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Amphibians are in trouble around the world. Awareness of the problem slowly grew in the 1980s. Among the earliest reported incidents were the disappearances of Golden Toads and Harlequin Frogs in the Monteverde Cloud Forest Reserve in Costa Rica in 1986–1987 (1), but soon there were many others. The Declining Amphibian Population Task Force, organized in 1991, served as a conduit for information arriving from many parts of the world and also was an important source of seed grant funding to encourage field research on amphibians, especially in understudied areas. Throughout the 1990s, reports continued to accumulate. Many amphibian biologists, especially those in apparently unaffected areas, were dubious and suspected that population fluctuations were being mistaken for monotonic declines. When long-term field studies (2) confirmed the early reports from Monteverde and reports of declines continued to accumulate, doubts essentially vanished. However, in many parts of the world, amphibians seemed to be doing well, and in discussing amphibian declines, it became standard to state, almost as a disclaimer, that the main reason for the decline was habitat destruction and conversion. But as data accumulated, it became apparent that the earliest reports of declines and disappearances from relatively undisturbed tropical upland habitats were not exceptional but were becoming typical. Tropical lowland environments seemed to be spared, but that perception is altered by an alarming new report by Whitfield *et al.* (3) in this issue of PNAS.

By the late 1990s, attention had shifted from documentation of amphibian declines to studies of causes and possible mitigation. Introduced trout eat tadpoles and froglets and were implicated in extinctions of populations of Mountain Yellow-Legged Frogs in the heavily protected national parks and wilderness areas of the Sierra Nevada of California. Experiments showed that frog populations rebounded when fish were removed (4). But other causes for this particular decline were also suggested (5), so even this apparently clear case was complicated.

A major breakthrough in the study of amphibian declines was the discovery of



Fig. 1. The Tink Frog (*Eleutherodactylus distema*), once a commonly encountered species with dense populations, is one of 17 species of amphibians and lizards that have experienced steep declines, on the order of 75%, over the past 35 years at the La Selva Biological Station in lowland northeastern Costa Rica. (Photo by B. Kubicki, Costa Rican Amphibian Research Center, Guayaquin, Costa Rica. Copyright 1995–2007 UC Regents. All rights reserved.)

dead frogs in Costa Rica and Australia and the detection of a new infectious agent, *Batrachochytrium dendrobatidis*, a chytrid fungus that can kill amphibians (6). At last there was a culprit for the tropical disappearances, and the chytrid was soon detected at many places around the world (7). Chytrid epidemics killed amphibians and led to the disappearance of many species at several sites in upland moist-to-wet forests in Costa Rica and Panama (8). Elsewhere, deaths from chytridiomycosis were also recorded. For example, the Mountain Yellow-Legged Frog populations that had been decimated by introduced fish now suffered local extinctions attributed mainly to the disease (9). The two species now recognized in the Mountain Yellow-Legged Frog complex recently were reported to have suffered population extinctions of 93.3% and 95.2%, based on study of 225 historical sites (10).

A bold claim that global climate change was driving the epidemics and causing amphibian extinctions in the tropics received much attention (11). Episodes of temperature change were found to be statistically correlated with the last appearances of various species of montane frogs. Global warming was seen as the key factor; climates were shifting in the direction of the inferred growth optimum of the chytrid, conse-

quently encouraging devastating outbreaks of disease. It is no surprise that intensive research activity has focused on this new disease, which has such profound biodiversity implications (12).

Results of a long-term monitoring program in lowland Costa Rica (3) raise important questions. The authors, with the help of many individuals and student classes over a 35-year period, conducted studies in primary forest and on abandoned cacao plantations at the La Selva Biological Station. They report major declines in the primary forest for populations of all terrestrial amphibians (see Fig. 1) and—adding a new twist to the decline puzzle—for all lizards as well. All 17 species of amphibians and lizards for which adequate samples were obtained declined by an average of $\approx 75\%$. Densities of these species have declined 4.1–4.5% per year since 1970. Although no local populations have gone extinct, the general nature of the decline is striking.

The fact that both lizards and amphibians have declined makes it unlikely that amphibian-specific disease, such as chytridiomycosis, is the primary cause. Furthermore, because lizards and amphibians differ so greatly in physiology and life-history biology, it is difficult to attribute cause. A perplexing aspect of the present study is that four species that declined in the primary forest sites increased in adjacent abandoned cacao plantations. Minimum temperatures have increased by $\approx 1^\circ\text{C}$ during the period of study, and the number of dry days per year has decreased by $\approx 50\%$. These facts led to the conclusion that the proximal cause of the decline is a reduction in standing leaf litter, in which the studied organisms live and find refuge, because trees retain leaves longer than in the past, because decomposition rates are higher than previously seen, or both. The increase in population densities in cacao is attributed to the leaf flush of these trees several times per year. The ultimate explanation offered

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