
Ecological Traits Predicting Amphibian Population Declines in Central America

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Abstract: *Amphibian populations are declining on all continents on which they occur, but not all species have been affected equally. Populations of some species are extirpated, others have declined but survive, some have not obviously declined, and some are increasing. If amphibian populations at multiple sites were affected by the same factors, then surviving species should share traits that promote persistence, whereas declining species should share traits that promote susceptibility. Identifying these traits can help diagnose potential causes and thus help to direct conservation actions. Using logistic regression, we quantified the vulnerability of amphibian populations in four areas in Central America. We analyzed a species-specific database of taxonomic identity, geographic and elevational range, elevational distribution, adult and larval habitat, activity period, and maximum adult body size. We found that (1) all four sites exhibited the same pattern of decline (there were no interactions between site and other variables); (2) declining populations shared aquatic habitats, restricted elevational ranges, and large body sizes; and (3) there was an interaction between body size and elevational range. The most significant variable in the model was lifetime aquatic index, a factor unrelated to demographic vulnerability and one that therefore might indicate the potential causative agent(s). Our results provide a predictive model with which to assess potential causes of population declines in other areas, and we generated a list of 52 species predicted to decline at a currently unaffected site in central Panama.*

Atributos Ecológicos Predicen Declinaciones Poblacionales de Anfibios en Centro América

Resumen: *Las poblaciones de anfibios están declinando en todos los continentes donde ocurren, pero no todas las especies han sido afectadas por igual. Algunas especies han sido extirpadas, otras han declinado pero sobreviven, algunas no han declinado notablemente y otras están aumentando. Si las poblaciones de anfibios en varios sitios fueran afectadas por los mismos factores, las especies sobrevivientes deberían compartir características que promuevan la persistencia mientras que las especies en declinación deberían compartir características que promuevan la susceptibilidad. La identificación de estas características puede ayudar a diagnosticar las causas potenciales y así ayudar a dirigir medidas de conservación. Utilizando regresión logística, cuantificamos la vulnerabilidad de las poblaciones de anfibios en cuatro áreas de Centro América. Analizamos una base de datos de identidad taxonómica de especies, rango geográfico y altitudinal, distribución altitudinal, hábitat de larvas y adultos, período de actividad y máxima talla corporal de adultos. Encontramos que (1) los cuatro sitios presentaron el mismo patrón de declinación (no hubo interacciones entre el sitio y otras variables), (2) las poblaciones en declinación compartieron hábitats acuáticos, rangos altitudinales restringidos y tamaño corporal grande y (3) hubo interacción entre el tamaño corporal y el rango altitudinal. La variable más significativa del modelo fue el índice de vida acuática, un factor no relacionado con la vulnerabilidad demográfica y que, por lo tanto, podría indicar el agente causal potencial. Nuestros resultados proporcionan un modelo predictivo para evaluar las causas potenciales de declinación poblacional en otras áreas, y generamos una lista de 52 especies de declinación prevista en un sitio actualmente no afectado del centro de Panamá.*

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Introduction

Populations of amphibians across the globe have been declining for many years (Alford & Richards 1999; Houlahan et al. 2000), and given the high endemism and restricted ranges of many Latin American species (Duellman 1999; Savage 2002), some may now be extinct. Hypothesized causes of amphibian declines in Latin America are varied (reviewed by Young et al. 2001) but include habitat loss, climate change (patterns of temperature, rainfall, and UV-B radiation), disease, exotic species (predators, competitors, pathogens), chemical contamination (toxins, endocrine disruption), and potential interactions among several factors. Most declines of amphibians in Latin America have occurred at higher elevation (>500 m) over short periods of time (2–3 years), and have affected about half of the species in a region (Young et al. 2001). Anecdotal evidence suggests that taxa more associated with riparian habitats have declined more than terrestrial species, but this has not been tested. Three general response patterns have been observed among amphibian species at sites of decline: (1) populations decline and disappear, (2) populations decline but persist, or (3) populations do not decline (Pounds et al. 1997; Lips 1998). Causal mechanisms of population susceptibility or survival at a site are unknown, but a combination of species-level traits and environmental characteristics are thought to be involved (e.g., Harries et al. 1996). Although habitat loss and alteration have resulted in the direct loss of amphibian populations, they cannot explain the decline of populations in protected reserves.

This problem is not specific to amphibians: populations of all taxa are disappearing around the globe. Many of these losses are directly or indirectly attributed to human activities (McKinney 1997). In many cases, declining species share ecological, life-history, or demographic traits thought to make them vulnerable to various threats. These traits include restricted ranges, specialized habitats or niches, small population size, fluctuating abundance, long generation times, low reproductive rates, migratory stages, complex life cycles, and large body size (Rabinowitz et al. 1986; Lande 1988; Pimm et al. 1988; McKinney 1997; Williams & Hero 1998; Dulvy & Reynolds 2002; Reed & Shine 2002). These traits are correlated with patterns of extinction in both extant taxa (Brown 1971; Bibby 1994; Angermeier 1995; Bennett & Owens 1997; Foufopoulos & Ives 1999; Jennings et al. 1999) and fossil taxa (Jablonski & Chaloner 1994; Lessa & Farina 1996; McKinney 1997). These traits alone probably do not cause declines, but they make a species susceptible to continued decline following some initial perturbation.

Rarely have amphibian populations been observed during a decline, which would help identify causative agents. Commonly, researchers have returned to sites after absences of months or years and could not find previously abundant species when appropriate habitats were

searched during appropriate times (e.g., Coloma 1995). Because the actual process of decline is rarely observed, analyzing species-specific survival is one of the few ways to identify causes consistent with a particular pattern. This approach also has limitations, however, because the quantity and quality of data vary among sites, species, and researchers. Given financial and logistical constraints, few researchers have been able to investigate the potential role of multiple agents at a particular site. Multidisciplinary research that can simultaneously investigate the roles of various factors at several sites will be most successful at identifying common causes. Until that happens, we are limited to comparing patterns among multiple sites, species, or life stages to determine whether those species that decline share particular demographic or ecological traits. If the same factors cause declines at multiple sites, then surviving species should share traits that promote persistence, whereas species that decline should share a different suite of traits that make them more susceptible to decline (Jablonski 1986; Arita et al. 1990; Laurance 1991; Harries et al. 1996; Davies et al. 2000).

Our objectives were to compare ecological factors between declining and surviving populations of amphibians at four sites that have experienced large-scale amphibian population declines. We assessed the relative contributions of, and interactions among, ecological factors known to influence population declines of animals, as well as specific variables hypothesized to be involved in amphibian population declines. We determined which factor or combination of factors was associated with declining species at all sites and whether sites differed in causal factors. We also used our model to predict which species would decline at El Copé, a site in central Panama, which is thus far unaffected but is geographically and ecologically similar to the sites where declines have occurred. We expected to identify particular demographic traits associated with declines (e.g., McKinney 1997), but we also hoped to find species-specific ecological characteristics correlated with declines that might suggest potential causes. This was especially important because we had data from two sources, one that attributed declines to the effects of global climate change (Pounds et al. 1997, 1999) and the other that attributed declines to a pathogenic fungus (Lips 1998, 1999; Lips et al. 2003).

Methods

Study Sites

MONTEVERDE CLOUD FOREST PRESERVE, PUNTARENAS, COSTA RICA

This 10,500-ha reserve is located at 1400 m elevation in the Cordillera de Tilarán of northwestern Costa Rica (Fig. 1). Habitat is lowland rainforest to premontane rainforest (Holdridge 1982). The average temperature is 19° C,

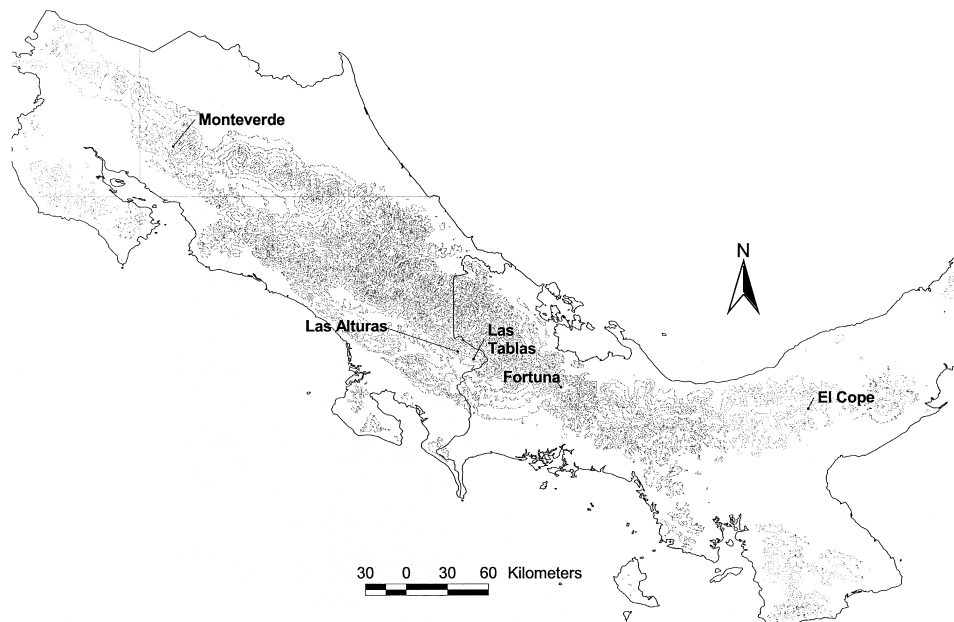


Figure 1. Location of amphibian population study sites (Environmental Systems Research Institute 1993) in Costa Rica and Panama.

with annual rainfall of 2500 mm (Clark et al. 2000). The species composition, abundance, and ecology of the Monteverde amphibian fauna are well known, and extensive, long-term hydrologic, climatic, and land-use data are available (Nadkarni & Wheelwright 2000). We used amphibian decline data published by Pounds et al. (1997) and Pounds and Fogden (2000) to determine the original species richness and patterns of decline among these species (Table 1).

FINCA LAS ALTURAS, PUNTARENAS, COSTA RICA

This field station is located on a private ranch on the Pacific slope of the Cordillera de Talamanca (Fig. 1). The field station is approximately 35 km north of San Vito (8°48'N, 82°55'W) at approximately 1400 m elevation. The station property is adjacent to the Parque Internacional La Amistad (207,000 ha) portion of the Amistad Bio-

sphere Reserve. Land uses include cattle ranching, logging, and small-scale coffee plantations. Rainbow trout (*Onchorhynchus mykiss*) have been introduced to the Río Cotón in both Las Alturas and Las Tablas. Mean annual temperature is approximately 22° C, and mean annual rainfall is 3000 mm. Herpetological collections conducted by K.R.L. and colleagues in the area during 1990–1991 (before decline) documented 26 amphibian species in 21 days (K.R.L., unpublished data). On two trips in 1998 and 2001 (after decline), only 11 species were found in twice the time and four times the area searched. Monitoring continues at 3- to 5-year intervals (Table 1).

ZONA PROTECTORA LAS TABLAS, PUNTARENAS PROVINCE, COSTA RICA

Finca Jaguar, a private farm approximately 40 km north-northeast of San Vito (8°55'N, 82°44'W) is located at 1900 m elevation within the Zona Protectora Las Tablas

Table 1. Amphibian species diversity and survey efforts at each of four decline sites and one unaffected site (El Copé).*

Site	Survey effort	No. species known at site	No. species used in analysis
Monteverde	weekly surveys for 11 years; 16 ponds, 16 streams; 2 × 15 km transect	60	58
Las Alturas	4 visits in 4 years; 45 transects 38 km, 158 hours; 181 captures	31	31
Las Tablas	8 visits in 7 years; 263 transects 108 km, 470 hours; 1460 captures	23	21
Fortuna	8 visits in 8 years; 248 transects 147 km, 347 hours; 992 captures	58	56
El Copé	6 visits in 5 years; 268 transects 82 km, 509 hours; 7286 captures	68	55

*Data from Monteverde are from Pounds et al. (1997) and Pounds & Fogden (2000); all other data from K.R.L. (unpublished data).

in the Cordillera de Talamanca (Fig. 1). The farm supports small-scale cattle ranching and apple orchards but is surrounded by extensive tracts of cloud forest (lower montane rainforest of Holdridge 1982) within the Amistad Biosphere Reserve. Mean annual temperature is 15° C, and mean annual rainfall is approximately 3500 mm. K. Lips has monitored amphibian populations along five streams, three trails, and flooded pastures since 1990 and has compiled a list of 23 amphibian species known from this site during a 3-year study of the natural history of a riparian treefrog (Lips 1995). Lips (1998) described patterns of decline observed in 1993–1994 and provided survey methods at this site. In 1991–1993 (before declines), K.R.L. ran 94 nocturnal transects (37 km, 267 hours) in which she made 1238 frog captures and encountered 23 amphibian species. She has returned five times since declines, during which time she ran 169 transects (72 km, 203 hrs) and captured only 222 individuals of 13 species (Table 1).

RESERVA FORESTAL FORTUNA, CHIRIQUÍ, PANAMA

This is an upland site (1,000–1400 m elevation) about 70 km east-southeast of Las Tablas (8°42'N, 82°14'W). Fortuna is situated in a high valley created by the Río Chiriquí and the joining of the Cordillera de Talamanca from the west and the Cordillera Central from the east (Fig. 1). Rainbow trout were stocked in the nearby Río Chiriquí Viejo in 1925; by 1938 they were abundant at many elevations over 2000 m (Hildebrand 1938). Tilapia and carp were introduced to the lake in 1992. Today, human modifications include a hydroelectric dam, an oil pipeline, and a highway running along the western edge of the 19,000-ha reserve (Lips 1999). Mean annual temperature is about 18° C, and mean annual rainfall is 4500 mm (Cavalier et al. 1996). K. Lips has been monitoring amphibian populations at this site since 1993 and has compiled a list of 57 amphibian species known from this site based on her efforts and those of two biotic surveys conducted in 1976 (Addames 1977) and 1982 (Martínez 1984). K. Lips made two visits prior to die-offs (29 transects, 16.7 km, 48 hours) and made 280 captures of 39 species. Lips (1999) described methods and survey efforts at this site and analyzed patterns of mortality and subsequent population declines during 1996–1997. Lips returned five times following the decline, during which time she ran 169 transects (101 km, 234 hours) and captured 361 individuals of 40 species (Table 1).

PARQUE NACIONAL G. D. OMAR TORRÍJOS H. EL COPÉ, COCLÉ, PANAMA

This 25,275-ha reserve is located (8°40'N, 80°37'17"W) on the eastern end of the Cordillera Central (Fig. 1) at elevations between 500 and 1000 m elevation. Portions of this park were selectively logged in the late 1970s, and amphibian survey transects and collections were done

in this matrix of secondary forest. Land uses in this economically poor province include small-scale agriculture, home gardens, coffee plantations, and some cattle ranching. Mean annual temperature is about 22° C, and mean annual rainfall is estimated at ≤ 3000 mm. K. Lips has been monitoring amphibian populations at this site since 1997. During six visits, she ran 268 transects (818 km, 509 hours) along six streams and four trails, during which time she caught 7286 individuals of 68 species (Table 1).

Data Collection

We used species diversity and abundance data from ongoing monitoring programs conducted by K.R.L. at three decline sites, all located within protected reserves (Las Tablas and Las Alturas, Costa Rica, and Fortuna, Panama; Table 1), and a list of amphibian species and responses to decline from the Monteverde Cloud Forest Preserve in northern Costa Rica (Pounds et al. 1997; Pounds & Fogden 2000). We also used a list of species from ongoing monitoring efforts at Parque Nacional El Copé, Panama (K.R.L., unpublished data), a site similar in composition of habitat and species (Fig. 1) but which has not experienced declines. Currently, all life stages of amphibians are being monitored along permanent terrestrial and riparian transects at all these sites through a combination of diurnal and nocturnal visual and audio surveys. The amount of data collected prior to and following declines varied in the number of years, transects, and species studied for each site (Tables 1 & 2) but was sufficient in terms of area and time expended (Table 1) to document the magnitude of losses observed at other sites in Latin America (Young et al. 2001).

For K.R.L.'s three sites, populations of common species were considered in decline if abundance was reduced by $\geq 75\%$ or, in the case of uncommon but regularly encountered species, if individuals were not found during repeated surveys of the same sites conducted at the same time of the year. A population was not considered in decline if abundance was greater than, equal to, or within 75% of historic levels when the same habitats were resurveyed during the same season. Many tropical frogs have prolonged breeding periods (Crump 1974; Wells 1977), especially many terrestrial *Eleutherodacty-*

Table 2. Amphibian species shared among sites (above diagonal) and numbers of endemic species (italicized, on diagonal) used in the analysis.

	<i>Monteverde</i>	<i>Las Alturas</i>	<i>Las Tablas</i>	<i>Fortuna</i>	<i>El Copé</i>
Monteverde	23	22	9	26	21
Las Alturas		2	11	19	17
Las Tablas			6	7	3
Fortuna				10	37
El Copé					15

lus and stream-breeding species we analyzed. Adults of many riparian species spend their entire lives along streams, do not migrate seasonally to breed, and are often territorial (e.g., Wells 1977; Lips 2001). Likewise, many species of *Eleutherodactylus* have direct development, may reproduce year round (e.g., Crump 1974; Joglar 1998; Donnelly 1999), and do not migrate to breed. Therefore, when intensive surveys produce few individuals of few species, it can often be attributed to population declines rather than to seasonal migration out of the site.

It can be difficult to define population status when populations fluctuate naturally or when individuals show seasonal changes in abundance. This is true not only for amphibian populations but also for many other taxa (e.g., World Conservation Union (IUCN) Red List). In the case of these declines from upland Latin America, however, the magnitude (80–90% of individuals, 50% of species) and rapidity (2–4 years) of these declines and the lack of any subsequent recovery (5–10 years) suggests that our criteria are sufficient to diagnose declines for species we used in our analyses. For the above reasons, and because we conservatively coded each population as either declining (i.e., experiencing population losses of $\geq 75\%$) or not, we are confident in our ability to detect this magnitude of change. This is true for both the number of species and the number of individuals. For example, during a 3-day trip to Fortuna in 1993, K.R.L. found 34 species, whereas on a 20-day trip in 2000 she found only 23 species. As an example of reduced individual abundance, we offer the change in capture rate from an average of 12.5 *Hyla calypsa* per 400 m in 4 months in 1991 to a total of 5 individuals of all species captured at Las Tablas in 7 days in 2001.

A considerable number of species co-occurred at multiple sites, which we treated as replicate observations because there is growing evidence that population risk is generally correlated with species risk (McKinney 1997). Because of the high species overlap among sites (Table 2), our database of species-specific responses at multiple sites in Central America allowed us to construct models with which to predict the persistence of the same or ecologically similar species at a healthy site.

We analyzed specific factors thought to contribute to amphibian population losses, and ecological, demographic, and life-history traits that might be associated with declines. Initially these included demographic traits (e.g., clutch size, longevity) and ecological traits (e.g., body size, dispersal distance) shown to be correlated with population declines in other taxa, as well as traits that might make a species susceptible to particular factors hypothesized to have been involved in declines. For example, because UV-B radiation has been suggested as being involved in some amphibian declines (e.g., Blaustein et al. 1994), we coded each species according to whether it was active during the day or night, hypothesizing that

if UV-B radiation were directly involved in adult mortality at any of these sites, diurnal species might be more likely to decline. For two reasons, we also included habitat used by each species. First, an aquatic pathogenic fungus has been associated with some declines (Berger et al. 1998; Lips et al. 2003). We hypothesized that if this chytrid fungus were involved in declines at any of these sites, then the more aquatic species should decline. Second, reduced rainfall has been proposed as being involved in other Neotropical amphibian declines (e.g., Pounds & Crump 1994; Pounds et al. 1999). If this were true, we hypothesized that species that depend on rainfall or other temporary water sources (e.g., puddle and bromeliad breeders, leaf-litter *Eleutherodactylus* species) might be more likely to decline than those living in permanent water bodies.

We searched the literature for data on all species at each site, but because details on the natural history, reproductive habits, and population demographic features of many upland amphibians are unknown (e.g., Duellman 2001; McCranie & Wilson 2002; Savage 2002), we eliminated from the analysis those traits (e.g., clutch size, longevity, dispersal distance) for which information was not available for a majority of our species. We found published information on 221 populations of 116 amphibian species (100 anuran, 13 salamander, 3 caecilian) belonging to nine families (seven anuran, one salamander, one caecilian) that occurred at one or more of the four decline sites. We included the species' geographic distribution (combined area for those countries where species was reported); the total extent of a species' elevational range (number of meters of elevation inhabited by a species); whether the elevational distribution was low (<500 m), moderate (500–1000 m), or high (over 1000 m); maximum adult body size (mm snout-to-vent length); adult habitat; larval habitat; and activity period (diurnal, nocturnal). We included both total elevational distribution of a species' habitat which might reflect a larger number of populations and thus the probability of recolonization and persistence, and whether a species inhabited a particular 500-m elevational section of the mountain (e.g., low, high), which might indicate the role of UV-B radiation, temperature, or other elevation-specific factors. We coded adult and larval habitat as exclusively terrestrial (1), occupying ponds or multiple habitats (2), or exclusively riparian (3). Adult and larval habitat were correlated (e.g., most terrestrial adults had direct-developing non-aquatic eggs and most riparian adults had riparian eggs and/or larvae), so we averaged the coded values for both stages to produce a lifetime "aquatic index" that ranged from 1 to 3.

Statistical Analyses

We used logistic regression to examine the effect of the independent variables listed above on the probability of

Table 3. Univariate results of logistic regression analysis examining the effect of independent variables on probability of decline.^a

Variable ^b	Coefficient	SE	df	χ^2	p
Lifetime aquatic index	0.988	0.237	1	20.31	<0.0001
Site	—	—	3	12.60	0.0056
Elevational range	-7.83×10^{-4}	3.20×10^{-4}	1	6.31	0.0120
Elevational distribution	—	—	3	9.05	0.0287
ln(max. SVL)	0.701	0.327	1	4.82	0.0282
Family	—	—	4	10.25	0.0364
ln(geographic distribution)	-0.121	0.114	1	1.12	0.2893
Activity period	—	—	2	2.44	0.2960

^aValues of χ^2 and p are from likelihood-ratio tests.

^bAll species are included for each variable except caecilians, which were not included in snout-to-vent length analysis; only species belonging to families Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, Plethodontidae were included in analysis of family.

decline. One goal was to determine which factors, alone and in combination, had significant effects on the probability of the decline. A second goal was to develop a model with which to predict the species likely to decline at El Copé. We constructed models using the model building strategy described by Hosmer and Lemeshow (2000) and conducted all analyses with the logistic regression platform in JMP 4.02 (SAS Institute 2000).

We first examined the relationship between population decline (coded yes or no) and each of eight independent variables: aquatic index, site, elevational range, elevational distribution, maximum snout-to-vent length, family, geographic distribution, and activity period (Table 3). The analysis of family was restricted to the Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, and Plethodontidae because we had sufficient observations only for these families. Maximum snout-to-vent length and geographic distribution both had highly skewed distributions and were log-transformed before analysis (Tabachnick & Fidell 2001). Caecilians were not used in the regression involving snout-to-vent length because their elongated bodies were not comparable to the much shorter frogs and salamanders. We excluded from further consideration variables for which p was >0.25 , eliminating geographic range and activity period and retaining aquatic index, site, elevational range and distri-

bution, maximum snout-vent-length, and family (Table 3). Variables were tested for significance with likelihood-ratio tests.

We next fitted a combined model including all six remaining independent variables. Aquatic index, site, elevational range, and maximum snout-vent-length were statistically significant ($p < 0.05$) and retained for further analysis, whereas family and elevational distribution were eliminated by this criterion. We then fitted models involving these four variables and each pairwise interaction (six total) and tested each interaction for significance ($p < 0.05$). Only one interaction was included per model. A significant interaction was detected only between elevational range and maximum snout-to-vent length. Our final model consisted of the four variables and this one pairwise interaction (Table 4). A chi-square goodness-of-fit test was used to assess the overall adequacy of the model.

We also fitted a model including the same variables as in the final model but excluding site effects to generate predictions about future declines independent of site. As a measure of the model's predictive ability, we calculated the area under the receiver operating characteristic curve (Hosmer & Lemeshow 2000). The model was then used to predict the probability of decline for each of the 55 amphibian species at El Copé. This site is simi-

Table 4. Final logistic regression model of probability of amphibian decline incorporating all variables found significant in previous analyses as well as significant interactions (see text for details).*

Factor	Coefficient	SE	df	Odds ratio	χ^2	p
Intercept	-6.409	1.837	—	—	—	—
Lifetime aquatic index	1.332	0.279	1	14.36	28.70	<0.0001
Site (overall)	—	—	3	—	17.05	0.0007
Fortuna	0.290	0.329	1	1.787	—	—
Las Alturas	0.652	0.416	1	3.687	—	—
Las Tablas	0.353	0.485	1	2.026	—	—
Elevational range	-1.16×10^{-3}	4.20×10^{-4}	1	0.069	9.63	0.0019
ln(max. SVL)	1.587	0.444	1	38.67	14.86	0.0001
Elevational range \times ln(max. SVL)	-2.33×10^{-3}	7.92×10^{-4}	1	0.015	10.06	0.0015
Whole model	—	—	7	—	60.47	<0.0001

*All species except for caecilians are included. Values of χ^2 and p are from likelihood-ratio tests.

Table 5. Numbers of amphibian species and populations and the percentage of those populations that showed declines for each family used in the analysis of the four decline sites.

Taxa	No. species	No. populations	Populations declining (%)
Anurans			
Ranidae	3	7	100
Microhylidae	2	2	100
Dendrobatidae	5	5	80
Hylidae	25	39	74
Bufo	9	19	68
Centrolenidae	6	16	56
Leptodactylidae	33	60	45
Salamanders			
Plethodontidae	13	15	47
Caecilians			
Caeciliidae	3	3	0

lar to the four decline sites in species and habitat composition, but at this point it has not experienced population declines.

Results

When found at multiple sites, a species was similar in its response among all sites, with approximately 68% of species showing the same response at 2 (15 of 22 species), 3 (9 of 13 species), and 4 (4 of 6 species) sites. All families of amphibians were heavily affected by declines (except caecilians), although the percentage of populations affected differed among families (Table 5), as has been reported for both historic and modern extinctions (Harries et al. 1996; Nee & May 1997). Given the large number of ecologically diverse congeners used in our model, we suggest that species-specific traits such

as habitat or reproductive mode obscured any phylogenetic signal in these speciose families. Some of these traits are likely correlated with phylogeny at subfamilial levels (e.g., all *Atelopus* spp. but not all *Bufo* spp. declined), but no well-resolved phylogenies of these families are available.

Our initial logistic regressions showed significant effects for most of the independent variables (Table 3). Habitat, as described by our aquatic index, was the most significant factor associated with decline for every site (Fig. 2a). Patterns of decline were similar in kind but differed in magnitude between Monteverde and the other three sites (Fig. 2b). Both elevational range and elevational distribution were significant in the univariate analysis (Table 3; Fig. 2c). Large frogs declined more than small frogs (Fig. 2d). Neither geographic range nor activity period influenced the probability of decline (Table 3).

We combined all significant factors from the univariate analyses (Table 3) into the final model. Elevational distribution and family were no longer significant and were eliminated, so our final model included only the first four variables in Table 3 and one pairwise interaction (Table 4). A goodness-of-fit test was not significant ($\chi^2 = 158.7$, $df = 155$, $p = 0.401$), indicating that the model provided an adequate description of these data. Examination of the regression coefficients and associated odds ratio suggests that all variables are important in determining the probability of decline, although aquatic index was always the most statistically significant variable. Similar to the univariate results (Table 3; Fig. 2), in the full model probability of decline increased with aquatic index and body size and decreased with elevational range.

There was no interaction between site and any other factor; the effect of site was predominantly to the result of the difference between Monteverde (which had a lower

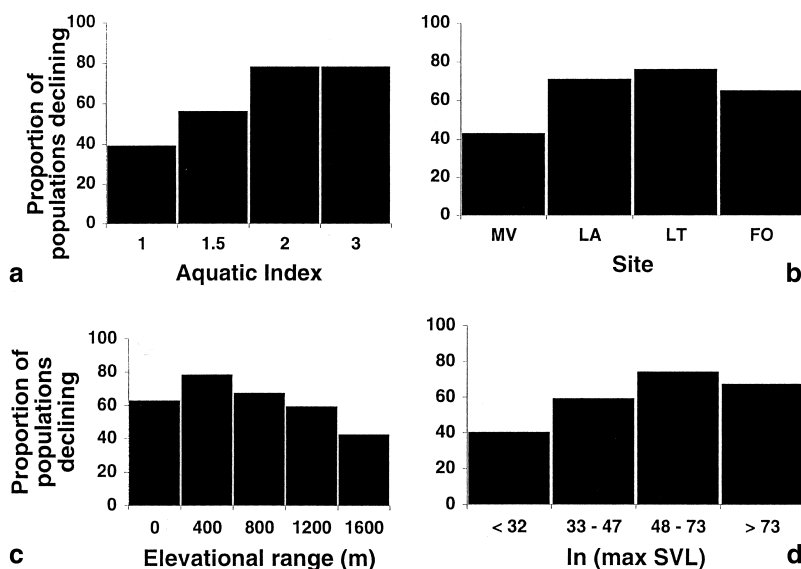


Figure 2. (a) Effect of habitat use on pattern of decline. Aquatic index was the average of adult and pre-metamorphic habitats. Aquatic species were significantly more likely to decline than terrestrial species. (b) Site effect on patterns of decline of amphibian populations. Site abbreviations from left to right represent Monteverde, Las Alturas, Las Tablas, and Fortuna. (c) Effect of elevational range on observed pattern of decline. Endemic species tended to decline, whereas wide-spread species tended to survive. (d) Effect of body size on observed patterns of decline. Categories represent equally sized quartiles of the log-transformed body sizes of all species used in the analysis.

rate of decline) and the other three sites. When the Monteverde data were dropped from the analysis, the site effect was not significant ($p = 0.663$).

There was a significant interaction between body size and elevational range, with a consistent relationship between probability of decline and elevational range for large-bodied frogs, but no consistent relationship for small-bodied frogs. In particular, large body size increased the probability of decline, but this effect was ameliorated by large elevational range. One species, *Bufo marinus*, appeared responsible for much of the interaction: it is extremely large, has a broad elevational range, and did not decline at any site.

We used a reduced model without site effects to predict the probability of decline for the amphibian species at El Copé in central Panama (Appendix 1). The coefficients in the model were similar to those in the full model (Table 4), and the area under the receiver operating characteristic curve was large (0.81), indicating that the model was accurate in predicting which species declined in the data (Hosmer & Lemeshow 2000). The model predicted 33 species as likely to decline ($p \geq 0.67$), 10 species as unlikely to decline ($p \leq 0.33$), and 9 species as intermediate in probability of decline ($0.33 < p < 0.67$). Populations of most riparian species were predicted to decline, as were some pond breeders (e.g., *Leptodactylus pentadactylus*) and terrestrial species with aquatic reproductive modes (e.g., *Dendrobates auratus*). Survivors were those that were exclusively terrestrial (e.g., *Eleutherodactylus caryophyllaceus*, *E. vocator*) and a few species that breed primarily in pools or puddles (e.g., *Bufo marinus*, *Smilisca phaeota*).

Discussion

Extirpation of amphibian populations at four upland sites in Costa Rica and Panama was nonrandom with respect to adult and larval habitat, species' elevational range, site, maximum snout-vent-length, and an interaction between elevational range and maximum snout-vent-length.

Our model indicated that aquatic index, which estimated the degree of dependence on riparian habitats over a species' lifespan, was the most significant factor associated with declines at all sites. This was not unexpected because anecdotal evidence suggested that riparian amphibians were more affected than terrestrial species. At Monteverde, Las Tablas, and Fortuna, for example, most riparian amphibians (including some of the most abundant species) have disappeared and not recovered, whereas many forest frog species have persisted (Pounds et al. 1997; Lips 1998, 1999). This is particularly interesting because this is not a trait traditionally associated with vulnerability to decline for any modern or historic species (McKinney 1997).

Some amphibian declines in Latin America have been attributed to infection by *Batrachochytrium dendrobatidis*, an amphibian-specific aquatic fungus (Berger et al. 1998). This fungus grows best at cool temperatures (15–23° C; J. E. Longcore, personal communication) and was the only pathogen common to all dead frogs collected from Las Tablas, Costa Rica (Lips et al. 2003), and Fortuna, Panama (Berger et al. 1998). Chytrid fungus has not been found in frogs from Monteverde, but Puschendorf (2002) has identified this fungus in two frogs collected from sites geographically intermediate to Monteverde and K.R.L.'s three sites, suggesting that it could be a currently undiagnosed factor at Monteverde.

Patterns of decline among amphibian populations were of the same kind but differed in magnitude between Monteverde and those of south-central Costa Rica and western Panama (Fig. 2b), suggesting that similar factors were involved in declines at all sites. Because there were no interactions between site and any other factor, the reduced level of decline at Monteverde was presumably the result of the larger faunal pool and greater sampling effort, which reduce the chance of concluding that a population has declined. Similar patterns of decline at all sites might indicate that the chytrid fungus was involved in declines at Monteverde, that climatic factors may have indirectly contributed to declines at the three other sites, or that both factors were involved in declines at all sites.

Pounds et al. (1999) detected reductions in rainfall at Monteverde, which, they hypothesized, contributed to population declines of many amphibian, reptilian, and avian populations. Alexander and Eischeid (2001) found, however, that Costa Rica was only slightly drier than normal immediately prior to amphibian population declines and that amphibian declines were not observed when climate was at its most extreme. They concluded that climate change might have indirectly contributed to declines in amphibian populations (e.g., Carey et al. 2001; Kiesecker et al. 2001). It might be expected that terrestrial leaf-litter frogs such as species of *Eleutherodactylus* might be more sensitive to reduced moisture levels, but we found that aquatic species declined more often. Additional studies to investigate species-specific moisture relationships are needed to explore potential mechanisms of decline.

We found no evidence that activity period was directly related to decline, suggesting that UV-B was not a direct cause of adult mortality. We cannot rule out indirect effects of UV-B through interactions with other aspects of the biology of amphibians (e.g., diet, larval ecology, pathogens) or their environment (Middleton et al. 2001).

Elevational range significantly contributed to the probability of decline (Fig. 2c). In Latin America, amphibian endemism is positively correlated with elevation (Campbell 1999), with the result that most endemic species are restricted to mountain tops (e.g., Campbell 1998;

McCranie & Wilson 2002; Savage 2002). Elevational range probably absorbed some of the variation resulting from elevational distribution because we used species-level and not population-level data. Population-specific data should produce more accurate models, but these data were not available.

Catastrophic events, global climate change, disease, introduced predators, or other threats driving the global loss of biodiversity are more likely to cause declines in an isolated, endemic, or otherwise rare species than in a widespread, common species with numerous subpopulations (Brown 1971; Margules et al. 1994; Davies et al. 2000). For example, many documented amphibian population declines have occurred at sites above 500 m elevation. Our model could not discriminate among three hypotheses that could all produce this pattern: (1) rare endemic species (i.e., those with restricted elevational ranges) are more susceptible to extinction than widespread species; (2) high-elevation species (which are the endemic species) were affected by a temperature-sensitive chytrid fungus; and (3) climate change is causing the upward migration and subsequent shrinking or loss of populations (Pounds et al. 1997). The fact that elevational range contributed to declines, but the particular elevation inhabited did not, may indicate the high susceptibility of endemic populations and the importance of recolonization, or that both moderate- and high-elevation populations (as we defined them) may have been affected by the same factors.

Many pond-breeding amphibians from the temperate zone have a metapopulation structure and depend on dispersal among subpopulations for persistence (Berven & Grudzien 1990; Sjogren 1991; Gulve 1994; Alford & Richards 1999). Metapopulation structure might contribute to species persistence at a site and thus confound our ability to detect whether a population persisted or was recolonized, but our analysis could not discriminate between these two processes. Accurate conclusions regarding metapopulation structure and historic dispersal patterns of riparian amphibians depend on population genetic studies because of the difficulty of quantifying long-term movements of adults and the potential contribution of larval dispersal in these open systems.

At high elevations large frogs (e.g., *Eleutherodactylus punctariolus*, *E. bufoniformis*, *Gastrotheca cornuta*) declined, whereas at low elevations large species survived (e.g., *Bufo marinus*, *Smilisca phaeota*). Frogs of all sizes with large elevational ranges survived, suggesting that population density may be important in influencing population survival. For example, large-bodied frogs with small geographic ranges would be doubly handicapped because, all else being equal, they would have a lower density than would small frogs with a range of the same size.

When we applied our model to the database of ecological traits of frogs from El Copé, many species had a high

probability of decline and few had a high probability of survival (Appendix 1). For example, *Bufo marinus* (large elevational range, pond breeder), *Dendrobates minutus* (small body size, bromeliad breeder), and several *Eleutherodactylus* species (e.g., *E. vocator*, *E. bransfordii*, and *E. ridens*; small body size and terrestrial habits) had very low probabilities of decline.

Rare species are statistically more likely to go extinct than common species because rare species generally have some combination of small geographic range, specialized habitat, and low abundance (Rabinowitz et al. 1986). Our results indicate that ecological factors associated with rarity contributed to the probability of decline in this upland tropical frog fauna, but that the most significant factor was lifetime aquatic index, a factor not correlated with rarity (McKinney 1997). We hypothesize that this indicates a possible clue to the cause of declines at all four sites, and propose that chytrid fungal infection is consistent with these patterns, although we cannot rule out other causes, especially as cofactors.

Generally, theories of extinction (e.g., island biogeography) deal with statistical properties of species assemblages and ignore details of ecology and population structure; these theories cannot predict the extinction of individual species (Lande 1988). We must develop predictive models of species-level extinction probabilities for conservation purposes because most legislation operates at the level of species (e.g., the U.S. Endangered Species Act). We restricted our analyses to four similar upland sites to create a predictive model that can be further refined with additional demographic and ecological data or that could be used to analyze species-specific patterns of decline at other Neotropical upland sites (e.g., Ecuador, Venezuela). We encourage application of this model to other data sets to test the generality of these findings to amphibian declines in other habitats (e.g., lowland areas) or on other continents (e.g., Australia).

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Appendix 1. El Copé anuran and salamander species and the probability (in parentheses) of declining as predicted from a full logistic regression model similar to Table 5, but without a site effect.*

Probability of decline		
High (n = 33)	Medium (n = 9)	Low (n = 10)
<i>Atelopus zeteki</i> (1.0)	<i>Colostethus flotator</i> (0.64)	<i>Bufo marinus</i> (0.15)
<i>Bufo coniferus</i> (0.73)	<i>Hemiphractus fasciatus</i> (0.61)	<i>Dendrobates minutus</i> (0.11)
<i>Bufo baematiticus</i> (0.98)	<i>Smilisca pbaeota</i> (0.44)	<i>Eleutherodactylus bransfordii</i> (0.29)
<i>Centrolene euknemos</i> (0.91)	<i>Eleutherodactylus cerasinus</i> (0.36)	<i>E. caryophyllaceus</i> (0.29)
<i>C. ilex</i> (0.92)	<i>E. cruentus</i> (0.37)	<i>E. crassidigitus</i> (0.22)
<i>C. prosoblepon</i> (0.89)	<i>E. fitzingeri</i> (0.61)	<i>E. diastema</i> (0.18)
<i>Cochranella albomaculata</i> (0.87)	<i>E. gaigei</i> (0.55)	<i>E. pardalis</i> (0.18)
<i>C. granulosa</i> (0.88)	<i>E. gollmeri</i> (0.40)	<i>E. podiciferus</i> (0.26)
<i>C. spinosa</i> (0.70)	<i>Bolitoglossa colonnea</i> (0.55)	<i>E. ridens</i> (0.21)
<i>Hyalinobatrachium colymbiophyllum</i> (0.84)		<i>E. vocator</i> (0.14)
<i>H. pulveratum</i> (0.84)		
<i>H. valerioi</i> (0.84)		
<i>C. inguinalis</i> (0.93)		
<i>C. nubicola</i> (0.89)		
<i>C. pratti</i> (0.83)		
<i>C. talamancae</i> (0.75)		
<i>Dendrobates auratus</i> (0.72)		
<i>D. vicente</i> (0.73)		
<i>Gastrotheca cornuta</i> (0.99)		
<i>Hyla colymba</i> (0.97)		
<i>H. palmeri</i> (0.99)		
<i>Phyllomedusa lemur</i> (0.79)		
<i>Eleutherodactylus bufoniformis</i> (0.99)		
<i>E. noblei</i> (0.67)		
<i>E. punctariolus</i> (0.99)		
<i>Leptodactylus labialis</i> (0.77)		
<i>L. pentadactylus</i> (1.00)		
<i>L. poecilochilus</i> (0.88)		
<i>Nelsonophryne aterrima</i> (0.93)		
<i>Bolitoglossa schizodactyla</i> (0.72)		
<i>Oedipina collaris</i> (0.93)		
<i>Oedipina parvipes/complex</i> (0.69)		
<i>Rana warszewitschii</i> (0.69)		

*Species were classified as having a high ($p \geq 0.67$), medium ($0.33 < p < 0.67$), or low ($p \leq 0.33$) probability of declining.