibian abundance and disease prevalence, field crews obtained the first *Bd*-positive sample on 23 September 2004 (Figure 1). Within one week, several dead frogs had been found, and shortly thereafter as many as 19 dead frogs were found in a single day. After four months, researchers had found 350 dead frogs, representing 40 species among eight families of anurans and salamanders, all of which were heavily infected with *Bd*. This report was the first definitive link between catastrophic population declines of amphibians and the sudden appearance of *Bd* at a site. Within six months, amphibian abundance had been reduced by more than 75%, with 50% of species missing and almost all species affected to some degree. Nocturnal surveys prior to October 2004 often produced as many as 170 captures, representing as many as 23 species, but those same transects now produce no more than five or six frogs, representing only two or three species. Within a remarkably short space of time, the amphibian community of El Copé has been devastated by this disease, and is not anticipated to recover, because populations have been greatly reduced and because *Bd* persists at this site.

Although many diseases can impact host populations by causing temporary or permanent declines in abundance, only recently has disease been considered a major cause of species extinctions (de Castro and Bolker 2005). Theoretical work on disease ecology predicts that, as an epidemic infectious disease reduces the abundance of its hosts, there is an increase in the relative abundance of immune individuals; thus, disease transmission is reduced to zero, such that the pathogen becomes extinct before the host. *Bd* is unusual in that it affects a broad taxonomic array of species, and is highly virulent killing most infected individuals. These are classic traits of invasive or novel pathogens, and the arrival of *Bd* in the Neotropics, and its subsequent extermination of the native fauna, is similar to the effect smallpox had when it was introduced from Europe to the Americas by Christopher Columbus and his crew.

A large number of amphibian species have already been identified as hosts of *Bd*, and it is likely that both the environment and the frogs are potential disease reservoirs (Lips *et al.* 2006). When populations begin to decline, they can be wiped out in a short period of time with little chance of recovery or replenishment from other populations. It is this lethal combination of an exotic virulent pathogen (with a broad host range) invading a highly endemic amphibian fauna with small geographic distributions that produces high levels of species extinction in very short periods of time. In conclusion, we can expect to see many more losses of amphibian species from the Neotropics, as this disease continues to expand its range. Worse yet, bioclimatic modeling (e.g., Ron 2005; and see Essay 11.4) suggests that *Bd* can survive in many other parts of the globe, and is likely to infect hundreds, if not thousands, of additional species in Africa and Asia.

Many questions remain regarding how the relationships among *Bd*, amphibian hosts, and environmental conditions produce such a wide range of amphibian population responses. We are beginning to appreciate the complex challenges involved in mitigating or even reversing impacts of emerging infectious diseases. We also know that traditional conservation efforts that are tied to habitat protection are inadequate by themselves in such instances, so effective solutions remain elusive. Trade and transport of amphibians and other wildlife may spread *Bd* (Hanselmann *et al.* 2004), but the actual frequency and impact of these factors is not known. Regional and local climatic conditions may influence the growth and survival of *Bd* (Pounds *et al.* 2006), but until a mechanism is identified that can link global or regional climate changes to individual mortality or reduced population growth, we cannot hope to design effective conservation measures that would mitigate these impacts. At this time, while we can effectively treat animals in captivity (Nichols *et al.* 2001), we cannot control the spread of *Bd* in the wild, or treat animals or ecosystems *in situ*. Another problem is that *Bd* is difficult to detect because it is microscopic and may persist in ecosystems for undetermined periods of time.

Chytridiomycosis is an alarming model system for disease-driven extinctions of an entire fauna. For one emerging infectious disease to appear so suddenly and have such uncontrollable effects on global biodiversity, demands an immediate response. We are facing the synchronous extinction of a significant proportion of an entire group of vertebrates, and we propose that it is no longer correct to speak of global amphibian declines but, more appropriately, of global amphibian extinctions.

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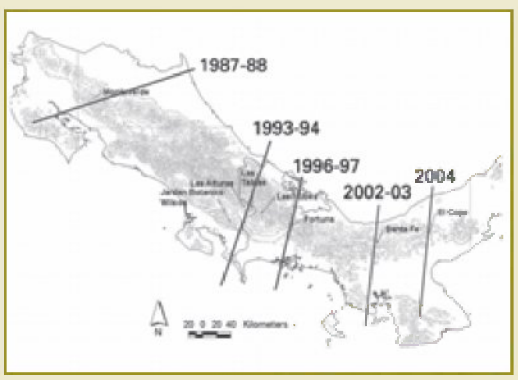

Figure 1. *Timelines of sequential catastrophic declines of amphibians, as a result of chytridiomycosis, in Costa Rica and Panama. Modified from Lips* et al. *(2006).*

An undescribed species of Eleutherodactylus *found dead floating in a stream during a die off near El Cope, Panama in 2004. © Forrest Brem & Roberto Brenes*