

Are we in the midst of the sixth mass extinction? A view from the world of amphibians

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Many scientists argue that we are either entering or in the midst of the sixth great mass extinction. Intense human pressure, both direct and indirect, is having profound effects on natural environments. The amphibians—frogs, salamanders, and caecilians—may be the only major group currently at risk globally. A detailed worldwide assessment and subsequent updates show that one-third or more of the 6,300 species are threatened with extinction. This trend is likely to accelerate because most amphibians occur in the tropics and have small geographic ranges that make them susceptible to extinction. The increasing pressure from habitat destruction and climate change is likely to have major impacts on narrowly adapted and distributed species. We show that salamanders on tropical mountains are particularly at risk. A new and significant threat to amphibians is a virulent, emerging infectious disease, chytridiomycosis, which appears to be globally distributed, and its effects may be exacerbated by global warming. This disease, which is caused by a fungal pathogen and implicated in serious declines and extinctions of >200 species of amphibians, poses the greatest threat to biodiversity of any known disease. Our data for frogs in the Sierra Nevada of California show that the fungus is having a devastating impact on native species, already weakened by the effects of pollution and introduced predators. A general message from amphibians is that we may have little time to stave off a potential mass extinction.

chytridiomycosis | climate change | population declines |
Batrachochytrium dendrobatidis | emerging disease

Biodiversity is a term that refers to life on Earth in all aspects of its diversity, interactions among living organisms, and, importantly, the fates of these organisms. Scientists from many fields have raised warnings of burgeoning threats to species and habitats. Evidence of such threats (e.g., human population growth, habitat conversion, global warming and its consequences, impacts of exotic species, new pathogens, etc.) suggests that a wave of extinction is either upon us or is poised to have a profound impact.

The title of our article, suggested by the organizers, is an appropriate question at this stage of the development of biodiversity science. We examine the topic at two levels. We begin with a general overview of past mass extinctions to determine where we now stand in a relative sense. Our specific focus, however, is a taxon, the Class Amphibia. Amphibians have been studied intensively since biologists first became aware that we are witnessing a period of their severe global decline. Ironically, awareness of this phenomenon occurred at the same time the word “biodiversity” came into general use, in 1989.

Five Mass Extinctions

It is generally thought that there have been five great mass extinctions during the history of life on this planet (1, 2). [The first two may not qualify because new analyses show that the magnitude of the extinctions in these events was not significantly higher than in several other events (3).] In each of the five events, there was a profound loss of biodiversity during a relatively short period.

The oldest mass extinction occurred at the Ordovician–Silurian boundary (≈439 Mya). Approximately 25% of the

families and nearly 60% of the genera of marine organisms were lost (1, 2). Contributing factors were great fluctuations in sea level, which resulted from extensive glaciations, followed by a period of great global warming. Terrestrial vertebrates had not yet evolved.

The next great extinction was in the Late Devonian (≈364 Mya), when 22% of marine families and 57% of marine genera, including nearly all jawless fishes, disappeared (1, 2). Global cooling after bolide impacts may have been responsible because warm water taxa were most strongly affected. Amphibians, the first terrestrial vertebrates, evolved in the Late Devonian, and they survived this extinction event (4).

The Permian–Triassic extinction (≈251 Mya) was by far the worst of the five mass extinctions; 95% of all species (marine as well as terrestrial) were lost, including 53% of marine families, 84% of marine genera, and 70% of land plants, insects, and vertebrates (1, 2). Causes are debated, but the leading candidate is flood volcanism emanating from the Siberian Traps, which led to profound climate change. Volcanism may have been initiated by a bolide impact, which led to loss of oxygen in the sea. The atmosphere at that time was severely hypoxic, which likely acted synergistically with other factors (5). Most terrestrial vertebrates perished, but among the few that survived were early representatives of the three orders of amphibians that survive to this day (6, 7).

The End Triassic extinction (≈199–214 Mya) was associated with the opening of the Atlantic Ocean by sea floor spreading related to massive lava floods that caused significant global warming. Marine organisms were most strongly affected (22% of marine families and 53% of marine genera were lost) (1, 2), but terrestrial organisms also experienced much extinction. Again, representatives of the three living orders of amphibians survived.

The most recent mass extinction was at the Cretaceous–Tertiary boundary (≈65 Mya); 16% of families, 47% of genera of marine organisms, and 18% of vertebrate families were lost. Most notable was the disappearance of nonavian dinosaurs. Causes continue to be debated. Leading candidates include diverse climatic changes (e.g., temperature increases in deep seas) resulting from volcanic floods in India (Deccan Traps) and consequences of a giant asteroid impact in the Gulf of Mexico (1, 2). Not only did all three orders of amphibians again escape extinction, but many, if not all, families and even a number of extant amphibian genera survived (8).

A Sixth Extinction?

The possibility that a sixth mass extinction spasm is upon us has received much attention (9). Substantial evidence suggests that an extinction event is underway.

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When did the current extinction event begin? A period of climatic oscillations that began about 1 Mya, during the Pleistocene, was characterized by glaciations alternating with episodes of glacial melting (10). The oscillations led to warming and cooling that impacted many taxa. The current episode of global warming can be considered an extreme and extended interglacial period; however, most geologists treat this period as a separate epoch, the Holocene, which began $\approx 11,000$ years ago at the end of the last glaciation. The Holocene extinctions were greater than occurred in the Pleistocene, especially with respect to large terrestrial vertebrates. As in previous extinction events, climate is thought to have played an important role, but humans may have had compounding effects. The overkill hypothesis (11) envisions these extinctions as being directly human-related. Many extinctions occurred at the end of the Pleistocene, when human impacts were first manifest in North America, in particular, and during the early Holocene. Because naive prey were largely eliminated, extinction rates decreased. Extinctions were less profound in Africa, where humans and large mammals coevolved. Most currently threatened mammals are suffering from the effects of range reduction and the introduction of exotic species (12). In contrast to the overkill hypothesis, an alternative explanation for the early mammalian extinctions is that human-mediated infectious diseases were responsible (13).

Many scientists think that we are just now entering a profound spasm of extinction and that one of its main causes is global climate change (14–16). Furthermore, both global climate change and many other factors (e.g., habitat destruction and modification) responsible for extinction events are directly related to activities of humans. In late 2007, there were 41,415 species on the International Union for Conservation of Nature Red List, of which 16,306 are threatened with extinction; 785 are already extinct (17). Among the groups most affected by the current extinction crisis are the amphibians.

Amphibians in Crisis

Amphibians have received much attention during the last two decades because of a now-general understanding that a larger proportion of amphibian species are at risk of extinction than those of any other taxon (18). Why this should be has perplexed amphibian specialists. A large number of factors have been implicated, including most prominently habitat destruction and epidemics of infectious disease (19); global warming also has been invoked as a contributing factor (20). What makes the amphibian case so compelling is the fact that amphibians are long-term survivors that have persisted through the last four mass extinctions.

Paradoxically, although amphibians have proven themselves to be survivors in the past, there are reasons for thinking that they might be vulnerable to current environmental challenges and, hence, serve as multipurpose sentinels of environmental health. The typical life cycle of a frog involves aquatic development of eggs and larvae and terrestrial activity as adults, thus exposing them to a wide range of environments. Frog larvae are typically herbivores, whereas adults are carnivores, thus exposing them to a wide diversity of food, predators, and parasites. Amphibians have moist skin, and cutaneous respiration is more important than respiration by lungs. The moist, well vascularized skin places them in intimate contact with their environment. One might expect them to be vulnerable to changes in water or air quality resulting from diverse pollutants. Amphibians are thermal-conformers, thus making them sensitive to environmental temperature changes, which may be especially important for tropical montane (e.g., cloud forest) species that have experienced little temperature variation. Such species may have little acclimation ability in rapidly changing thermal regimes. In general, amphibians have small geographic ranges, but this is accentuated in most terrestrial species (the majority of

salamanders; a large proportion of frog species also fit this category) that develop directly from terrestrial eggs that have no free-living larval stage. These small ranges make them especially vulnerable to habitat changes that might result from either direct or indirect human activities.

Living amphibians (Class Amphibia, Subclass Lissamphibia) include frogs (Order Anura, $\approx 5,600$ currently recognized species), salamanders (Order Caudata, ≈ 570 species), and caecilians (Order Gymnophiona, ≈ 175 species) (21). Most information concerning declines and extinctions has come from studies of frogs, which are the most numerous and by far the most widely distributed of living amphibians. Salamanders facing extinctions are centered in Middle America. Caecilians are the least well known; little information on their status with respect to extinction threats exists (18).

Amphibians are not distributed evenly around the world. Frogs and caecilians thrive in tropical regions (Fig. 1). Whereas caecilians do not occur outside the tropical zone, frogs extend northward even into the Arctic zone and southward to the southern tips of Africa and South America. Salamanders are mainly residents of the North Temperate zone, but one subclade (Bolitoglossini) of the largest family (Plethodontidae) of salamanders has radiated adaptively in the American tropics. The bolitoglossine salamanders comprise nearly 40% of living species of salamanders; $\approx 80\%$ of bolitoglossines occur in Middle America, with only a few species ranging south of the equator.

The New World tropics have far more amphibians than anywhere else. Fig. 1 shows the number of species in relation to the size of countries (all data from ref. 21). The Global Amphibian Assessment completed its first round of evaluating the status of all then-recognized species in 2004 (18), finding 32.5% of the known species of amphibians to be “globally threatened” by using the established top three categories of threat of extinction (i.e., Vulnerable, Endangered, or Critically Endangered); 43% of species have declining populations (17). In general, greater numbers as well as proportions of species are at risk in tropical countries (e.g., Sri Lanka with 107 species, most at risk; nontropical New Zealand has an equivalent proportion, but has only 7 species) (Fig. 2). Updates from the Global Amphibian Assessment are ongoing and show that, although new species described since 2004 are mostly too poorly known to be assessed, $>20\%$ of analyzed species are in the top three categories of threat (22). Species from montane tropical regions, especially those associated with stream or streamside habitats, are most likely to be severely threatened.

We present a case study from our own work to explore the reasons underlying declines and extinctions of amphibians.

Rana in the Sierra Nevada of California

One of the most intensively studied examples of amphibian declines comes from the Sierra Nevada of California. The mountain range spans thousands of square kilometers of roadless habitat, most of which is designated as National Park and Forest Service Wilderness Areas, the most highly protected status allowable under U.S. law. The range contains thousands of high-elevation (1,500- to 4,200-m) alpine lakes, as well as streams and meadows, that until recently harbored large amphibian populations. Biological surveys conducted nearly a century ago by Grinnell and Storer (23) reported that amphibians were the most abundant vertebrates in the high Sierra Nevada. Because large numbers of specimens were collected from well documented localities by these early workers, the surveys provide a foundation on which current distributions can be compared. Of the seven amphibian species that occur $>1,500$ m in the Sierra Nevada, five (*Hydromantes playcephalus*, *Bufo boreas*, *B. canorus*, *Rana muscosa*, and *R. sierrae*) are threatened. The best studied are the species in the family Ranidae and include the Sierra Nevada Yellow-legged Frog (*R. sierrae*) and

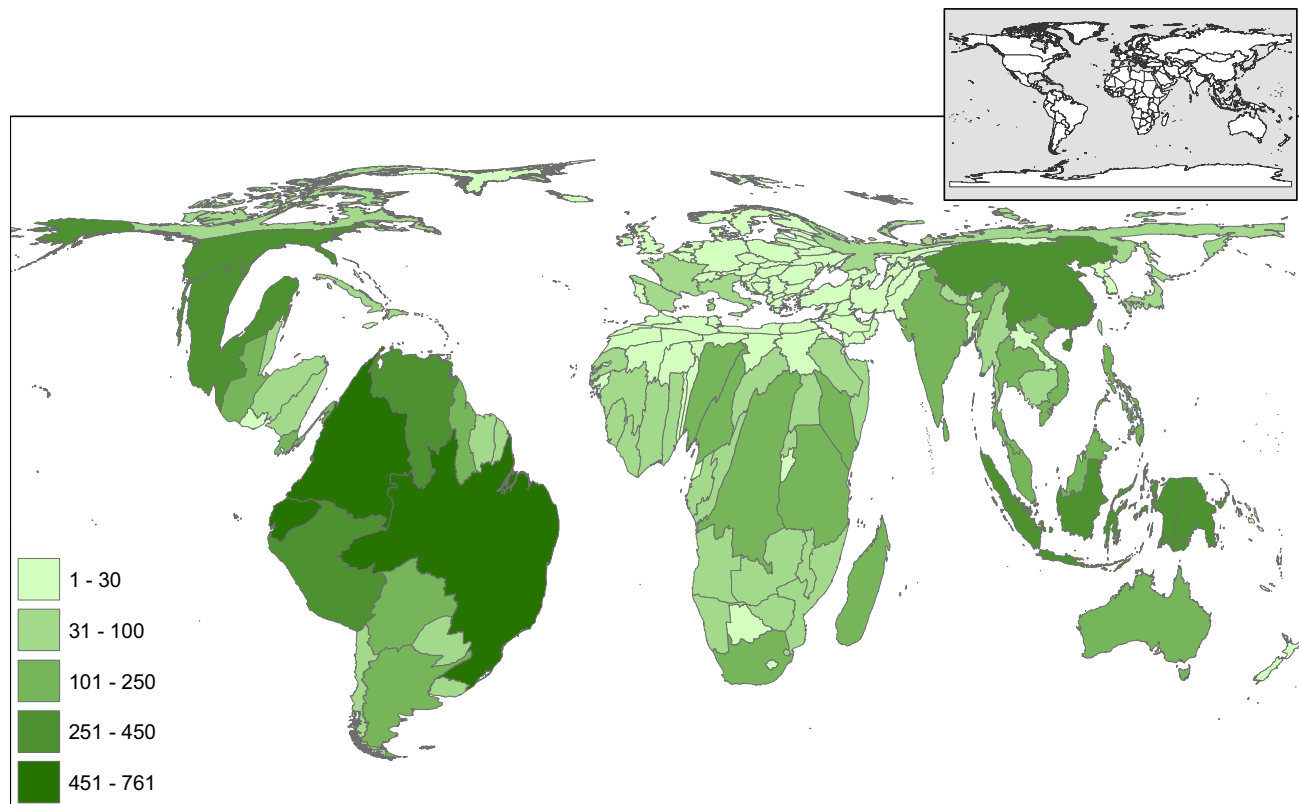


Fig. 1. Global amphibian species diversity by country visualized using density-equalizing cartograms. Country size is distorted in proportion to the total number of amphibian species occurring in each country relative to its size. (*Inset*) Baseline world map. Brazil (789 species) and Colombia (642) have the largest number of species. China (335) has the largest number of species in the Old World. The Democratic Republic of the Congo (215) has the largest number from continental Africa. However, 239 species are recorded from Madagascar. Australia has 225 species, and Papua New Guinea has 289. In North America, Mexico has the largest number of species (357). There are 291 species in the United States. Prepared by M. Koo (see *Acknowledgments*).

Southern Yellow-legged Frog (*R. muscosa*) (24). In the 1980s, field biologists became aware that populations were disappearing (25), but the extent of the problem was not fully appreciated until an extensive resurvey of the Grinnell-Storer (23) sites disclosed dramatic losses (26). Especially alarming was the discovery that frogs had disappeared from 32% of the historical sites in Yosemite National Park. Furthermore, populations in most remaining sites had been reduced to a few individuals.

The yellow-legged frogs, which had been nearly ubiquitous in high-elevation sites in the early 1980s, are ideal subjects for ecological study. Their diurnal habits and their use of relatively simple and exposed alpine habitats make them readily visible and easy to capture. Typically these frogs occurred in large populations, and rarely were they found >2 m from the shores of ponds, lakes, and streams. Censuses throughout the Sierra Nevada began in the early 1990s and intensified in this century. Although most of the frog habitat in this large mountain range is protected in national parks and wilderness areas, yellow-legged frogs are now documented to have disappeared from $>90\%$ of their historic range during the last several decades (24). The most recent assessment lists them as Critically Endangered (18). Factors implicated in the declines include introduced predatory trout (27), disease (28), and air pollution (29, 30). Experiments that extirpated introduced trout led to rapid recovery of frog populations (31). Thus, for a time, there was hope that, simply by removing introduced trout, frog populations would persist and eventually spread back into formerly occupied habitat. Curiously, multiple attempts at reintroduction in the more western parts of the range clearly failed (32). Hundreds of dead frogs were encountered at both reintroduction and many

other sites in the western part of the range (28), and it became apparent that predation was not the only factor affecting the frogs' survival.

In 2001, chytridiomycosis, a disease of amphibians caused by a newly discovered pathogenic fungus [*Batrachochytrium dendrobatidis* (Bd)] (33) was detected in the Sierra Nevada (34). Subsequently, a retrospective study disclosed that Bd was found on eight frogs (*R. muscosa*, wrongly identified as *R. boylei*) collected on the west edge of Sequoia and Kings Canyon National Parks in 1975 (35). Infected tadpoles of these species are not killed by Bd. When tadpoles metamorphose, the juveniles became reinfected and usually die (36). However, tadpoles of yellow-legged frogs in the high Sierra Nevada live for 2 to 4 years, so even if adults and juveniles die, there is a chance that some individuals might survive if they can avoid reinfection after metamorphosis.

The disease is peculiar in many ways (37, 38). Pathogenicity is unusual for chytrid fungi, and Bd is the first chytrid known to infect vertebrates. The pathogen, found only on amphibians, apparently lives on keratin, present in tadpoles on the external mouth parts and in adults in the outer layer of the skin. The life cycle includes a sporangium in the skin, which sheds flagellated zoospores outside of the host. The zoospores then infect a new host or reinfect the original host, establishing new sporangia and completing the asexual life cycle. Sexual reproduction, seen in other chytrids, is unknown in Bd (39). Much remains to be learned about the organism (38). For example, despite its aquatic life cycle, Bd has been found on fully terrestrial species of amphibians that never enter water, and the role of zoospores in these forms is uncertain. No resting stage has been found, and

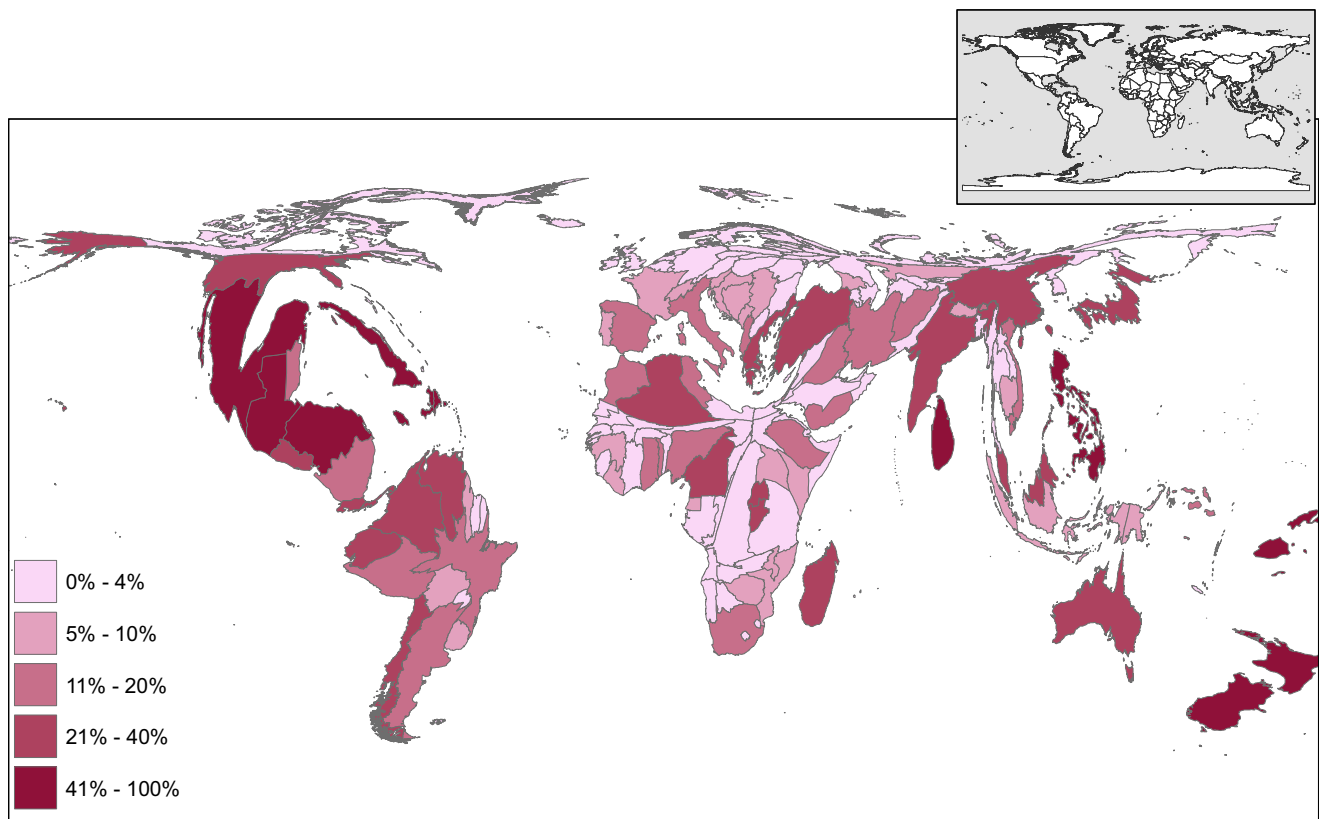


Fig. 2. Percentage of amphibian fauna in each country in the top three categories of threat (Critically Endangered, Endangered, and Threatened) (22). (Inset) Baseline world map. Visualization based on density-equalizing cartograms prepared by M. Koo.

no alternative hosts are known. Vectors have not been identified. It is relatively easy to rid a healthy frog of the fungus by using standard fungicides (40). Yet the fungus is surprisingly virulent. Finally, and importantly, how the fungus causes death is not clear, although it is thought to interfere with oxygen exchange and osmoregulation (41).

With associates, we have been studying frog populations in alpine watersheds within Yosemite, Sequoia, and Kings Canyon National Parks for over a decade. We recently showed that yellow-legged frogs are genetically diverse (24). Mitochondrial DNA sequence data identified six geographically distinct haplotype clades in the two species of frogs, and we recommended that these clades be used to define conservation goals. Popula-

tion extinctions, based on historical records, ranged from 91.3% to 98.1% in each of the six clades, so challenges for conservation are daunting. In the last 5 years, we have documented mass die-offs (Fig. 3) and the collapse of populations due to chytridiomycosis outbreaks (28). Although the mechanism of spread is unknown, it may involve movements of adult frogs among lakes within basins or possibly movements of a common, more vagile, and terrestrial frog, *Pseudacris regilla* (on which Bd has been detected), ahead of the *Rana* infection wave. Mammals, birds, or insects also are possible vectors. We have followed movements of *R. muscosa* and *R. sierrae* using pit tags and radio tracking from 1998 to 2002 (42), and we believe that movement between local populations may be spreading the disease. The environ-

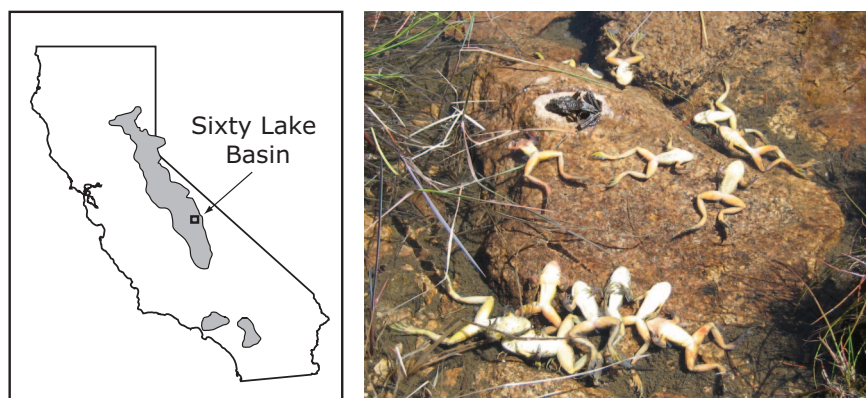


Fig. 3. Distribution of the critically endangered yellow-legged frogs in California. Chytridiomycosis outbreaks have had devastating effects (*Rana muscosa* photographed in Sixty Lake Basin, August 15, 2006).

ment in this area (2,500–3,300 m) is harsh for amphibians, with isolated ponds separated by inhospitable solid granite that lacks vegetation. Small streams join many of the lakes in each basin. The maximum movement of frogs, (≈ 400 m) was in and near streams; most movements are < 300 m. Our results are compatible with those of another study (43), which included a report of a single overland movement event. If chytridiomycosis sweeps through the Sierra Nevada the way it has through Central America (44), then population and metapopulation extinctions may be a continuing trend; we may be on the verge of losing both species.

It might be possible to arrest an epidemic. Laboratory treatments have shown that infected animals can be cleared of infection within days (40); if the dynamics of the disease can be altered or if animals can survive long enough to mount an immunological defense, then survival might be possible. Survival of infected frogs after an apparent outbreak has been seen in Australia (45), but is unknown in the Sierra Nevada frogs. The yellow-legged frogs of the Sierra Nevada are an ideal species in which to test this because they live in discreet habitat patches, are relatively easy to capture, and are highly philopatric.

Common Themes in Amphibian Declines

In the early 1990s, there was considerable debate about whether amphibians were in general decline or only local fluctuations in population densities were involved (46, 47). A definitive 5-year study that involved daily monitoring of a large amphibian fauna at the Monteverde Cloud Forest Preserve in Costa Rica showed that 40% (20 species of frogs) of the species had been lost (48). These instances involved some extraordinary species, such as the spectacularly colored Golden Toad (*Bufo perigrinus*) and the Harlequin Frog (*Atelopus varius*). Particularly striking about this case is the highly protected status of the Preserve, so habitat destruction, the most common reason for species disappearances in general, can be excluded. The start of this decline was pinpointed to the late 1980s. At about the same time, disappearances of species from protected areas in the Australian wet tropics were recorded (49). Both species of the unique gastric brooding frogs from Australia (*Rheobatrachus*) disappeared. Declines in other parts of the world included most species of the generally montane, diurnal frogs of the genus *Atelopus* from South and lower Central America, and species of *Bufo* and *Rana* from the Sierra Nevada of California (20, 25, 44). At first all of these declines were enigmatic, but eventually two primary causal factors emerged: the infectious disease chytridiomycosis and global warming (20, 44).

Chytridiomycosis was detected almost simultaneously in Costa Rica and Australia (33). From the beginning, it was perceived as a disease with devastating consequences. It quickly swept through Costa Rica and Panama, leaving massive declines and local extinctions in its wake (44). More than half of the amphibian species in lower montane forest habitats suffered declines on the order of 80%, and several disappeared. This extinction event had been predicted on the assumption that chytridiomycosis would continue its sweep southward from Monteverde, in northwestern Costa Rica (see below), to El Cope in central Panama (44). Attention is now focused on eastern Panama and northwestern Colombia, where chytridiomycosis has yet not had evident impact.

Carcasses of animals from the Monteverde extinction event are not available, and it is not known whether Bd was responsible for frog deaths. However, Bd has been detected in many preserved specimens that were collected at different elevations along an altitudinal transect in Braulio Carrillo National Park in 1986 (50). The park is in northern Costa Rica ≈ 100 km southeast of Monteverde. Given the high prevalence of Bd in the specimens surveyed, it seems reasonable to assume that Bd also was

present at Monteverde. Of course, there are many more species present in tropical areas (67 at El Cope, Panama) (44) than in the Sierra Nevada (seven at high elevations, but three most commonly, only two of which are aquatic), and hence there are many more opportunities for the spread of Bd among tropical species. The average moisture content of the air in the tropical environments is doubtless much higher, on average, in Central America than in the Sierra Nevada, where a characteristic dry summer rainfall pattern prevails and where there is no forest canopy because of the altitude and substrate. Although we do not know the mechanism of spread, conditions in Central America appear more suitable for the spread of an aquatic fungus.

Amphibians tend to have broader ranges in temperate regions than in the tropics. Despite many population extinctions in temperate regions, there have been few extinctions. Accordingly, the tropical species of amphibians are more at risk, but not just because of their typically small geographic ranges. Because they occur in rich, multispecies communities, the species become infected simultaneously.

Climate change has been implicated in declines since the documentation of disappearances at Monteverde (51, 52). Unusual weather conditions were initially implicated with amphibian declines. Large increases in average tropical air and sea surface temperatures were associated with El Niño events in the late 1980s; substantial warming had already occurred since the early 1970s. Temperature increases were correlated with increases in the height at which clouds formed at Monteverde and consequent reductions in the deposition of mist and cloud water critical for maintenance of cloud forest conditions during the dry season (20). Simulations using global climate models showed that greenhouse warming could have the effect of raising the cloud line by as much as 500 m at Monteverde during the dry season (20, 52).

A more general effect of climate change has been proposed for the disappearance of 100 species of tropical montane frogs of the genus *Atelopus*, which is widespread in southern Central and northern South America. A detailed correlational analysis revealed that ≈ 80 species were last seen immediately after a warm year (20). Several species disappeared from Ecuador during 1987–1988, which included the most extreme combination of dry and warm conditions in 90 years (53). Authors of this article document that the mean annual temperature in the Ecuadorian Andes has increased by $\approx 2^\circ\text{C}$ during the last century.

Pounds and coworkers (20) hypothesized that climate change, precipitation, and increased temperature have acted synergistically in favor of the growth of the infectious chytrid fungus. They argue that global warming has shifted temperatures closer to the presumed optimal conditions for *B. dendrobatidis* at Monteverde and the other intermediate elevation areas of the Central and South American highlands, where most of the extinctions of *Atelopus* have occurred. Warming has increased cloud cover in these areas, which had the effect of elevating already higher nighttime temperatures, thus favoring fungal growth. The hypothesis has yet to be tested.

Is Global Warming a Real Extinction Threat?

The Intergovernmental Panel on Climate Change (IPCC) reached consensus that climate change is happening and that it is largely related to human activities (15). Estimates of global warming during the next century vary, but generally fall in the range of 2°C to 4°C , whereas rises as high as 7°C are projected for much of the United States and Europe, with even higher temperatures expected in northern Eurasia, Canada, and Alaska (15). Such rises would have devastating effects on narrowly distributed montane species, such as cloud forest and mountain-top salamanders and frogs in Middle and South America. The physiology of ectotherms such as amphibians and their ability to

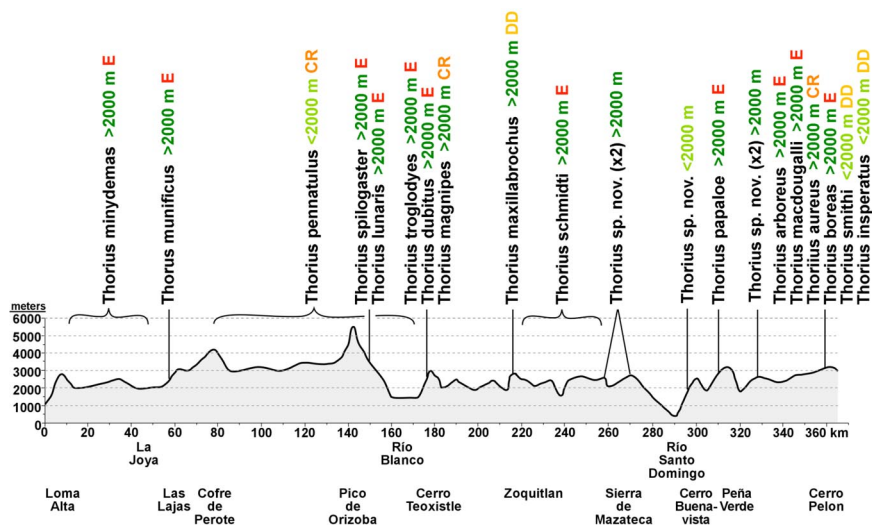


Fig. 4. A diagrammatic profile of the Sierra Madre Oriental from north-central Veracruz to northern Oaxaca, Mexico. The range extends in a generally north-northeast to south-southwest direction, but the section from Cofre de Perote to Loma Alta extends mainly east-northeast and has been straightened. This mountain system is home to 17 described and several unnamed species of Minute Salamanders, genus *Thorius*. Most of the species are clustered between 1,500 and 3,000 m. All of the species that have been evaluated are Endangered (E) or Critically Endangered (CR) and at risk of extinction, and three have been found so infrequently that they are categorized as Data Deficient (DD) (22).

acclimate also are important considerations for these species (54). With climate change (already 2°C changes in temperature have been recorded in montane Ecuador) (53), altitudinal limits of plant and animal communities will shift upward and amphibians must either move with them or acclimate until adaptation occurs. Even small increases in temperature lead to significant metabolic depression in montane salamanders (55). Impacts of the different warming scenarios are all dramatic and severe (see fig. TS.6 in ref. 15). The first event predicted by the IPCC panel, “Amphibian Extinctions Increasing on Mountains,” is now an empirical fact.

In previous publications, we showed that many tropical plethodontid salamanders have very narrow altitudinal limits and are often restricted to single mountains or local mountain ranges (56). With few exceptions, species found above 1,500–2,000 m have narrow distributional limits. We have surveyed extensively a mountainous segment of eastern Mexico from the vicinity of Cerro Cofre de Perote (≈4,000 m) in central western Veracruz in the north to Cerro Pelon (≈3,000 m) in northern Oaxaca in the south. These two peaks, separated by ≈280 km, lie along the eastern crest of the Sierra Madre Oriental, a nearly continuous range that is broken only by Rio Santo Domingo (Fig. 4). Otherwise the crest lies above 1,500 m, with many peaks that rise to ≈2,000 m or higher. There are 18 species of plethodontids on both Cofre de Perote and Pelon, but only two species—widespread lowland members of *Bolitoglossa*—are shared. To determine the geographical limits of the other species, we have been surveying the entire crest area since the 1970s. We have learned that most of the species on each mountain are endemic to it. When we searched in the intervening region, expecting to expand the known distributional ranges for different species, we instead discovered numerous undescribed species (many since named) almost every time we explored an isolated peak at >2,000 m. On a single short trip just 5 years ago to the Sierra de Mazateca, north of the Rio Santo Domingo (Fig. 4), we discovered two new species of *Pseudoeurycea* and at least one new species of *Thorius* (57). We suspect that many species disappeared without ever having been discovered because the area is heavily populated and has experienced extensive habitat modi-

fication. Furthermore, the newly discovered species are endangered and survive in what appear to be suboptimal, disturbed habitats or in small fragments of forest. The majority of species along altitudinal transects in this area are found at >2,000 m in cloud forests that are being forced upward by global warming. On Cerro Pelon, eight of the species are found only at >2,200 m, and six of them range to the top of the mountain and into extinction. Global warming threatens to force them off the mountain and into extinction.

The section of the Sierra Madre Oriental we have been studying is home to 17 named and 3–5 as yet unnamed species of the plethodontid salamander genus *Thorius*, the Minute Salamanders. All but four of these species occur exclusively at >2,000 m, often on mountains that rise only a little above that level. Of the 17 named species, 11 are listed as Endangered and 3 are listed as Critically Endangered; the remaining 4 species are so rare and poorly known that they can only be listed as Data Deficient (Fig. 4) (18). We consider this region to be a hot spot of extinction, and yet it is still very incompletely known. Based on our studies of altitudinal transects elsewhere in Middle America, we expect that the situation we have described for eastern Mexico is typical of mountainous parts of the entire region.

What Will We Lose?

The amphibians at greatest risk of extinction are likely to be those with relatively few populations in areas undergoing rapid habitat conversion because of human activities. Populations that are already reduced in size are especially susceptible to other stressors, such as introduced species and disease. Tropical montane species are at special risk because of global warming. These already stressed species, reduced to a few populations, also are likely to be hit hardest by Bd. However, a paradoxical fact is that new species of amphibians are being described at an unprecedented rate. In 1985, the first comprehensive account of all amphibian species reported ≈4,000 species (58). That number has now risen to >6,300, and species are being named at a rate exceeding 2% per year. Some of these species are cryptic forms that were found as a result of molecular systematic studies, but the vast majority are morphologically distinctive species mainly from tropical regions (Fig. 5). These biologically unique species

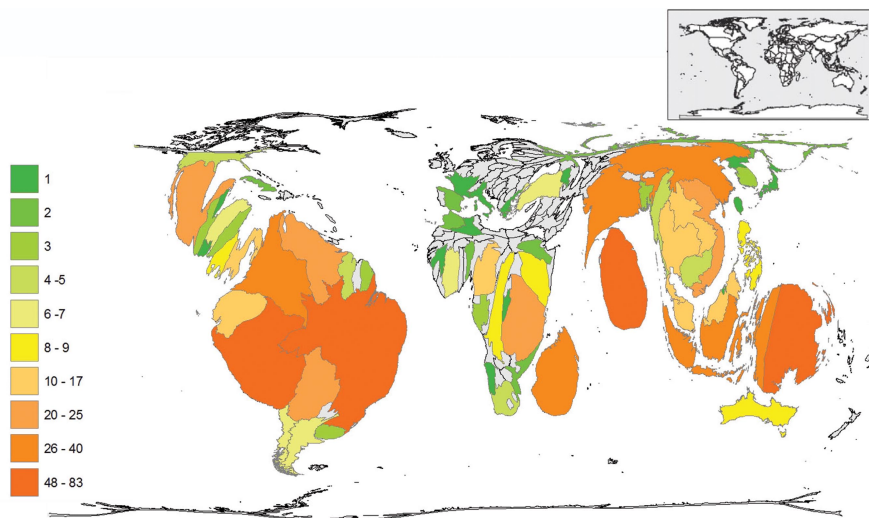


Fig. 5. Distribution of species of amphibians discovered and named during the period 2004–2007. Color scale bar indicates number of new species per country. (Inset) Baseline world map. Visualization is based on density-equalizing cartograms prepared by M. Koo.

often have been found as a byproduct of the heightened interest in amphibians and consequent field research. Field surveys in still relatively unstudied parts of the world (e.g., New Guinea and nearby islands, Madagascar) have resulted in many new discoveries. Among the most spectacular discoveries during this decade are a frog from India that is so distinct that it was placed in a new family (59) and a salamander from South Korea that is the only member of the Plethodontidae from Asia (60). It is impossible to know what has been overlooked or has already been lost to extinction, but there is every reason to think that the losses have been substantial.

The rate of extinction of amphibians is truly startling. A recent study estimates that current rates of extinction are 211 times the background extinction rate for amphibians, and rates would be as high as 25,000–45,000 times greater if all of the currently threatened species go extinct (61).

Despite these alarming estimates, amphibians are apparently doing very well in many parts of the world, and many thrive in landscapes heavily modified by human activities. Species such as the Cane Toad (*Bufo marinus*), the American Bullfrog (*Rana catesbeiana*), and the Clawed Frog (*Xenopus laevis*) have proven to be potent invasive species, and they have not yet been shown to be afflicted by chytridiomycosis. Attempts are being made to mitigate anticipated losses of amphibian species. Promising research on bacterial skin symbionts of amphibians suggests that they may have antifungal properties (62, 63), possibly opening pathways for research on changing the outcomes of fungal attacks. Local extinctions have been so profound and widespread in Panama that a major initiative has been launched to promote *in situ* as well as *ex situ* captive breeding programs. Species will be maintained in captivity until solutions to problems such as chytridiomycosis, local habitat destruction, or others can be mitigated, at which time reintroduction programs will be developed (64). Although amphibians are suffering declines and extinctions, we predict that at least some frogs, salamanders, and caecilians will survive the current extinction event on their own or with help, even as their ancestors survived the four preceding mass extinctions.

What Is the Principal Cause of the Present Extinction Spasm?

Human activities are associated directly or indirectly with nearly every aspect of the current extinction spasm. The sheer magnitude of the human population has profound implications because of the demands placed on the environment. Population growth,

which has increased so dramatically since industrialization, is connected to nearly every aspect of the current extinction event. Amphibians may be taken as a case study for terrestrial organisms. They have been severely impacted by habitat modification and destruction, which frequently has been accompanied by use of fertilizers and pesticides (65). In addition, many other pollutants that have negative effects on amphibians are byproducts of human activities. Humans have been direct or indirect agents for the introduction of exotic organisms. Furthermore, with the expansion of human populations into new habitats, new infectious diseases have emerged that have real or potential consequences, not only for humans, but also for many other taxa, such as the case of Bd and amphibians (66). Perhaps the most profound impact is the human role in climate change, the effects of which may have been relatively small so far, but which will shortly be dramatic (e.g., in the sea) (16). Research building on the Global Amphibian Assessment database (18) showed that many factors are contributing to the global extinctions and declines of amphibians in addition to disease. Extrinsic forces, such as global warming and increased climatic variability, are increasing the susceptibility of high-risk species (those with small geographic ranges, low fecundity, and specialized habitats) (67). Multiple factors acting synergistically are contributing to the loss of amphibians. But we can be sure that behind all of these activities is one weedy species, *Homo sapiens*, which has unwittingly achieved the ability to directly affect its own fate and that of most of the other species on this planet. It is an intelligent species that potentially has the capability of exercising necessary controls on the direction, speed, and intensity of factors related to the extinction crisis. Education and changes of political direction take time that we do not have, and political leadership to date has been ineffective largely because of so many competing, short-term demands. A primary message from the amphibians, other organisms, and environments, such as the oceans, is that little time remains to stave off mass extinctions, if it is possible at all.

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