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Tests of Null Models for Amphibian Declines on a Tropical Mountain

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Abstract: *Many of the recent, widespread declines and disappearances of amphibian populations have taken place in seemingly undisturbed, montane habitats. The question of whether the observed patterns differ from those expected from natural population dynamics is the subject of an ongoing controversy with important implications for conservation. We examined this issue for the Monteverde region of Costa Rica's Cordillera de Tilarán, where a multi-species population crash in 1987 led to the disappearance of the endemic golden toad (*Bufo periglenes*) and many other species. Focusing on long-term studies of other amphibian assemblages, we developed probabilistic null models for the number of disappearances. Tests of these models at Monteverde suggest that the patterns observed there are highly improbable in the context of normal demographic variability. Twenty species of frogs and toads (40% of the anuran fauna) were missing throughout our 1990–1994 surveys of a 30-km² area. Not all organisms in this area had declined accordingly: the relative frequency of absences was much greater for anurans than for breeding birds. Nevertheless, anuran habitats, most of which are protected within the Monteverde Cloud Forest Preserve, seemed unchanged, and none of the breeding-bird species known to be sensitive to deforestation was missing. Thus, only factors other than direct, obvious human impacts can explain the amphibian declines. Consistent with our tests of null models, analyses of recent population trends do not support the hypothesis that the 1987 crash was an extreme fluctuation from which populations are recovering. Surviving species for which baseline data are available—stream-breeding glass frogs (*Hyalinobatrachium fleischmanni* and *Centrolenella prosoblepon*) and a pond-breeding treefrog (*Hyla pseudopuma*)—remained far less abundant than they were before the crash and showed no increase during 1990–1994. We documented an increase only for one terrestrial-breeding rain frog (*Eleutherodactylus diastema*).*

Pruebas de Modelos Nulos para Disminuciones de Anfibios en una Montaña Tropical

Resumen: *Muchas de las disminuciones y desapariciones recientes de poblaciones de anfibios en varias partes del mundo se han producido en hábitats que aparentemente no han sido alterados. La pregunta de si los patrones observados difieren de lo que es predicho por la dinámica natural de poblaciones es el tema de una controversia actual que tiene consecuencias importantes para la conservación. Se examinó esta pregunta para la región de Monteverde en la Cordillera de Tilarán, Costa Rica, donde un colapso de poblaciones en 1987 produjo la desaparición del endémico sapo dorado (*Bufo periglenes*) y muchas otras especies. Centrándose en estudios a largo plazo sobre anfibios de otras regiones, se desarrollaron modelos nulos probabilísticos con respecto al número de desapariciones. Al probarse estos modelos para Monteverde se sugiere que los patrones observados son poco probables dentro de los parámetros normales de la variabilidad demográfica. Durante 1990–1994 en un área de 30-km², veinte especies de ranas y sapos (el 40% de los anuros de la región) estuvieron ausentes. No todos los organismos del área disminuyeron de la misma forma: por ejemplo, la frecuencia relativa de especies ausentes fue mucho mayor para los anuros que para las aves que se reproducen en el área de estudio. Sin embargo, la mayoría de los hábitats de anuros están protegidos den-*

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tro de la Reserva Biológica Bosque Nuboso de Monteverde, y no parecía que habían cambiado. Además, ninguna de las especies de aves que son afectadas de manera negativa por la deforestación estuvo ausente. Por lo tanto, las disminuciones de anfibios sólo pueden ser explicadas por factores que no son los impactos obvios y directos causados por los seres humanos. De acuerdo con nuestras pruebas de modelos nulos, los análisis de tendencias recientes de abundancia no apoyan la hipótesis de que el colapso de 1987 fuera una fluctuación extrema de la cual las poblaciones están recuperándose. Las especies sobrevivientes de las que existen datos demográficos anteriores al colapso—ranas de vidrio (*Hyalinobatrachium fleischmanni* y *Centrolenella prosoblepon*), que se reproducen en quebradas, y una rana arborícola (*Hyla pseudopuma*) que pone buevos en lagunas y pozos—eran mucho menos abundantes durante 1990–1994 de lo que fueron antes de este evento y no se encontró evidencias de aumento. Se documentó un incremento solo en las poblaciones de *Eleutherodactylus diastema*, que se reproduce en hábitats terrestres.

Introduction

Reports of declining amphibian populations, particularly those in undisturbed montane environments on several continents, have caused alarm and controversy (Blaustein 1994; Pechmann & Wilbur 1994; Phillips 1994; Sarker 1996). The alarm stems from the suggestion, inherent in these reports, that agents more subtle than habitat loss and fragmentation may be threatening biodiversity. The controversy focuses on whether the observed patterns differ from those expected from normal population dynamics.

Pechmann and Wilbur (1994), elaborating the arguments of Pechmann et al. (1991), expressed doubt that the declines reflect anything more than natural fluctuations. They criticized Blaustein and Wake (1990), Wake (1991), Wake and Morowitz (1991), Wyman (1990), and others for being “alarmist.” If it turns out that these authors are “crying frog,” Pechmann and Wilbur warned, future reports of declining populations “may fall upon unsympathetic ears.” Furthermore, they argued, the “alarmist reports” may do a disservice to conservation by drawing attention away from known problems such as tropical deforestation.

Implying that subjectivity in the assessment of apparent declines has led to a misapprehension of their significance, Pechmann and Wilbur (1994) offered a “theoretical, empirical, and philosophical perspective” on interpreting the observed patterns. Although most of their discussion focused on how to tell whether extant populations are in decline, the “relevant examples” at which they directed their comments mostly involve disappearances. They commented briefly on rates of local extinction but provided little framework for judging whether the reported disappearances are unusual.

Travis (1994) recognized that our ability to judge the meaning of disappearances is central to the controversy: “The essential observation that causes concern is the extinction of one or more populations without recolonization during the lifetime of the funded project.” Travis also showed how ambiguous disappearances can be. If there are naturally few local populations per area and individuals disperse over relatively short distances, one might have to wait many years to judge whether recolonization of a site follows its expected course.

It is likewise difficult to interpret the absence of a species from all known sites in an area. Rare local populations might easily be overlooked, especially if they are reduced in size, and a temporary decline might therefore be mistaken for the extinction of a metapopulation or species. Furthermore, some regional extinctions are to be expected. Even the natural extinction of a species, though rare in ecological time, is not out of the question, and isolated, montane endemics such as the golden toad (*Bufo periglenes*) of Costa Rica may be prime candidates for this elusive event (Pechmann & Wilbur 1994).

Because the disappearance of a species from an area lies within the range of normal expectations, a fundamental question is whether the number of disappearances exceeds that expected for naturally fluctuating populations. We address this question for the assemblage to which the golden toad belongs. Although much attention has focused on the disappearance of this species, it is but one of many examples from the Monteverde region of Costa Rica’s Cordillera de Tilarán, where a multi-species population crash took place in 1987 (Crump et al. 1992; Pounds 1990, 1991; Pounds, in press; Pounds & Crump 1994; Pounds & Fogden 1996).

We formulated null models for the number of disappearances and analyzed 5 years of field observations (1990–1994) to test these models. We examined data for breeding birds to test an additional null hypothesis, proposed by Pechmann and Wilbur (1994), that amphibians have declined no more than other organisms. Because fluctuating populations are expected to rebound following apparent declines, we also analyzed recent trends for surviving species to ask whether abundance has increased since the 1987 crash.

Methods

Study System

Our study area is a 15-km-long, east-west belt that straddles the continental divide in Costa Rica’s Cordillera de Tilarán. This belt, which averages about 2 km in width and includes a representation of all the ecological life

zones and amphibian habitats of the region, extends from the 1100-m contour in the headwaters of the Rios Lagarto and Guacimal on the Pacific slope to 1700 m along the continental divide and down to 750 m along the Río Peñas Blancas on the Caribbean slope. The eastern two-thirds lies within the 10,500-ha Monteverde Cloud Forest Preserve, which adjoins the 17,200-ha Children's International Rain Forest. See Pounds and Crump (1994) for a map of the region and a description of climate.

We divided the study area into four zones: Pacific slope (1100–1450 m, zone A); upper slopes and continental divide (>1450 m, zone B); upper Peñas Blancas Valley (950–1450 m, zone C); and lower Peñas Blancas Valley (750–950 m, zone D). The natural vegetation of zone A is moist forest grading into premontane wet forest at the higher elevations. That of zone B is cloud forest and, along the ridge tops, elfin woodland. That of zones C and D is Caribbean-slope rain forest. Whereas the vegetation in zone A and the western edge of zone B is a mosaic of pasture, secondary forest, and primary-forest remnants, that of zones B–D is mostly primary forest. The map in Pounds and Crump (1994) illustrates forested and deforested areas as approximated from aerial photographs.

In the decade preceding the 1987 crash, there was no systematic monitoring, yet faunal surveys and ecological studies provide information on species composition, local distribution, and abundance of selected species during that period (Crump 1986, 1991; Crump et al. 1992; Crump & Pounds 1985, 1989; Crump & Townsend 1990; Hayes 1985, 1991; Hayes et al. 1989; Jacobson 1985; Jacobson & Vandenberg 1991; Pounds, in press; Pounds & Crump 1987, 1994; Timmerman & Hayes 1981; Van Devender 1980). Fifty-three species of anurans, five species of salamanders, and two species of caecilians are known from the region. All inhabited our study area. Two of us are long-term residents who have become familiar with the fauna and have witnessed the recent changes (JAP since 1982; MPLF since 1977).

Habitats do not appear to have changed during the past 15 years. Sites comprising a sample of 16 streams and 16 ponds and swamps look much the same as they did in the early 1980s. Most of these are protected within the Monteverde Preserve. Opportunities for dispersal between sites, though greatest in zones B, C, and D, likewise seem unchanged.

Tests of Null Models for the Number of Disappearances

MODEL FORMULATION

One method for calculating the expected number of disappearances would rely on the historical record for the area in question. For most areas, however, the record is limited, and even where it is substantial, this approach is problematic. In the decade preceding the 1987 crash at Monteverde, faunal surveys and ecological studies sug-

gested no spate of disappearances. It would introduce bias, however, to judge normal faunal stability by examining the years of greatest stability. Furthermore, even if there were data showing that species composition had remained constant for, say, 50 years, this bias would still be a problem: the most extreme fluctuations might be rare even on multi-decade time scales.

We developed an alternative approach that bases null models on long-term studies of other amphibian assemblages. The available data suggest that populations ordinarily “range from highly variable to highly stable” (Pechmann & Wilbur 1994). Focusing on examples at the former end of the spectrum, we constructed null models in which the expected numbers of disappearances presumably lie near the upper extreme of what is normal. For each model, we defined no single expected number but rather a probability distribution that corresponds to the range of possibilities. First we estimated the likelihood that a single species would disappear from an area. We then calculated the probability that a particular number of species would disappear simultaneously. Because we considered two possible outcomes, disappear or persist, a binomial distribution gives the latter probability (Batschelet 1979).

Pechmann and Wilbur (1994) opened their paper with an illustration of how natural fluctuations can be mistaken for alarming declines. Mocking recent articles, they paraphrased Bragg's (1954) note on toad populations in Cleveland County, Oklahoma as though it were a new alarmist report: “The dwarf American toad, *Bufo americanus charlesmitbi*, . . . has all but disappeared . . .” Interjecting accounts of other “catastrophic die-offs,” they did not reveal the source or the outcome until several paragraphs later: “By 1958, populations of *B. americanus* . . . had recovered . . .” Bragg (1960) documented patterns for this and 14 other species (12 anurans & 2 salamanders) in a 25-year study (1935–1959). Pechmann and Wilbur intended to convey a simple message—that we have heard it all before. Yet by choosing Bragg's work to illustrate how unstable amphibian populations can be, they tacitly offered it as a basis for null models. They also emphasized a 12-year study of 4 species (1 anuran & 3 salamanders) breeding in a seasonal pond (Rainbow Bay) on the upper coastal plain of South Carolina (Pechmann et al. 1991). Numbers of individuals arriving at this pond fluctuated dramatically from year-to-year and sometimes fell to zero. These studies, which together provide 423 species-years of observations, form the empirical basis of our null models.

PROBABILITY OF SINGLE-SPECIES DISAPPEARANCE

The probability of disappearance (here defined operationally as the absence of adults during a year or more) varies according to the spatial scale. A species is more likely to disappear from a single pond, for example, than

from an area with 10 similar ponds. The spatial scale of null models should therefore match that of the area in question. Because our study lies between that of Bragg (1960) and that of Pechmann et al. (1991) in spatial scale, a reasonable estimate of the probability of disappearance may lie between the values obtained from these studies.

We calculated two estimates of the likelihood that a single species would disappear. The first, which equals the number of disappearances divided by the number of species-years of observation, gives the average per-species probability of disappearance in any year chosen at random (ω). Of course, rather than fluctuate entirely at random, populations respond in varying degrees to droughts and other disturbances (Bragg 1960; Pechmann et al. 1991). Bragg hypothesized, for example, that the repeated disappearance and reappearance of the western chorus frog (*Pseudacris t. triseriata*) resulted from range contraction during dry years and range expansion during rainy years. Thus, our second estimate, which equals the number of disappearances divided by the product of the number of species times the number of disturbances, gives the average per-species probability of disappearance in response to a natural disturbance (λ).

Calculations of ω suggest that disappearances are ordinarily less common than Pechmann and Wilbur might have us believe. Six species of anurans in Bragg's study fluctuated strongly, yet we estimated that only four disappearances took place during 1935–1959. The western chorus frog was absent during the first 3 years but appeared in 1938. We assumed that this species disappeared in 1935. Of course, it quite possibly was absent before Bragg's study as well, yet we made this assumption to ensure, conservatively, that any bias in our estimate is toward the high side. Because the western chorus frog disappeared and reappeared twice more, we estimated that it disappeared three times in all. The dwarf American toad (*B. a. charlesmithi*) disappeared and reappeared once. Bragg (1960) did not always clarify exactly how long these species were absent. To be conservative, we assumed that each was missing during half of the study, so there were 25 species-years in which disappearance was not possible because the species in question was already absent. We therefore reduced the total number of species-years (15 species \times 25 years = 375) by 25, leaving 350. Thus $\omega \approx 4$ disappearances \div 350 species-years \approx 0.011. Applying the same methods to the data from Rainbow Bay (Pechmann et al. 1991), we estimated that two disappearances took place during 1979–1990: the salamanders *Ambystoma opacum* and *A. tigrinum* each disappeared and reappeared once. Total species-years was 48 (4 species \times 12 years). Reducing this by 8 (the number of species-years in which populations were absent or greatly reduced), we obtained $\omega \approx 2$ disappearances \div 40 species-years \approx 0.05. Thus, on the spatial scale of our study, the average probability that a

species would disappear in any year chosen at random may lie in the range of 1–5%.

Because disappearances are more likely during disturbances, λ is a more conservative basis for null models than ω . In Bragg's study, density fluctuations and disappearances appeared to correspond to three dry spells. Hence $\lambda \approx 4$ disappearances \div (15 species \times 3 disturbances) \approx 0.089. At Rainbow Bay (Pechmann et al. 1991), the fluctuations and disappearances seemed to correspond to four disturbances: dry weather in 1981, 1985, and 1988–1989, plus an unidentified event postulated here to explain the absence of *A. opacum* at the beginning of the study (1979–1980). Thus $\lambda \approx 2$ disappearances \div (4 species \times 4 disturbances) \approx 0.125. A reasonable estimate of λ might therefore lie between 0.089 and 0.125. For a conservative argument, we adopted the larger value for our principal null model.

Because environmental and demographic variability may increase, up to a point, with the length of the sampling period, this value could underestimate the natural probability of disappearance. Ultimately, of course, one can only judge whether the observed number of disappearances is unusual in the context of known variability. Nevertheless, to consider a hypothetical extreme, we arbitrarily doubled our estimate of λ in our second null model (i.e., $\lambda = 0.25$). According to this model, a species ordinarily has a one-in-four chance of disappearing from our study area in response to a natural disturbance.

PROBABILITY OF SIMULTANEOUS *D*-SPECIES DISAPPEARANCE

Given λ , one can calculate the probability that the number of disappearances (D) would equal a theoretical expected number of disappearances (X_i), where X_i may range from zero to N (the total number of species). First, one must tally the possible ways (combinations, disregarding order) in which X_i out of N species could disappear (e.g., Batschelet 1979):

$$\binom{N}{X_i} = \frac{N(N-1)\cdots(N-X_i+1)}{X_i!} \quad (1)$$

For our study area, $N = 50$. Hence, there are 50 ways that a single species could disappear. There are, however, 2,118,760 ways that five species could disappear. A binomial distribution gives the probability that $D = X_i$:

$$p(D = X_i) = \binom{N}{X_i} \lambda^{X_i} (1-\lambda)^{N-X_i} \quad (2)$$

This equation expresses the likelihood, in the context of natural demographic variability as characterized by λ , that exactly 0, 1, 2, ..., or N species would disappear at the same time. The critical issue, however, is the probability that, by chance alone, the number of disappearances would exceed a particular expected number (X_i). A cumulative binomial distribution gives this probability:

$$p(D > X_i) = \sum_{Y = X_i + 1}^N \binom{N}{Y} \lambda^Y (1 - \lambda)^{N - Y}. \quad (3)$$

We used these equations to generate probability distributions corresponding to our two null models: 1) that based on known fluctuations ($\lambda = 0.125$) and 2) that based on a hypothetical extreme of demographic variability ($\lambda = 0.25$; Fig. 1).

SAMPLING METHODS AND TESTS

To test each model, we compared the *number of species missing* (M) to the cumulative probability distribution corresponding to the range of possible expected numbers of disappearances (X_i ; eq. 3; Fig. 1b). Because the *number of disappearances* (D) could not be known with certainty, we used M as a surrogate. We examined $p(D > X_i)$ for the largest value of X_i that M exceeded. Setting $\alpha = 0.05$, we rejected the null model if this probability was less than 0.05. The procedure is equivalent to assessing the random probability, in the context of our models, that the number of absences would be as large or larger than that observed.

Field work to assess M began in 1990, when it was clear that the scarcity of amphibians reflected more than a lull in activity. Conducting regular searches (at least weekly), we targeted particular species and timed visits to sites according to weather and activity patterns. We scanned vegetation and listened for vocalizations but, because of time constraints, did not rake leaf litter, dig soil, or open moss mats, bromeliads, etc. Our field methods were thus suitable only for anurans, and we restricted our analyses to them. In defining which species we would ordinarily expect to find in a given year, we omitted rare ones, which were absent throughout 1990–1994 and hard to find even before the declines (*Hyla fimbriemembra*, *Nelsonophryne aterrima*, and *Eleutherodactylus cuaquero*). We included the highly arboreal *H. miliaria* and *Anoteca spinosa*, which are more often heard than seen, because their vocalizations and calling sites had been documented (Fogden, unpublished). Thus $N = 50$ (Appendix).

We tested the null models for the total study area and each of the four zones. We therefore recalculated eq. 3 for the corresponding N for each zone. Although the spatial scale varied among analyses, in every case it lay between that of Cleveland County, Oklahoma (Bragg 1960) and that of Rainbow Bay in South Carolina (Pechmann et al. 1991).

We also repeated our tests with different definitions of “missing”: absent in 1990 or absent throughout 1990–1994. Whereas the former corresponds to the definition of disappearance used in formulating null models, the latter provides more conservative tests. In a given year it is possible to overlook some species—especially fossorial,

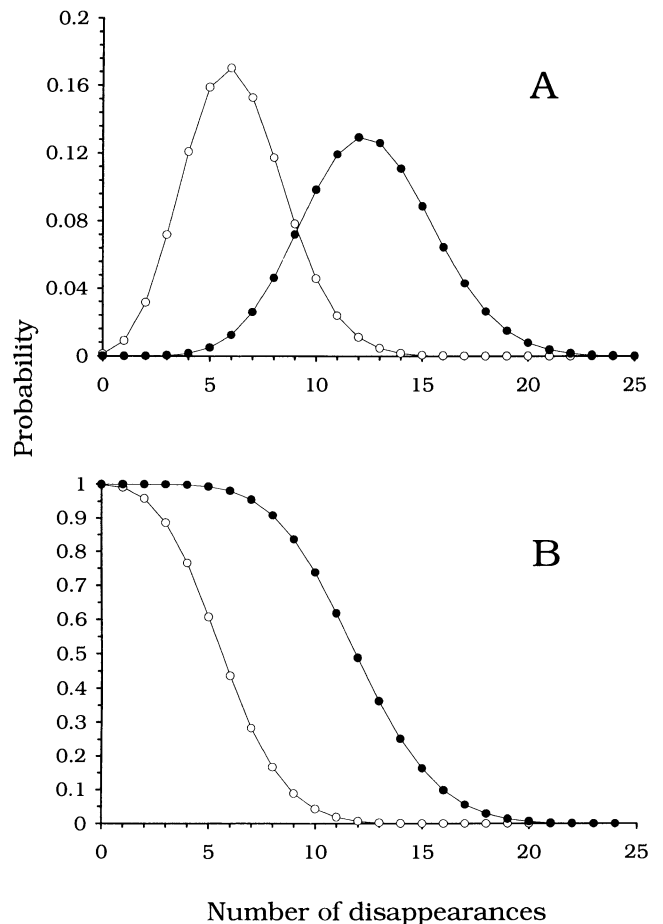


Figure 1. Binomial probability distributions for the number of disappearances. Probabilities give the likelihood that the number of disappearances would equal a particular expected value (A; eq. 2) or exceed this value (B; eq. 3). Numbers of disappearances are theoretical expected values (X_i), which may range from zero (no disappearances) to N (disappearance of the entire assemblage). Probabilities are calculated for $N = 50$, but only the lower half of the range of X_i is graphed. Open symbols are for $\lambda = 0.125$, shaded ones for $\lambda = 0.25$, where λ is the average per-species probability of disappearance in response to a natural environmental disturbance.

explosive breeders (*Bufo periglenes* and *Hypopachus variolosus*)—but this is unlikely during 5 consecutive years.

Our models and tests did not consider the duration of absence. Although this parameter might reflect the severity of declines, we know too little about natural population structure to judge how expected rates of recolonization at Monteverde might compare to those elsewhere. By examining populations on a regional scale, however, we may shed some light on whether the observed patterns differ from those expected from normal metapopulation dynamics.

COMPARABILITY OF ASSEMBLAGES AND THE VALIDITY OF TESTS

Our study focuses on tropical lower montane amphibians, whereas the null models are based on temperate lowland ones. Comparability would be a critical issue, however, only if populations of the former were inherently unstable compared to those of the latter, and we are aware of no suggestion that they are. To the contrary, Pechmann and Wilbur (1994) viewed humid tropical habitats as “presumably favorable,” though populations there do fluctuate (e.g., Barbault 1991). Nevertheless, the Monteverde assemblage differs from those represented in our null models in taxonomic composition, diversity of breeding modes, and patterns of habitat use—characteristics that could influence probabilities of disappearance.

We thus examined patterns of presence and absence in relation to family, breeding mode, and habitat. Where associations could affect the validity of our tests of null models, we repeated these tests while excluding, from our sample of species at Monteverde, those belonging to categories (of the relevant variable) not represented in the models.

We categorized species as indicated in the Appendix. Breeding modes fall into three classes: (1) eggs and tadpoles aquatic; (2) eggs out of water, tadpoles aquatic; and (3) direct development within encapsulated, terrestrial eggs (Duellman & Trueb 1986). Habitats likewise fall into three categories: (1) ponds and swamps; (2) streams; and (3) forest, independent of bodies of water. Some species could be included in two habitat categories. *Rana warszewitschii*, for example, breeds in both lentic and lotic waters. In this and similar cases, we classified species according to the habitat used most frequently in our study area.

Family, breeding mode, and habitat are not independent of one another. All forest-dwelling species not associated with bodies of water (forest habitat) are terrestrial breeders (mode 3) and belong to the genus *Eleutherodactylus* (Leptodactylidae). Three other members of this genus, however, follow the same reproductive mode but frequent stream margins (Appendix). Within the constraints set by this non-independence of variables, we used χ^2 analyses of contingency tables to test for associations between species characteristics and *presence-absence* in 1990 (2-tailed; Yates-corrected where $df = 1$; Sokal & Rohlf 1969).

Comparisons with Breeding Birds

Where amphibians have declined, Pechmann and Wilbur (1994) argued, so have other organisms, and the causes are direct, obvious human impacts such as habitat destruction. According to these authors, “there are no analyses that compare population changes in amphibians to those in other taxa” to substantiate the idea that recent declines and disappearances “fall more heavily on amphibians” or that “amphibians are provid-

ing an early warning” of subtle but critical changes in the environment.

We compared disappearances of anurans to those of breeding birds in our study area. Because birds have relatively impermeable skins and develop within amniotic eggs that require no free water, they are more isolated from their immediate physical environment than most amphibians (Blaustein & Wake 1990; Blaustein 1994). Presumably, therefore, they are comparatively well-buffered against certain environmental perturbations (e.g., droughts). Nevertheless, birds, like amphibians, may be bio-indicators. Many avian species require a large area of forest, and their presence or absence may thus indicate the extent of deforestation (e.g., Stiles & Skutch 1989). At Monteverde, examples of these species include the Bare-necked Umbrellabird (*Cephalopterus glabricollis*) and the Ornate Hawk-Eagle (*Spizaetus ornatus*). The only noticeable change in their habitats during the past 15 years is the reversion of pastures and homesites to forest, especially in the Peñas Blancas Valley (zones C & D), which was annexed to the preserve in the mid-1980s.

The bird data (gathered by MPLF) include 16 years of records for zones A and B (1979–1994) and 10 years for zones C and D (1985–1994). For each zone and the total study area, we compiled a list of species detected as breeding birds in three or more years during 1983–1992. The total list includes 268 representatives of 43 families (Fogden 1993).

We compared presence-absence patterns of anurans and breeding birds for 1993–1994. A bird species was scored as absent (in a particular zone or the total study area) if it was not detected as a breeding bird in either year. Our null hypothesis was that the proportion of species missing was no greater for anurans than for birds.

We also examined the bird data to test the null models formulated for amphibians (see Tests of Null Models for the Number of Disappearances). If anurans but not birds have declined in diversity, we should reject these models for the former but not the latter.

Analyses of Recent Population Trends

The hypothesis that amphibian declines represent natural fluctuations predicts that, following an apparent decline, abundance should increase as populations recover. Assuming normal conditions, then, populations that survived the 1987 crash at Monteverde should exhibit an increase in abundance if not a complete return to pre-crash levels.

During 1990–1994, we monitored the abundance of Fleischmann’s and emerald glass frogs (*Hyalinobatrachium fleischmanni* and *Centrolenella prosoblepon*, respectively), the meadow treefrog (*Hyla pseudopuma*), the red-eyed stream frog (*H. uranochroa*), and the common dink frog (*Eleutherodactylus diastema*). Pre-crash demographic data exist only for the glass frogs and *H.*

pseudopuma. We nevertheless monitored *E. diastema* because it had been one of the most abundant and widespread species in the area before the 1987 crash. We included *H. uranochroa* to study recolonization. From field notes we identified six previously inhabited stream sites within 2 km of each other in zone B. One of these was occupied in 1990.

For each species except *H. uranochroa*, we monitored three populations in zone A or B. Sites for glass frogs included the stream described by Hayes (1991) and Jacobson (1985) and similar ones nearby. Sites for *H. pseudopuma* included "site 1" of Crump and Townsend (1990) and two other seasonal ponds, one at a pasture-forest boundary (~300 m²) and the other in primary forest (~15 m²) within the preserve. We surveyed populations of *Eleutherodactylus diastema* along forest trails.

For each species except the explosively breeding *H. pseudopuma*, we performed monthly counts for each population during the wet season (May-October), the same times of year as in the previous studies. We counted adults in belt transects (6 × 100–200 m) and converted the numbers into observed densities. For *H. pseudopuma*, we did total counts when ponds filled. Because frogs of this species become highly concentrated for short periods, we did not convert the numbers into densities.

We calculated Spearman rank correlations (Sokal & Rohlf 1969) of abundance versus year for each population and species (averaging across populations). Our index of abundance for each population, except those of *H. pseudopuma*, was the annual maximum observed density in one set of analyses and the annual mean observed density (averaging across months) in another. For *H. pseudopuma*, we used the annual maximum number. In each analysis, to ask whether populations were recovering from the 1987 crash, we tested for evidence of an increase ($H_0: r_s \leq 0$ and $H_a: r_s > 0$; N = number of years =

5). We also compared our observations to pre-crash data where the latter were available.

Results

Natural Fluctuations or a Decline in Diversity?

The number of species missing exceeded that expected in the context of our null models (Table 1; Appendix [p. 1322]). Of the 50 species of anurans, 25 were absent in 1990, leading us to reject the null model based on known fluctuations ($\lambda = 0.125$) and that based on a hypothetical extreme of demographic variability ($\lambda = 0.25$). Five species reappeared during 1991–1994; thus 20, including the golden toad (*Bufo periglenes*), were missing throughout 1990–1994, leading us to again reject both null models. We also rejected them for each zone for both 1990 and 1990–1994 patterns. Accordingly, the relative frequency of absences did not differ among zones for either period ($\chi^2_{3df} \leq 0.565$; $p > 0.90$).

Reappearances seemed to be due to recolonization from outlying areas. All but that of *Hyalinobatrachium colymbiphylum* in 1994 took place on the perimeter of the study area at the lower altitudinal limits. All except that of *Rana warszewitschii* in 1991 occurred after several years of absence. *Bufo melanochloris*, *Eleutherodactylus biporcatus*, and *Hypopachus variolosus* reappeared in 1993.

The likelihood of disappearance following the 1987 crash appeared to be independent of family (Table 2). Disappearances afflicted each of the six families and none significantly more than others. The proportion of absences among the Leptodactylidae appeared relatively low but did not differ from that of the other five families combined ($\chi^2_{1df} = 2.17$; $p > 0.10$).

There was likewise no association between *presence-*

Table 1. Tests of null models for the number of disappearances of anuran species in the Monteverde region of Costa Rica's Cordillera de Tilarán.

Period	Parameter	Portion of study area (zones A–D)				
		A	B	C	D	Total (A–D)
1990	Total number of species (N)	24	26	26	29	50
	Number of species missing (M)	12	13	11	15	25
	Proportion missing (M/N)	0.500	0.500	0.423	0.517	0.500
	p for model I ($\lambda = 0.125$)*	0.0000091	0.0000038	0.0001469	0.0000004	0.0000000014
	p for model II ($\lambda = 0.25$)	0.0072	0.0052	0.0401	0.0018	0.000123
1990–1994	Number of species missing (M)	11	12	11	12	20
	Proportion missing (M/N)	0.458	0.462	0.423	0.414	0.400
	p for model I ($\lambda = 0.125$)	0.0000603	0.0000255	0.0001469	0.0000954	0.00000093068
	p for model II ($\lambda = 0.25$)	0.0213	0.0155	0.0401	0.0390	0.013918

* p is the random probability, in the context of normal demographic variability as defined by the null models, that the number of disappearances would be as large or larger than that observed. The null model is rejected if $p < 0.05$. See text for details regarding λ (the average per-species probability of disappearance in response to a natural environmental disturbance).

Table 2. Number of disappearances of anuran species at Monteverde in relation to family, breeding mode, and habitat.^a

Variable	Category ^b	Total number of species (N)	Number of species missing (M)	Proportion missing (M/N)
Family	Leptodactylidae	18	6	0.333
	Bufoidea	7	4	0.571
	Microhylidae	1	1	1.000
	Hylidae	14	8	0.571
	Centrolenidae	7	3	0.429
	Ranidae	3	3	1.000
Breeding mode	1. Eggs and larvae aquatic	22	13	0.591
	2. Eggs out of water, larvae aquatic	11	6	0.545
	3. Terrestrial (no larvae)	17	6	0.353
Habitat	1. Ponds, pools, or swamps	18	11	0.611
	2. Streams	18	11	0.611
	3. Independent of aquatic habitats	14	3	0.214

^aPatterns are for 1990. See text for statistical analyses.

^bAppendix lists species in each category.

absence and breeding mode (Table 2; $\chi^2_{2df} = 2.29$; $p > 0.31$). The proportion of absences appeared lowest for the 17 species of *Eleutherodactylus* frogs, which undergo direct development into froglets within encapsulated terrestrial eggs. Nevertheless, the pattern for this genus did not differ from that of all the other genera combined ($\chi^2_{1df} = 1.43$; $p > 0.10$). The three species of *Eleutherodactylus* associated with streams all disappeared.

There was an association between presence-absence and habitat (Table 2; $\chi^2_{2df} = 6.35$; $p < 0.042$). Patterns were identical for anurans ordinarily found near streams and those which frequented ponds or swamps. The 14 species of *Eleutherodactylus* independent of bodies of water, however, were less likely to be missing than the 36 species associated with aquatic habitats.

Because the amphibian assemblages represented in our null models include only aquatic breeders, these for-

est-dwelling *Eleutherodactylus* are the principal element of the Monteverde fauna that reduces its comparability to those assemblages. We thus retested the models for the 36 species normally associated with bodies of water. Of these species 22 were missing in 1990 and 18 were absent throughout 1990-1994, leading us to again reject both null models regardless of the time frame (Table 3). While the results were similar for the 18 species associated with ponds or swamps, the 14 species of *Eleutherodactylus* independent of bodies of water showed no significant departure from the expected patterns (Table 3).

Have Anurans Declined More than Breeding Birds?

The proportion of species missing during 1993-1994 was much greater for anurans than for breeding birds (Fig. 2). The pattern was similar for each of the four zones and the total study area (Fisher exact tests; $p < 0.0002$).

Table 3. Tests of null models for the number of disappearances of anuran species in different habitat classes at Monteverde.

Period	Parameter	Subset of species		
		Associated with aquatic habitats ^a	Associated with ponds, pools, or swamps ^b	Independent of bodies of water ^c
1990	Total number of species (N)	36	18	14
	Number of species missing (M)	22	11	3
	Proportion missing (M/N)	0.611	0.611	0.214
	<i>p</i> for model I ($\lambda = 0.125$) ^d	0.0000000000087	0.00000158	0.2510
	<i>p</i> for model II ($\lambda = 0.25$)	0.0000048	0.00124	0.7189
1990-1994	Number of species missing (M)	18	9	2
	Proportion missing (M/N)	0.500	0.500	0.143
	<i>p</i> for model I ($\lambda = 0.125$)	0.0000000525401	0.00012450	0.5374
	<i>p</i> for model II ($\lambda = 0.25$)	0.0010680	0.01935	0.8990

^aThese habitats include ponds, pools, swamps, and streams.

^bSpecies in this class, which excludes stream-dwellers, are a subset of those associated with aquatic habitats in general.

^cAll species in this category are terrestrial-breeding *Eleutherodactylus* frogs.

^dInterpretation of *p* in tests of the null models is the same as in Table 1.

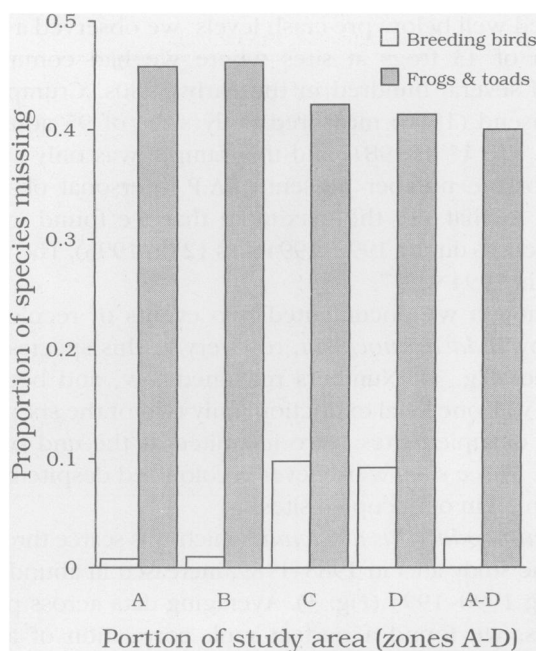


Figure 2. Comparison of presence-absence patterns for anurans and breeding birds at Monteverde. Patterns are for 1993–1994. See Tables 1 and 4 for sample sizes.

Virtually all disappearances of breeding birds occurred in zones C and D, where comparatively little deforestation had taken place and most former clearings had reverted to forest during the preceding decade (Fig. 2). Furthermore, none of the species known to be sensitive to deforestation was absent. The disappearances appeared to be largely due to the impact of forest regeneration on invasive, open-country birds. Of the 204 species that inhabited these zones, 42 frequented clearings and early successional growth, whereas 162 were primarily forest-dwelling. Species missing from one or both zones included a much higher proportion of the former (0.357) than the latter (0.043; Fisher exact test; $p < 0.0001$).

The relative frequency of absences among frogs and toads, though greater than that for breeding birds in gen-

eral, was similar to that of open-country birds whose farmland habitat had mostly reverted to forest. The proportion of anuran species missing from the total study area (0.40) was not distinguishable from the proportion of open-country bird species missing from the combined area of zones C and D (0.310; Fisher exact test; $p = 0.248$). Nevertheless, the habitats of anurans, like those of forest-dwelling birds, seemed unchanged.

In tests of the probabilistic null models for the number of disappearances, breeding birds in general showed no evidence of a decline in diversity (Table 4). Whereas the same was true for forest-dwelling species in zones C and D, we rejected model I ($\lambda = 0.125$) but not model II ($\lambda = 0.25$) for open-country birds in that area (Table 4).

Are Populations Recovering?

Except in the case of *Eleutherodactylus diastema*, we failed to reject the null hypothesis of no trend of increasing abundance during 1990–1994. The same was true for each population and species (averaging across populations). For species studied in transects, the results were similar regardless of whether we used the annual maximum observed density or the annual mean (averaging across months); we present the former.

Glass frogs (*Hyalinobatrachium fleischmanni* and *Centrolenella prosoblepon*) increased slightly in abundance during the first few years but then decreased (Fig. 3). Averaging data across populations of each species, we found no correlation between abundance and year in either case ($r_s \leq 0.30$; $p > 0.33$). There was likewise no correlation for any single population ($r_s \leq 0.48$; $p > 0.23$). Numbers of frogs, compared to what they had been before the 1987 crash, hovered near zero. Hayes (1991) estimated that 280–294 males of *H. fleischmanni* held territories along a 120-m segment of the Río Guacimal in 1980. Although we did not assess absolute densities, the numbers of frogs that we observed were extremely low relative to Hayes's estimates. The maximum found per 120 m of stream in any one census during 1990–1994 was eight (in 1993). The maximum at Hayes's site in 1994 was one. Jacobson (1985) marked 353 *C.*

Table 4. Tests of null models for the number of disappearances of breeding-bird species at Monteverde.^a

Parameter	Portion of study area (zones A–D)					Subset of species in zones C & D	
	A	B	C	D	Total (A–D)	Forest	Open-country
Total number of species (N)	122	102	132	173	268	162	42
Number of species missing (M)	1	1	13	16	7	4	13
Proportion missing (M/N)	0.008	0.010	0.098	0.092	0.026	0.025	0.310
p for model I ($\lambda = 0.125$) ^b	>0.9999	>0.9999	>0.8551	0.9254	>0.9999	>0.9999	0.00135
p for model II ($\lambda = 0.25$)	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	0.2336

^a Patterns are for 1993–1994; the null models are those formulated for amphibians.

^b Interpretation of p in tests of null models is the same as in Table 1.

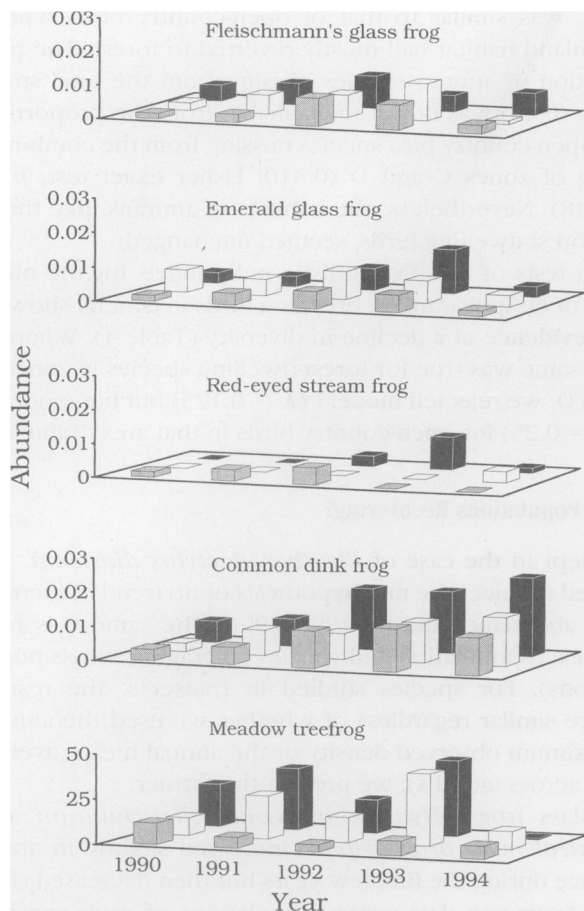


Figure 3. Year-to-year variation in the abundance of anuran species that survived the 1987 population crash at Monteverde. Patterned, black, and white columns represent the different sites for each species. For the explosively breeding meadow treefrog (*H. pseudopuma*), abundance is the annual maximum number observed at each pond. For all other species, abundance is the annual maximum observed density at each site. Data for Fleischmann's and emerald glass frogs (*Hyalinobatrachium fleischmanni* and *Centrolenella prosoblepon*) and the red-eyed stream frog (*Hyla uranochroa*) are from transects along streams. For the latter species, three other previously inhabited sites remained unoccupied throughout 1990–1994. Data for the common dink frog (*Eleutherodactylus diastema*) are from transects along forest trails.

prosoblepon in 1982 along an 80-m section of the same stream. The maximum that we observed per 80 m of stream in any one census was six (in 1993). The corresponding maximum in 1994 was two.

Our results were similar for *Hyla pseudopuma* (Fig. 3). Averaging data across populations, we found no correlation between abundance and year ($r_s = -0.30$; $p > 0.33$). Likewise, there was no correlation for any single population ($r_s \leq 0.13$; $p > 0.42$). Abundance again re-

mained well below pre-crash levels: we observed a maximum of 43 frogs at sites where we had commonly found several hundred in the early 1980s. Crump and Townsend (1990) measured body sizes of 95 adults at their "site 1" in 1981, and this sample was only a fraction of the number present (J.A.P., personal observation). At that site the maximum that we found in any one census during 1990–1994 was 12 (in 1993). The maximum in 1994 was 7.

Although we documented two events of recolonization by *Hyla uranochroa*, recovery in this species was limited (Fig. 3). Numbers remained low, and because there was one local extinction, only two of the six previously occupied sites were inhabited at the end of the study. Three sites were never recolonized despite being within 1 km of occupied sites.

Eleutherodactylus diastema, which was scarce throughout the study area in 1988–1989, increased in abundance during 1990–1994 (Fig. 3). Averaging data across populations, we found a perfect rank correlation of abundance with year (i.e., $r_s = 1.0$). Likewise, there was a positive correlation for each population ($r_s \geq 0.83$; $p < 0.05$). The populations monitored throughout the study were all in zone B. Nevertheless, abundance of this species increased in zone D as well: although it was scarce there in the late 1980s, the maximum observed density in 1993–1994 was similar to that in zone B (Wilcoxon signed ranks test, paired by month; $T = 30$, $N = 15$, $p > 0.16$). The results for *E. diastema* accord with our impression that many species of *Eleutherodactylus* increased in abundance during 1990–1994.

Discussion

The Case of the Golden Toad

The golden toad (*Bufo periglenes*) has figured prominently in the debate regarding the significance of amphibian declines. Published reports document that this species was locally abundant when discovered in the early 1960s (Savage 1966), during ecological studies in 1977 and 1982 (Jacobson & Vandenberg 1991) and shortly before populations crashed in 1987 (Crump et al. 1992; Pounds & Crump 1994). Focusing on the lack of continuous monitoring, Pechmann and Wilbur (1994) implied that the golden toad's disappearance may have been a repeat of history. Nevertheless, Wilford Guindon, who has patrolled the Monteverde Preserve almost constantly for 25 years, is emphatic that hundreds to thousands of toads were present every year during 1971–1987 (W. Guindon, personal communication). The species was thus locally abundant for at least 17 consecutive years leading up to its sudden disappearance.

During those years, golden toads spent most of their time in underground retreats, emerging to breed each

year during one to several 5- to 10-day periods in March–June. When few toads appeared in 1988 and 1989, Crump et al. (1992) suspected that many had stayed underground because of dry weather. Others have reiterated this idea as a possible explanation for the species' continued absence (Blaustein 1994; Blaustein et al. 1994; Pechmann & Wilbur 1994). By 1990, however, it was clear that this hypothesis was false (Pounds 1990). Many species were absent despite rainy weather, and some of them, including the harlequin frog (*Atelopus varius*) along the headwaters of the Río Lagarto, had previously been conspicuous year-round (Crump & Pounds 1989; Pounds & Crump 1994).

If the golden toad is extinct, Pechmann and Wilbur (1994) argued, it may have been “a likely candidate for natural extinction”. They noted, however, that natural extinctions of species have been rare or nonexistent in historical times. They might find it troubling, therefore, that Holdridge's toad (*Bufo holdridgei*), endemic to Costa Rica's Cordillera Central, also vanished from seemingly undisturbed habitats in the late 1980s (F. Bolaños, unpublished). Pechmann and Wilbur (1994) argued that biologists often have a “probability blind spot” that causes them to miscalculate odds when confronted with a seemingly improbable coincidence of rare events (“Preposterous Odds and the Birthday Problem”). Is our concern over the possibility of multiple species extinctions in protected habitats another manifestation of this bias? We would find the pattern disquieting even if we were unaware of the many declines and disappearances in highland areas of other continents (e.g., Carey 1993; Corn & Fogleman 1984; Czechura & Ingram 1990; Drost & Fellers 1996; Fellers & Drost 1993; Heyer et al. 1988; Kagarise Sherman & Morton 1993; LaMarca & Reinthaler 1991; Laurance et al. 1996; Weygoldt 1989).

Sufficient Evidence?

Echoing the call for routine monitoring, Pechmann and Wilbur (1994) implied that the controversy cannot be resolved until data accumulate over many years. McCoy (1994) advocated more-structured approaches to testing null hypotheses, yet he too suggested that we are in for a long wait “because of the sheer magnitude of the undertaking.” Although we agree that ongoing study is essential, we disagree that a solution to the “dilemma” lies beyond present knowledge.

The fundamental question is whether the observed declines and disappearances are improbable in the context of normal population dynamics. To address this question for a particular population, long-term data are needed, but in most cases they do not exist. We have avoided the problem by approaching the question at the level of the species assemblage. We have compared the observed number of disappearances to that predicted by null models based on populations that, according to Pechmann

and Wilbur (1994), are normally unstable. Our conclusion is that the observed patterns are indeed improbable.

There are conceivable alternatives to these models. Instead of the *average per-species probability of disappearance in response to a natural disturbance* (λ), one could use the *maximum proportion of species that have disappeared in any single event* (D_{\max}/N). Where the number of species (N) is small, however, as at Rainbow Bay (Pechmann et al. 1991), this ratio is highly sensitive to slight variation in D_{\max} . At any rate, values of D_{\max}/N for Bragg's study (0.13) and that of Pechmann et al. (0.25) do not exceed the range of λ in our models. Substitution of D_{\max}/N for λ would therefore not alter our conclusions.

Although our null models could underestimate the natural probability of disappearance, it appears more likely that the opposite is true. Model I ($\lambda = 0.125$) may overestimate this probability, not only because our assumptions were conservative, but also for three additional reasons. First, the amphibian populations examined by Pechmann et al. (1991) are one-fourth of those that breed at Rainbow Bay; the others might be comparatively stable. Second, because adults may skip breeding in some years, the patterns at Rainbow Bay may largely reflect behavioral rather than demographic variability. Third, Pechmann et al. reported numbers of adult females but not adult males. Because males could be present during years in which no females arrive, it is unclear whether absence of the latter implies disappearance as defined in our null models.

Whereas model I may be conservative, model II ($\lambda = 0.25$) almost certainly is. The species of plants and animals in our study area must ordinarily have less than a one-in-four chance of vanishing in response to any natural disturbance short of a volcanic cataclysm. Otherwise, many of them, particularly highland specialists with restricted altitudinal distributions, would have vanished long ago. Imagine, for example, 100 mountaintop species that have no chance of recolonization if they go extinct. If the mean per-species probability of disappearance in response to a severe natural disturbance that recurs once per century were 0.25, we could be 95% confident (from eq. 3) that 18 or more species would disappear in one century. We could likewise expect at least 14 of the remaining 82 to vanish in the following century. Continuing the progression, we could expect 80% or more of the species to be gone after a millennium (Fig. 4). Thus, if λ were as large as 0.25, it seems unlikely that speciation would keep pace with extinctions.

Moreover, the patterns for breeding birds strongly suggest that model II overestimates the natural probability of disappearance. Our failure to reject this model for invasive, open-country birds whose diversity had sharply declined because of forest regeneration is clearly a Type II error (failure to reject a false null hypothesis).

At any rate, our tests of null models attach probabilities to an interpretation that is obvious to the field natu-

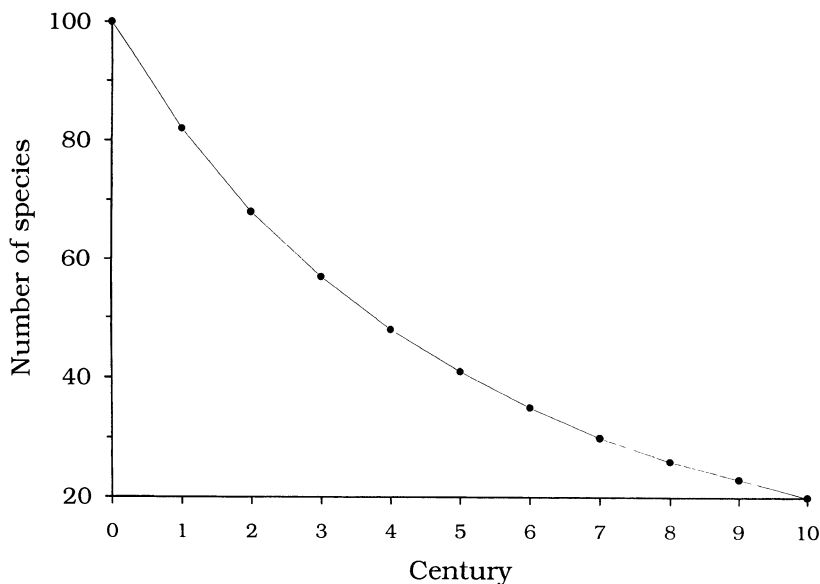


Figure 4. Hypothetical decay in the number of high-elevation species in response to a severe disturbance that recurs once per century. The number of species is that remaining (out of an initial 100) at the end of each century, after extinctions. The progression is based on the binomial distribution (eq. 3) and the assumption that a species ordinarily has a one-in-four chance of disappearing in response to each event (i.e., $\lambda = 0.25$).

ralist. It is extraordinary that half of the anuran species in a large assemblage would simultaneously disappear over a 30-km² area. Furthermore, salamanders have also declined. *Bolitoglossa robusta* and *B. subpalmata*, common before the 1987 crash, have been scarce in recent years. According to Pechmann and Wilbur (1994), "catastrophes" like that of the golden toad and other amphibians abound for everything from seals and sea urchins to desert cacti. We are aware of no other group of organisms, however, in which so many species have vanished from a seemingly intact forest.

Although we would not expect a single study to lay all skepticism to rest, there is sufficient evidence to warrant concern. We therefore call for an end to the debate. Scientific acumen can be brought into play in a manner relevant to conservation only if dialogue and research focus on causes and mechanisms of the declines, implications for biodiversity in general, and possible solutions.

Subtle Threats to Biodiversity

Pechmann and Wilbur (1994) criticized Blaustein and Wake (1990), Wyman (1990), Wake (1991), Wake and Morowitz (1990), and others for implying without justification that amphibian declines go beyond the "general biodiversity crisis." Blaustein (1994), who objected to Pechmann's and Wilbur's interpretation of what had been stated, concluded that the declines are not a distinct phenomenon. An important question, however, is whether all amphibian declines can be attributed to the principal known causes of this crisis—habitat loss and degradation due to *direct* human impacts. Although Pechmann and Wilbur (1994) argued that the answer is quite likely "yes," our results suggest otherwise.

In the early 1980s, when the Monteverde Preserve was one-third its present size and the idea of establishing the adjacent Children's International Rain Forest had not yet been conceived, logging activities threatened to reduce the forest to a small island in a sea of farmland (Pounds & Fogden 1996). There was ample doubt that the Bare-necked Umbrellabird, Ornate Hawk-Eagle, jaguar, mountain lion, and Baird's tapir would persist for long. No one worried, however, about the golden toad: it was locally abundant and its habitat seemed intact. Ironically, of all these endangered species, only the golden toad has vanished. Nevertheless, its disappearance and the larger phenomenon it has come to symbolize are certainly part of a taxonomically broader biodiversity crisis. Snakes and lizards, for example, have also declined at Monteverde, though to a lesser degree than anurans (Pounds in press).

The comparison of anurans and breeding birds helps put the amphibian declines at Monteverde in perspective. The proportion of species missing was much greater for anurans than for breeding birds in general. That for anurans, however, was equivalent to that of open-country birds whose farmland habitat had largely reverted to forest. The absence of any noticeable change in amphibian habitats and the persistence of bird species known to be sensitive to deforestation suggest that subtle but critical changes in the environment have taken place.

Pounds (1991) and Pounds and Crump (1994) hypothesized that warm, dry conditions were a key factor in the 1987 crash. Shortly before this crash, harlequin frogs (*Ateolopus varius*) along the headwaters of the Río Lagarto underwent an unprecedented shift in distribution within the habitat, apparently in response to desiccating conditions. The catastrophic nature of the declines, however, led Pounds and Crump (1994) to hypothesize that unusual

weather had not acted alone. Conditions may, for example, have set the stage for a pathogen outbreak.

Recent analyses suggest that the unusual weather of 1987 was a consequence of the 1986–1987 El Niño and a 24-year trend in the temporal patterns of daily precipitation (Pounds in press; A. Pounds, M. Fogden, & J. Campbell unpublished). This trend appears to be related to a recent bias toward warm sea-surface temperatures in the tropical Pacific, possibly a consequence of greenhouse warming (Graham 1995).

An underlying assumption of our null models is that the outcome of one natural disturbance is ordinarily independent of another—a condition required for application of the binomial distribution (Batschelet 1979). We followed this assumption because the species studied by Bragg (1960) and Pechmann et al. (1991) appeared to recover between events, as would be expected if populations were fluctuating but not declining. Where amphibians have declined, however, the underlying cause could be manifested as an increase in the frequency or intensity of disturbances and a resultant loss of this normal independence of effects.

Unnatural Metapopulation Dynamics?

We gathered 5 years of data before writing this article because in 1990 we expected amphibians to rebound quickly. Most of them have not. Of the 25 species missing in 1990, 80% were still absent at the end of our study in 1994. Observed waiting times for reappearance have thus exceeded those reported by Bragg (1960) and Pechmann et al. (1991). Expected waiting times are unknown, however, and even limited recovery might seem encouraging. Nevertheless, four of the five species that apparently recolonized our study area also inhabited adjacent foothills and lowlands, where we have seen little evidence of declines. Prospects of recovery are dim for montane specialists such as the golden toad (*Bufo periglens*) and the green-eyed frog (*Rana vibicaria*).

Rates of recolonization might naturally be low if there are few local populations per area and individuals disperse over relatively short distances (Travis 1994). Rates might be abnormally low, however, if populations have disappeared over a large area, if surviving populations are reduced in size and number, or if the agents responsible for the declines are still operative. Travis (1994) implied that to interpret the meaning of empty habitats one must be resigned to a long wait, for “even the lower [theoretical] waiting times [for recolonization] can be high in terms of human patience.” The alternative to waiting, however, is to assess declines at the metapopulation level by examining sites on a regional scale.

Following this approach at Monteverde, we have found evidence of a strong departure from normal metapopulation dynamics. Of the anuran species that persisted in our study area after the 1987 crash, many

seemed to lack viable source populations for recolonization of previously occupied sites. Those for which baseline data exist—*Hyalinobatrachium fleischmanni*, *Centrolenella prosoblepon*, and *H. pseudopuma*—were far less abundant than they were before the crash and showed no increase during 1990–1994. Accordingly, *Hyla uranochroa* failed to recolonize three previously inhabited sites despite the presence of small populations within 1 km. Only the terrestrial-breeding *Eleutherodactylus diastema* and many of its congeners not dependent on bodies of water seemed to be recovering.

Comparability and Margins for Error

These forest-dwelling *Eleutherodactylus*, the chief element of the Monteverde fauna that reduces its comparability to the assemblages represented in our null models, also tended to escape regional extinction. Population structure may be a key factor in the relative success of these species. Compared to amphibians associated with bodies of water, they tend to be more continuously distributed, and the comparatively large number of local populations may reduce their vulnerability to stochastic mechanisms of extinction in the wake of deterministic declines.

Inclusion of terrestrial *Eleutherodactylus* in our tests of null models, which are based on aquatic breeders, contributed to the conservative nature of our approach. When we repeated the tests while excluding these species, the results strengthened our conclusion that the number of disappearances exceeded that expected for naturally fluctuating populations. Of the 36 species associated with aquatic habitats, 22 were missing in 1990. Even if species ordinarily have a 45% chance of disappearing in response to a natural disturbance (i.e., $\lambda = 0.45$), we would still reject the null model of no departure from normal population dynamics ($p = 0.038$). If we base our estimate of λ on the patterns reported by Pechmann et al. (1991), the chances that so many species would be missing under normal conditions are less than one in one hundred billion. “Preposterous odds” indeed.

Despite continued field work at Monteverde since the completion of our analyses, we have observed little evidence of additional recovery. None of the anuran species missing throughout 1990–1994 reappeared in 1995–1996. Thus, almost a decade after the multi-species population crash, the amphibian fauna remains impoverished.

Acknowledgments

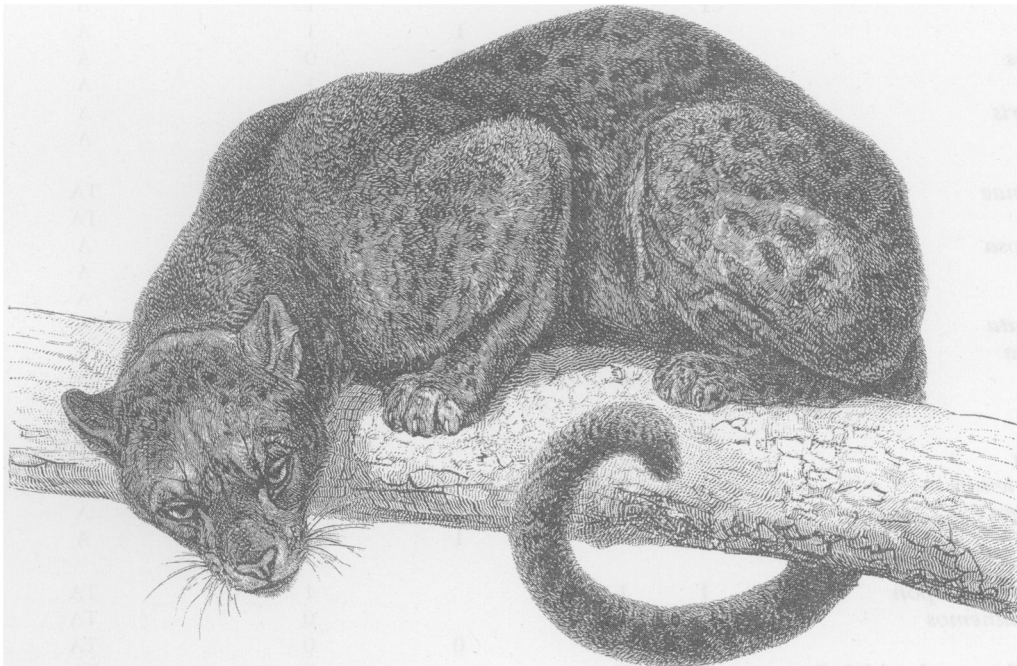
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Appendix

Frogs and toads of Monteverde.

Taxon	Presence-absence in zones A-D ^a				Overall (A-D)	Breeding mode ^b	Habitat ^c
	A	B	C	D			
Microhylidae							
<i>Hypopachus variolosus</i>	0	0			0	A	PSW
Leptodactylidae							
<i>Eleutherodactylus altae</i>			1	1	1	DT	F
<i>E. andi</i>		0	0	0	0	DT	S
<i>E. angelicus</i>	0	0	0	0	0	DT	S
<i>E. biporcatus</i>				0	0	DT	F
<i>E. bransfordii</i>	1	1	1	1	1	DT	F
<i>E. caryophyllaceus</i>				0	0	DT	F
<i>E. cerasinus</i>				0	0	DT	F
<i>E. crassidigitus</i>	1	1	1		1	DT	F
<i>E. cruentus</i>		1	1	1	1	DT	F
<i>E. diastema</i>	1	1	1	1	1	DT	F
<i>E. fitzingeri</i>			1	1	1	DT	F
<i>E. hylaeformis</i>		1	1		1	DT	F
<i>E. melanostictus</i>		1	1		1	DT	F
<i>E. podiciferus</i>	1	1	1		1	DT	F
<i>E. ridens</i>			0	1	1	DT	F
<i>E. rugulosus</i>				0	0	DT	S
<i>E. underwoodi</i>	1	1	1		1	DT	F
<i>Leptodactylus pentadactylus</i>				1	1	TA	PSW
Bufonidae							
<i>Atelopus varius</i>	0	0	0	0	0	A	S
<i>Bufo coccifer</i>	1				1	A	PSW
<i>B. coniferus</i>			1	1	1	A	PSW
<i>B. haematiticus</i>				0	0	A	S
<i>B. marinus</i>	1	1			1	A	PSW
<i>B. melanochloris</i>				0	0	A	S
<i>B. periglenes</i>		0			0	A	PSW
Hylidae							
<i>Agalychnis annae</i>	0	0	0		0	TA	PSW
<i>A. callidryas</i>				0	0	TA	PSW
<i>Anotheca spinosa</i>			0		0	A	PSW
<i>Hyla loquax</i>				1	1	A	PSW
<i>H. miliaria</i>				0	0	A	PSW
<i>H. angustilineata</i>		0			0	A	PSW
<i>H. pseudopuma</i>	1	1	1	0	1	A	PSW
<i>H. rivularis</i>	0	0	0		0	A	S
<i>H. rufioculis</i>	1		0	1	1	A	S
<i>H. tica</i>	0	0			0	A	S
<i>H. uranochroa</i>	0	1	1		1	A	S
<i>Phyllomedusa lemur</i>		0	0	0	0	TA	PSW
<i>Smilisca phaeota</i>				1	1	A	PSW
<i>S. sordida</i>	1			1	1	A	S
Centrolenidae ^d							
<i>Centrolenella prosoblepon</i>	1	1	1		1	TA	S
<i>Cochranella euknemos</i>	0				0	TA	S
<i>C. granulosa</i>	0			0	0	TA	S
<i>Hyalinobatrachium colymbiophyllum</i>	0	0			0	TA	S
<i>H. fleischmanni</i>	1	1			1	TA	S
<i>H. valerioi</i>			0	1	1	TA	S
<i>H. vireovittatum</i>			1	1	1	TA	S
Ranidae							
<i>Rana forreri</i>	0				0	A	PSW
<i>R. vibicaria</i>		0			0	A	PSW
<i>R. warszewitschii</i>	0	0	0	0	0	A	PSW

^aFor presence-absence, 1, present throughout 1990-1994; 0, absent throughout 1990-1994; 0, absent in 1990 but reappeared during 1991-1994; blank, not included in the sample for that zone. A species was omitted from zones where it was not known to occur or was so uncommon before the declines as to be easily overlooked. Likewise, three rare species were omitted altogether (*Hyla fimbriemembra*, *Nelsonophryne aterrima*, and *Eleutherodactylus cuaquero*). A, Pacific slope 1100-1450 m; B, upper slopes and continental divide >1450 m; C, upper Peñas Blancas Valley (Caribbean slope) 950-1450 m; D, lower Peñas Blancas Valley 750-950 m.

^bA, eggs and tadpoles aquatic; TA, eggs out of water, tadpoles aquatic; DT, direct development within encapsulated, terrestrial egg.

^cPSW, ponds and swamps; S, streams; F, forest (independent of bodies of water).

^dAll centrolenids listed were previously included in *Centrolenella*.