

BIODIVERSITY LOSS

Tropical snake diversity collapses after widespread amphibian loss

Elise F. Zipkin^{1*}, Graziella V. DiRenzo^{1,2}, Julie M. Ray³, Sam Rossman^{1,4}, Karen R. Lips⁵

Biodiversity is declining at unprecedented rates worldwide. Yet cascading effects of biodiversity loss on other taxa are largely unknown because baseline data are often unavailable. We document the collapse of a Neotropical snake community after the invasive fungal pathogen *Batrachochytrium dendrobatidis* caused a chytridiomycosis epizootic leading to the catastrophic loss of amphibians, a food source for snakes. After mass mortality of amphibians, the snake community contained fewer species and was more homogeneous across the study site, with several species in poorer body condition, despite no other systematic changes in the environment. The demise of the snake community after amphibian loss demonstrates the repercussive and often unnoticed consequences of the biodiversity crisis and calls attention to the invisible declines of rare and data-deficient species.

Long-term biodiversity trends indicate that species extinction rates over the past two centuries are up to 100 times higher than throughout the rest of human history (1). Despite tremendous data collection efforts worldwide, empirical evidence of the ecological impacts of these losses is often lacking. Scientists rarely have the ability to predict impending change, precluding the opportunity to collect adequate pre- and postdata to evaluate ecosystem responses to species declines. Yet biodiversity loss can cause cascading effects within ecosystems, such as coextinction of mutualist species, changes in energy flow and primary production, and reduced resiliency to climate and environmental change (2–4).

Without a clear understanding of these cascading sequences, we risk undermining options available for effective conservation (5).

Nowhere has biodiversity loss been more acute than in the tropics, which harbor two-thirds of described species (6). Recent assessments suggest that nearly 12% of animal species in tropical countries are classified as endangered, vulnerable, or near threatened, representing 64% of all such classified species worldwide (7). Amphibians, in particular, have suffered severe declines in the tropics from habitat loss, disease, and climate change (8, 9). Given that amphibians are important as both consumers and prey in aquatic and terrestrial habitats and that their abundance in the tropics can be quite high, the effects of amphibian losses likely permeate to other taxa within ecosystems (10).

We evaluated a Neotropical snake community for changes in species richness, community composition, occurrence rates, and body condition after the mass mortality of amphibians from chytridiomycosis caused by the invasive fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) (11, 12). Snakes are an understudied taxon in which almost one in four

assessed species has an unknown conservation status (13). The diets of tropical snakes include amphibians and their eggs, invertebrates (including oligochaetes and mollusks), lizards, snakes, birds, and mammals, with most species feeding on amphibians to some extent (table S1). Although amphibian declines are likely to negatively affect snakes through the loss of diet items, presumably many species could persist by shifting to other prey.

Our study occurred in Parque Nacional G. D. Omar Torrijos Herrera, 8 km north of El Copé, Panama. The amphibian community at the study site (hereafter “El Copé”) contained >70 species pre-epizootic (11). Amphibian abundance declined by >75% immediately after the *Bd* epizootic in late 2004, with extirpation of at least 30 species (11, 12). The study site is composed of mature secondary forest that remained undisturbed with no systematic changes documented within the abiotic environment (e.g., habitat, water quality, or contaminants; materials and methods). We conducted 594 surveys targeting all amphibians and reptiles on seven permanent transects during the 7 years pre-epizootic (December 1997 to December 2004) and 513 surveys on the same transects during the 6 years post-epizootic (September 2006 to July 2012).

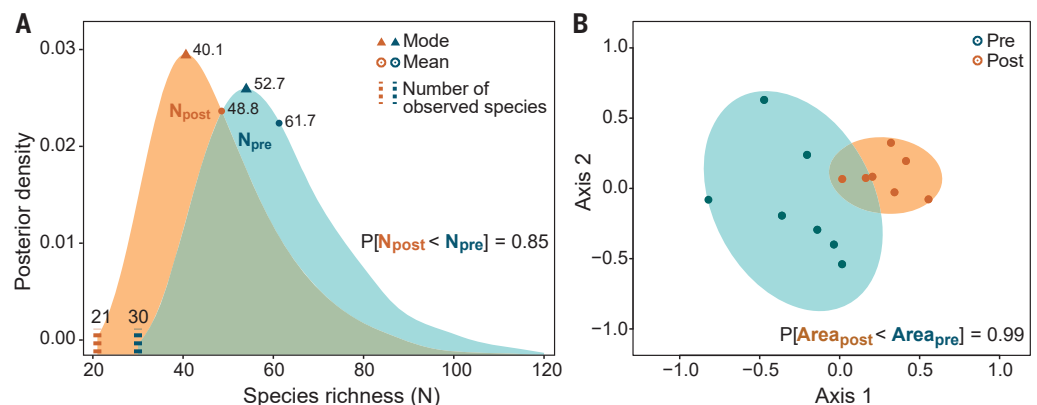
In El Copé, as with many tropical communities, a large fraction of species are rare and most are difficult to detect. For example, of the 36 snake species ever observed on our standardized transect surveys during the 13-year study, 12 were detected only once. In an effort to include the data from rarely observed species while also accounting for imperfect detection and ecological variations among species, we developed a hierarchical community model using a Bayesian approach for parameter estimation (14). Our model estimated occurrence rates, or the probability that both observed and unobserved species used the survey transects, which we utilized to calculate species richness pre- and post-epizootic (materials and

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Fig. 1. Snake species richness and composition before and after the epizootic that led to amphibian loss.

(A) Observed (dashed lines) and estimated snake species richness (posterior density plots with mean and mode) pre-epizootic (N_{pre} , blue) and post-epizootic (N_{post} , orange). (B) Standard ellipses representing observed snake composition pre-epizootic (blue) and post-epizootic (orange). Points within the ellipses show the dimensionless values of community composition for the seven transects pre- and post-epizootic. The smaller area of the post-epizootic ellipse indicates a more homogeneous snake community compared with pre-epizootic.



methods). We focused on estimating probabilities that species diversity and occurrence metrics changed from pre- to post-epizootic rather than reporting absolute values of these metrics, which are inherently imprecise owing to the many rare species within tropical snake communities.

After the epizootic, the total number of observed snake species declined from 30 to 21, with an estimated 0.85 probability that species richness was lower post-epizootic than pre-epizootic (Fig. 1A). Estimated species richness was considerably higher than the number of observed snake species because of a high probability that many species were present and went undetected during sampling. The mean

(61.7 versus 48.8), median (58 versus 45), and mode (52.7 versus 40.1) values of posterior distributions all indicate that snake species richness was higher pre-epizootic than post-epizootic (Fig. 1A), although the 95% credible intervals on richness estimates were wide both pre-epizootic (38 to 105) and post-epizootic (28 to 89). Results of a nonmetric multidimensional scaling analysis show that the observed snake community composition also changed from pre- to post-epizootic, as indicated by a shift of the centroid (0.93 probability of change) and reduction in area (0.99 probability of decrease) of standard ellipses comparing composition across survey transects (Fig. 1B). Collectively, these results reveal that the snake

community has fewer species and is more homogeneous post-epizootic.

Individual snake species responses to the loss of amphibians were variable, but most fared worse post-epizootic. Despite low detection power for many species (figs. S1 and S2), we were able to confidently estimate the probability that occurrence rates changed from pre- to post-epizootic for almost half of the observed snake species (tables S2 and S3). Of the 17 species with at least five total observations, nine had occurrence rates that were lower post-epizootic (with ≥ 0.72 probability), four had occurrence rates that were higher, and the remaining four species experienced no substantial change (Fig. 2). We compared body condition (ratio of mass to snout-to-vent length squared) for the six snake species with at least five samples both pre- and post-epizootic (table S4). Four of the six species had ≥ 0.97 probability of decreased body condition post-epizootic, whereas two had body conditions that increased (Fig. 3). Although there is no single life history or diet attribute that provides a clear explanation of the species results (table S1), snakes that declined post-epizootic may have had a difficult time switching their diets as amphibians declined and prey availability shifted. For example, *Sibon argus*, which has been documented feeding on amphibian eggs at higher levels than the three other *Sibon* species [primarily molluscivores; (15)], experienced the most severe declines of its genus despite otherwise similar habitat requirements and behaviors. Although most snake species were negatively affected by the loss of amphibians, a few exploited this change, increasing in occurrence and/or body condition. Thus, the Bd epizootic indirectly produced a large number of “loser” snake species but also a few “winners,” an ecological phenomenon frequently observed after disturbance leading to biotic homogenization (16).

Our analyses demonstrate that widespread amphibian losses led to a smaller, less diverse

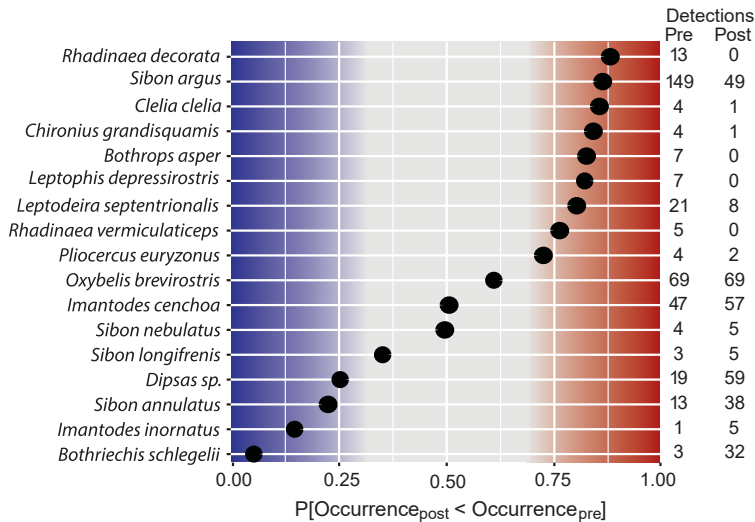


Fig. 2. Changes in snake species occurrence rates after the epizootic that led to amphibian loss. Probabilities (black circles) that occurrence rates were lower post-epizootic than pre-epizootic for the 17 snake species with at least five total detections across both time periods. High values (red-shaded zone) indicate that the occurrence rate decreased after the epizootic, whereas low values (blue-shaded zone) indicate that the occurrence rate increased. The gray zone represents no change. The number of detections pre- and post-epizootic on standardized survey transects is shown for each snake species to the right of the figure.

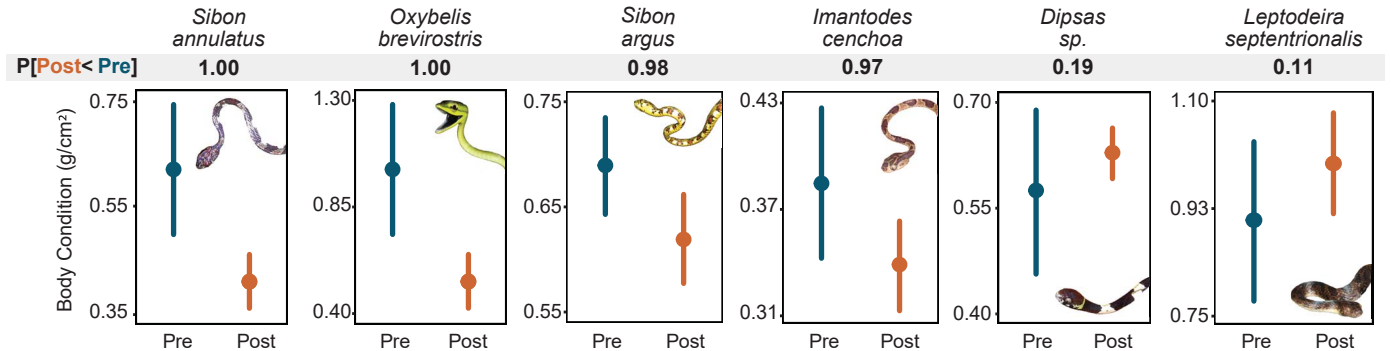


Fig. 3. Average body condition for snake species before and after the epizootic that led to amphibian loss. Body condition for the six snake species with at least five samples available both pre-epizootic (blue) and post-epizootic (orange). Mean values (circles) and 95% credible intervals (lines) are plotted for each species

in both time periods. Probabilities that body condition was lower post-epizootic than pre-epizootic are shown for each species above the individual plots. High probabilities (close to 1) indicate that body condition decreased after the epizootic, whereas low probabilities (close to zero) indicate that body condition increased.

snake community, even with uncertainty in the exact number of species that declined. Although there are no direct effects of the *Bd* pathogen on snakes, many of our focal species (table S1) as well as others in Central America (17) have been observed preying on amphibian adults and/or eggs. Our results suggest that the snake community may be dependent on amphibians for a large portion of their diet and/or the loss of amphibians disrupted the food web to such an extent that other taxonomic groups (e.g., lizards, another major food source) have also declined. The loss of amphibians and snakes might well cascade upward through effects on higher-order predators, such as raptors and mammals (17), potentially causing substantial changes to the food web structure. Indeed, top-down effects from amphibian losses on the food web are well documented, including changes to algae and detritus biomass, reduced energy flow between streams and surrounding forested habitats, and lower rates of nitrogen turnover (10, 18). Together, these results demonstrate the indirect and cascading effects of the invasive *Bd* pathogen and highlight the negative consequences of amphibian losses on other taxonomic groups through both top-down and bottom-up processes.

The extent of global biodiversity loss is likely underestimated because cascading effects of disappearing species can lead to invisible declines of sympatric species. Tracking these processes is particularly challenging because certain taxa and geographic locations are understudied,

resulting in data deficiencies. However, data deficiencies can also arise because some species are rare or have elusive behaviors and life history strategies, such that it can be difficult to quantify species losses even with extensive sampling and advanced statistical models. Despite a lack of data for many species, it is clear that biodiversity loss is a global problem (1). Our results suggest that ecosystem structures could deteriorate faster than expected from indirect and cascading effects generated by disease, invasive species, habitat loss, and climate change. Fast-moving policies are essential for effective adaptation to ongoing species changes and to mitigate the impacts of the world's biodiversity crisis (19).

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ACKNOWLEDGMENTS

We thank the many people who contributed to data collection. L. Brown, M. Farr, S. Saunders, A. Shade, A. Wright, and E. Zylstra provided comments on the manuscript, and M. Newman helped with figure design. **Funding:** E.F.Z. was funded by NSF EF-1702635 during model development. G.V.D. was supported by NSF PRFB-1611692. Field work was funded by NSF DEB-0717741 and DEB-0645875 to K.R.L. and IBN-0429223, IBN-0429223, and IOB-0519458 to J.M.R. and A. Savitzky. The Smithsonian Tropical Research Institute and Ministerio de Ambiente provided logistical support in Panama. **Author contributions:** All authors conceived of the research. K.R.L. and J.M.R. led data collection. E.F.Z., G.V.D., and S.R. built the models. All authors contributed to the interpretation of results. E.F.Z., G.V.D., and K.R.L. wrote the paper. All authors contributed edits. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data and code are available at <https://zipkinlab.github.io/#community2020Z> and are archived at Zenodo (20).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/367/6479/814/suppl/DC1
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Supplementary Text
Figs. S1 and S2
Tables S1 to S4
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2 July 2019; accepted 23 January 2020
10.1126/science.aay5733

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Science **367** (6479), 814-816.
DOI: 10.1126/science.aay5733

Cascading impacts of prey loss

The global pandemic caused by the amphibian fungal pathogen *Batrachochytrium dendrobatidis* has decimated frog populations around the world. This decline has been called out as a potential catastrophe for amphibian species. What has been less explored are the impacts of amphibian declines on other members of their ecological communities. Using survey data collected over 13 years, Zipkin *et al.* looked at diversity and body condition of a tropical snake community heavily affected by chytridiomycosis. They found that affected snake communities were less diverse and most species were in decline, except for a few "winning" species.

Science, this issue p. 814

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Supplementary Materials for
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Published 14 February 2020, *Science* **367**, 814 (2020)

DOI: 10.1126/science.aay5733

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Materials and Methods

Study Site

Our study site is a 4 km² area within the Parque Nacional G. D. Omar Torrijos Herrera, a protected national park located 8 km north of the town of El Copé de La Pintada, Coclé Province in central Panama (8° 40' N, 80° 37' 17" W [21; see 22 for site map]). The park is located on the Continental Divide, while the study area is contained entirely on the Atlantic facing slope at the top of the watershed with a mean elevation of 750 m. Average temperature and cumulative precipitation do not vary considerably within the annual cycle, although May to November tends to have higher rainfall (23). The national park is comprised primarily of mature secondary forest cover and contains several connected streams within the same tributary. Although the study site occurs within the protected area, land use surrounding the park includes small-scale agriculture, home gardens, coffee plantations, and cattle ranching (21).

Amphibian abundance at the study site (hereafter “El Copé”) declined rapidly in late 2004 following the arrival of the amphibian-killing fungus *Batrachochytrium dendrobatidis* (*Bd*), the causative agent of chytridiomycosis (9, 11, 12, 24). Prior to the arrival of *Bd*, the abundance of amphibians at El Copé had been stable from at least 1997 (the first year for which data are available; 12). *Bd* spread quickly to all environments and species (25), causing amphibian mass mortality and the eventual extirpation of 40% of amphibian species (11, 26). Our study took place from 1997 to 2012 during which no systematic changes to the abiotic environment and habitat of this remote site have been documented by any of the long-term studies in the area (11, 25, 27). Water quality, exotic predators, land-use, and commercial harvesting all remained constant or varied randomly before, during, and immediately after the loss of amphibians, with no evidence that mortality was caused by contaminants (12). There are also no industries or intensive large-scale uses of agrochemicals affecting this area, and although wind could transport contaminants, prevailing winds do not originate from urban or agricultural areas (reviewed in 12). Thus, the only major change documented in El Copé during our study period was the catastrophic loss of amphibians caused by the *Bd* epizootic in late 2004 (10, 11, 12, 18, 23, 24, 27).

Data Collection

All amphibians and reptiles were surveyed repeatedly along four stream (each ~200 m) and three terrestrial (each ~400 m) transects every year from December 1997 to July 2012 (11, 12, 21, 22, 24). Field teams of two to eight people (typically two) conducted encounter surveys by slowly walking each transect and using visual and audio cues to locate amphibians and reptiles within two meters horizontal distance and three meters vertical distance from the stream bank or trail. Our analyses excluded records that could not be identified to the species level (note that *Dipsas* *sp.* denotes a single species that is yet to be described). When possible, we captured snakes and measured their snout-to-vent length (cm) and mass (g). Surveys occurred throughout the entire year with the most effort annually in June and July. For all analyses, we excluded data from January 2005 to August 2006 following the peak of the epizootic (end of 2004). We expected the snake community to be in flux during this time following a temporal lag from the loss of amphibians, and thus in a transitory state. We conducted a total of 594 surveys in the time

period pre-epizootic (1997-2004; with an average of 84 ± 22 [mean \pm SE] surveys per transect) and 513 surveys post-epizootic (2006-2012; with an average number of 73 ± 39 [mean \pm SE] surveys per transect).

Statistical Analyses

Our objective was to compare snake species richness and community composition in El Copé before (1997-2004) and after (2006-2012) the epizootic. For species with sufficient data (see Main Text), we also evaluated whether there were changes in species-specific occurrence rates and body condition.

We conducted all analyses using a Bayesian approach with Markov chain Monte Carlo (MCMC) in the programs R (28) and JAGS (29) unless otherwise indicated. Bayesian inference methods are especially appropriate for our analyses as sample sizes at both the species and community levels were generally low. Using a Bayesian approach allowed us to calculate probabilities of decline or change in parameter estimates post-epizootic as compared to pre-epizootic. For each model, we used independent, diffuse prior distributions (as suggested by 30, 31) and assessed convergence using the \hat{R} statistic and through visual examination of the MCMC chains (32). Models are described below with the JAGS code provided in the Supplementary Text.

Community occurrence model. We developed a hierarchical community model (33) to estimate snake occurrence rates and species richness pre- and post-epizootic (Supplementary Text: Code S1). As compared to traditional approaches for quantifying biodiversity, community occurrence models are powerful tools because they preserve the identity of individual species while accounting for variable and imperfect species detection (34, 35 [Chapter 11]). Community occurrence models also lead to increased precision on inferences of rare and elusive species by assuming that species-specific parameters are random effects drawn from community-level distributions (36).

Species occurrence on a transect $Z_{i,j,t}$ is a binary variable in which $Z_{i,j,t} = 1$ if species i occurs on transect j during time period t , and zero otherwise. The occurrence state is assumed to be the outcome of a Bernoulli random process where $Z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t} \cdot w_{i,t})$ and $\psi_{i,j,t}$ is the probability that species i occurs on transect j during time period t . The parameter $w_{i,t}$ indicates whether species i exists within the El Copé snake community in time period t (i.e., pre-epizootic and post-epizootic). We specified the occurrence model using a logit-link function where $\text{logit}(\psi_{i,j,t}) = u_{i,t}$. We assumed that each of the intercept values ($u_{i,t}$, species occurrence rates in time period t , on the logit scale) were drawn from a community-level normal distribution with means, μ_t , that differed based on the time period t with a shared variance, σ^2 such that $u_{i,t} \sim N(\mu_t, \sigma^2)$.

The data, $X_{i,j,t,k}$, consist of a one if species i is observed on transect j during time period t and survey replicate k and a zero otherwise. True occurrence of a species on a transect, $Z_{i,j,t}$, is observed imperfectly. Repeated sampling on transect j on multiple occasions ($k > 1$) over a period of time when the community remains closed (i.e., no changes in occurrence) allows for the distinction between species absence and non-detection. For our study, we assumed that snake species occurrence status remained closed within each time period t but could change between the pre- and post-epizootic

time periods. Tropical snake species are fairly long-lived and stationary with small home ranges (37, 38); thus, our closure assumption is reasonable and consistent with previous research (39). However, a more accurate interpretation of occurrence in this case is whether a snake species “used” the habitat on a transect at some point during the specific time period. In such cases, the occurrence rate parameter $\psi_{i,j,t}$ can be interpreted as the probability that species i used transect j during time period t .

We define the detection model as $X_{i,j,t,k} \sim \text{Bern}(p_{i,j,t,k} \cdot Z_{i,j,t})$, where $p_{i,j,t,k}$ is the detection rate (i.e., probability) of species i on transect j in time period t during survey replicate k , given that the species is present ($Z_{i,j,t} = 1$). Thus, detection is a fixed zero when a species is not present because $Z_{i,j,t} = 0$ in that case. We modeled species detection using a logit-link function where: $\text{logit}(p_{i,j,t,k}) = v + \rho(u_{i,t} - \mu_t)$ in which v is the detection rate (on the logit scale) for species with average occurrence rate (i.e., μ_t) and ρ is an effect based on the species’ occurrence rate. Thus, the model assumes that species detection is correlated with its occurrence (e.g., increased occurrence generally means higher abundance which leads to higher detection; 36, 40, 41, 42). For positive values of ρ (the *a priori* expectation and indeed the outcome in the snake community [Table S3]), detection increases with occurrence. The inclusion of ρ in our model allows for estimation of detection rates that vary across species and time periods without including a large number of additional species-level parameters that would be inestimable given the constraints of our data (i.e., large numbers of non-detections for many species). Thus, a species’ detection rate may change from pre- to post-epizootic based on changes in its occurrence rate, but species detection is constant across transects and survey replicates within a given time period.

To estimate species richness in time period t (N_t) including the number of species not observed (but present) during sampling, we augmented the data with m all-zero encounter histories, where m is a constant that is much greater than n , the total number of species observed ($n = 36$) across both time periods (33, 43). The value of m is not critical, but it should be larger than the possible size of the community. We set $m = 200$, such that maximum possible richness was above the known number of snake species in Panama (44) and much higher than we would expect at a single study site. We then define N_t as a random variable that comes from a uniform distribution:

$N_t \sim \text{uniform}(0, M)$, where $M = n + m$. The probability a species i exists within the community in time t , $w_{i,t}$, is characterized by a Bernoulli random process in which $w_{i,t} \sim \text{Bern}(\Omega_t)$ for species $i = 1, 2, \dots, n, n + 1, \dots, N_t, N_t + 1, \dots, M$. The parameter Ω_t describes the probability that species i is a true member of the community during time period t and is estimated with all other parameters in the model (14, 43). If $w_{i,t} = 1$ then the species is a member of the community and the occurrence rate is $\psi_{i,j,t}$ because $Z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t} \cdot 1)$. However, if $w_{i,t} = 0$, then the species is not present in the community at time t and the occurrence rate on any transect is a fixed zero as $Z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t} \cdot 0)$. We calculated species richness including unobserved species by summing the $w_{i,t}$ values separately for each time period (t) pre- and post-epizootic.

We did not include amphibian abundance as a covariate in the model because the number of amphibians observed on transects is essentially a binary predictor between pre- and post-epizootic time periods (i.e., average of 58 amphibians captures per survey in the years prior to the epizootic versus 3.5 amphibian captures per survey in the years

following the epizootic; 11). In early iterations of the model, we explored adding covariates to the occurrence (e.g., habitat: stream versus terrestrial, length of transect) and detection (e.g., time spent on a survey, number of people conducting survey, survey time period) components of the model. However, convergence was poor in models with covariates and estimates were extremely imprecise.

We evaluated the fit of our model to the snake community data using a posterior predictive check (32 [Chapter 8]) with a Bayesian p-value (35 [Chapter 2], 36). To do this, we defined a discrepancy measure (D) as the sum of the observed data minus their expected values squared. A similar discrepancy metric is computed for a simulated dataset (D_{sim}) generated using the parameter estimates from the model. Both discrepancy metrics were then computed for each iteration of the MCMC algorithm. The Bayesian p-value is defined as the probability that $D > D_{sim}$ in which extreme values (e.g., less than 0.05 or greater than 0.95) indicate poor model fit. The Bayesian p-value for our community model was 0.64, indicating that the model is appropriate for the data.

We compared the posterior distributions of the species richness estimates to make inferences on the probability that species richness was lower post-epizootic than pre-epizootic. To do this, we subtracted species richness estimates ($N_{post} - N_{pre}$) for each iteration of the MCMC and calculated the proportion of iterations that were negative. This proportion is interpreted as the probability that species richness is lower post-epizootic than pre-epizootic. We similarly calculated the probability that occurrence rate for each species was lower post-epizootic than pre-epizootic. As detection probabilities were quite low, we calculated the power to detect each species pre- and post-Bd as $1 - (1 - p_{i,t})^{\bar{K}_t}$ where \bar{K}_t is the average number of surveys conducted per transect in time period t (e.g., $\bar{K}_{pre} = 84$ and $\bar{K}_{post} = 73$). Thus, we define detection power as the probability of observing a species on at least one survey occasion conditional on that species using a transect within a given time period.

Community composition ordination analysis. We used a non-metric multidimensional scaling analysis (NMDS; 45) and a multivariate normal t -test (32) analyzed with a Bayesian approach to determine if snake community composition on transects: 1) changed between the time periods pre- and post-epizootic by comparing the centroids of standard ellipses and 2) was more homogeneous post-epizootic than pre-epizootic by comparing the area of the standard ellipses (Supplementary Text: Code S2). We pooled the data for observed snake species into an array $Y_{i,j,t}$ in which $Y_{i,j,t} = 1$ if species i was detected at transect j at any time during time period t and zero otherwise. Thus, for this analysis, we only considered species that were observed during sampling. We ran the NMDS using the Jaccard dissimilarity index and extracted estimates of transect-level snake assemblage composition (45). Points closer in phase-space have more similar community composition than points further apart. The final NMDS was conducted in two-dimensions and had a stress of 0.16. Using the extracted values, we ran a multivariate normal t -test to evaluate if the mean and variance of the two-dimensional points for each of the seven transects differed pre- and post-epizootic. We used the covariance matrix and centroid mean estimates from the t -test to create standard ellipses with the ellipse package in R (46) for each time period (pre-and post-epizootic).

To determine the probability that the centroids of the standard ellipses were different pre- and post-epizootic, we calculated the Euclidean distance between the centroids of the

standard ellipses pre- and post-epizootic, and then compared that distance to the distance between the standard ellipses pre-epizootic and a null distribution. The null distribution was generated using values from the posterior of the centroid estimates pre-epizootic. Then, we calculated the proportion of iterations in which the Euclidean distance between the centroids of the standard ellipses pre- and post-epizootic was greater than the distance of the centroids of the standard ellipses pre-epizootic and a null distribution. The results of this analysis can be interpreted as the probability that the centroids of the standard ellipses pre- and post-epizootic are more different than would be expected by chance.

To determine the probability that the area of the standard ellipse post-epizootic was smaller than the area of the standard ellipse pre-epizootic, we used the values of the covariance matrix as estimated in the multivariate *t*-test pre- and post-epizootic. We calculated the eigenvalues of the covariance matrix for each iteration of the MCMC. The eigenvalues represent the variance magnitude in the direction of the largest spread of the data. We took the square root of the eigenvalues to calculate the standard deviation. We then calculated the proportion of MCMC iterations in which the standard deviation is smaller post-epizootic as compared to pre-epizootic to determine the probability that the two values were different, similar to the approach for estimating differences in species occurrence and richness in the hierarchical community model.

Body condition analysis. We defined body condition using Quetelet's Index (47): as an individual snake's mass divided by standardized snout-to-vent length squared. Body condition data were difficult to obtain for many observed snakes and thus, sample sizes were low. We augmented our dataset with additional data collected on opportunistic surveys during the same time periods (i.e., snakes observed on permanent transects but not during a standardized survey period or on trails leading to permanent transects). The effort to obtain snake body condition data (particularly within opportunistic surveys) increased after the arrival of *Bd*, leading to larger sample sizes post-epizootic (Table S3). We limited the body condition analysis to the six species that had at least five captures (i.e., body condition samples) pre-epizootic and five captures post-epizootic. While many snake species are sexually dimorphic, there is no evidence that diet differs by sex. We did not have information on sex for many individuals in our sample. As such, our analyses implicitly assume that the sex ratio of species (or individuals captured) did not change from pre- to post- epizootic.

We used *t*-tests (32), run separately for each species using a Bayesian approach, with body condition as the response variable and time period (pre- versus post-epizootic) as the explanatory variable (Supplementary Text: Code S3). Given the small sample sizes, we assumed equal variances for each species across the two time periods. To estimate the probability that body condition for each snake species was higher pre-epizootic as compared to post-epizootic, we calculated the proportion of MCMC iterations in which mean body condition pre-epizootic minus mean body condition post-epizootic was positive (i.e., greater than zero).

Supplementary Text

Code S1.

JAGS code for the hierarchical community occurrence model to estimate snake species occurrence and richness during the time periods before and after the epizootic that lead to amphibian mass mortality. The model also estimates detection rates for each species in the two time periods. We ran three chains for a total length 208,343 after a burn-in of 166,677, and thinned the posterior chains by 25, which left 5,000 samples to approximate the posterior distribution. The number of iterations and burn-in were decided using an update function, allowing us to run a minimum number of iterations to achieve convergence. The model is described in the *Community occurrence model* section of the Materials and Methods.

```
model {
# Indexing: species = i, t = time period, j = transect,
# k = sampling event

# Define prior distributions for community-level model
# parameters: omega (probability that a species is a true
# member of the community), u.mu (average species occurrence
# probability), u.sigma (standard deviation on occurrence
# among species) v.mu (average species detection probability),
# rho (correlation between occurrence and detection)

# Note dnorm(0, 0.368) creates a uniform probability between 0
and
# 1 when transformed to the logit scale following Lunn et al.
(2012)

for (t in 1:nPeriod){
  omega[t] ~ dunif(0,1)
  u.mu[t] ~ dnorm(0, 0.368)
}

v.mu ~ dnorm(0, 0.368)
u.sigma ~ dgamma(0.1, 0.1)
u.tau <- 1/(u.sigma*u.sigma)
rho ~ dnorm(0,0.368)      }

# Specify the likelihood for the community model

for (i in 1:nSum){
  for (t in 1:nPeriod){

# Define the species-level prior distributions
w[i,t] ~ dbern(omega[t])
u[i,t] ~ dnorm(u.mu[t], u.tau)

# Create a loop to estimate the Z matrix (true occurrence
# for species i at transect j in time period t)
```

```

    for (j in 1:nTran){
      # psi = species occurrence probability
      logit(psi[i,j,t]) <- u[i,t]
      psi.mu[i,j,t] <- psi[i,j,t]*w[i,t]
      Z[i,j,t] ~ dbern(psi.mu[i,j,t])
    }
  }
  for (k in 1:nSamples) {
    # Estimate species detection using the data matrix X
    logit(p[k,i]) <- v.mu + rho*(u[i,period[k]]-
      u.mu[period[k]])
    mu.p[k,i] <- p[k,i]*Z[i,transects[k],period[k]]
    X[k,i] ~ dbern(mu.p[k,i])

    # Create simulated dataset to calculate the fit statistic,
    # the Bayesian p-value discrepancy measure
    Xnew[k,i] ~ dbern(mu.p[k,i])
    d[k,i]<- abs(X[k,i] - mu.p[k,i])
    dnew[k,i]<- abs(Xnew[k,i] - mu.p[k,i])
    d2[k,i]<- pow(d[k,i],2)
    dnew2[k,i]<- pow(dnew[k,i],2)
  }
}

# Calculate the discrepancy measure, defined as
# mean(p.fit > p.fitnew) using only observed species (1-36)
p.fit<-sum(d2[1:nSamples,1:36])
p.fitnew<-sum(dnew2[1:nSamples,1:36])
p.diff<-step(p.fit - p.fitnew)
}

```

Code S2.

JAGS code for the multivariate *t*-test using observed snake species composition across all transects to determine if standard ellipse centroids and areas (as estimated from a non-metric multidimensional scaling analysis) differed pre- and post-epizootic. We ran three chains of length 15,000 with a burn-in of 5,000, thinned the posterior chains by 5, and an adaptation length of 10,000. The model is described in the *Community composition ordination analysis* section of the Materials and Methods.

```
model {
# Indexing: transect = i
# Define the (uninformative) priors for the parameters
# Pre
# Variance-covariance matrix
sigma.pre[1] ~ dgamma(0.01, 0.01)
sigma.pre[2] ~ dgamma(0.01, 0.01)
rho.pre ~ dunif(-1, 1)
# Mean/centroid location
mu.pre[1] ~ dnorm(0, 0.01)
mu.pre[2] ~ dnorm(0, 0.01)

# Post
# Variance-covariance matrix
sigma.post[1] ~ dgamma(0.01, 0.01)
sigma.post[2] ~ dgamma(0.01, 0.01)
rho.post ~ dunif(-1, 1)
# Mean/centroid location
mu.post[1] ~ dnorm(0, 0.01)
mu.post[2] ~ dnorm(0, 0.01)

# Likelihood for multi-variate normal t-test
for(i in 1:7){
  # Pre-Bd
  y.pre[i,1:2] ~ dmnorm(mu.pre[1:2], prec.pre[1:2, 1:2])

  # Post-Bd
  y.post[i,1:2] ~ dmnorm(mu.post[1:2], prec.post[1:2, 1:2])
}

# Construct covariance matrix and corresponding precision matrix.
# Pre
prec.pre[1:2,1:2] <- inverse(cov.pre[,])
cov.pre[1,1] <- sigma.pre[1] * sigma.pre[1]
cov.pre[1,2] <- sigma.pre[1] * sigma.pre[2] * rho.pre
cov.pre[2,1] <- sigma.pre[1] * sigma.pre[2] * rho.pre
cov.pre[2,2] <- sigma.pre[2] * sigma.pre[2]
# Post
prec.post[1:2,1:2] <- inverse(cov.post[,])
cov.post[1,1] <- sigma.post[1] * sigma.post[1]
cov.post[1,2] <- sigma.post[1] * sigma.post[2] * rho.post
cov.post[2,1] <- sigma.post[1] * sigma.post[2] * rho.post
cov.post[2,2] <- sigma.post[2] * sigma.post[2]
}
```

Code S3.

JAGS code for the *t*-tests to determine if snake body condition (mass divided by standardized snout-to-vent length squared) differed for the six species with a sufficient number of samples both pre- and post-epizootic. We ran three chains of length 10,000 with a burn-in of 5,000, thinned the posterior chains by 5, and an adaptation length of 10,000. The model is described in the *Body condition analysis* section of the Materials and Methods.

```
model {
# Indexing: species = i, individual = j

for (i in 1:nSpecies) {

  # Define the (vague) priors for the parameters
  # Means pre- (mu1) and post- (mu2) Bd
  mu1[i] ~ dnorm(0,0.01)
  mu2[i] ~ dnorm(0,0.01)

  # Standard deviation (sigma) and precision (tau)
  sigma[i] ~ dunif(0, 10)
  tau[i] <- 1 / (sigma[i] * sigma[i])

  # t-test likelihood
  # y1 is the body condition data pre-Bd
  for (j in 1:n1[i]) {
    y1[i,j] ~ dnorm(mu1[i], tau[i])
  }

  # y2 is the body condition data post-Bd
  for (j in 1:n2[i]) {
    y2[i,j] ~ dnorm(mu2[i], tau[i])
  }

  # Derived quantity to estimate the probability
  # that average species-specific body condition changed
  delta[i] <- mu1[i] - mu2[i]

  # Calculate if delta is positive
  P.delta[i] <- step(delta[i])
}
}
```




Fig. S1.

Power to detect the 36 observed snake species before and after the epizootic that led to amphibian mass mortality (listed alphabetically). Detection power was calculated using the average number of surveys per transect: 84 in the seven-year period pre-epizootic (blue) and 73 in the six-year period post-epizootic (orange). Mean estimates (points) with 50% (thick lines) and 95% (thin lines) credible intervals shown.

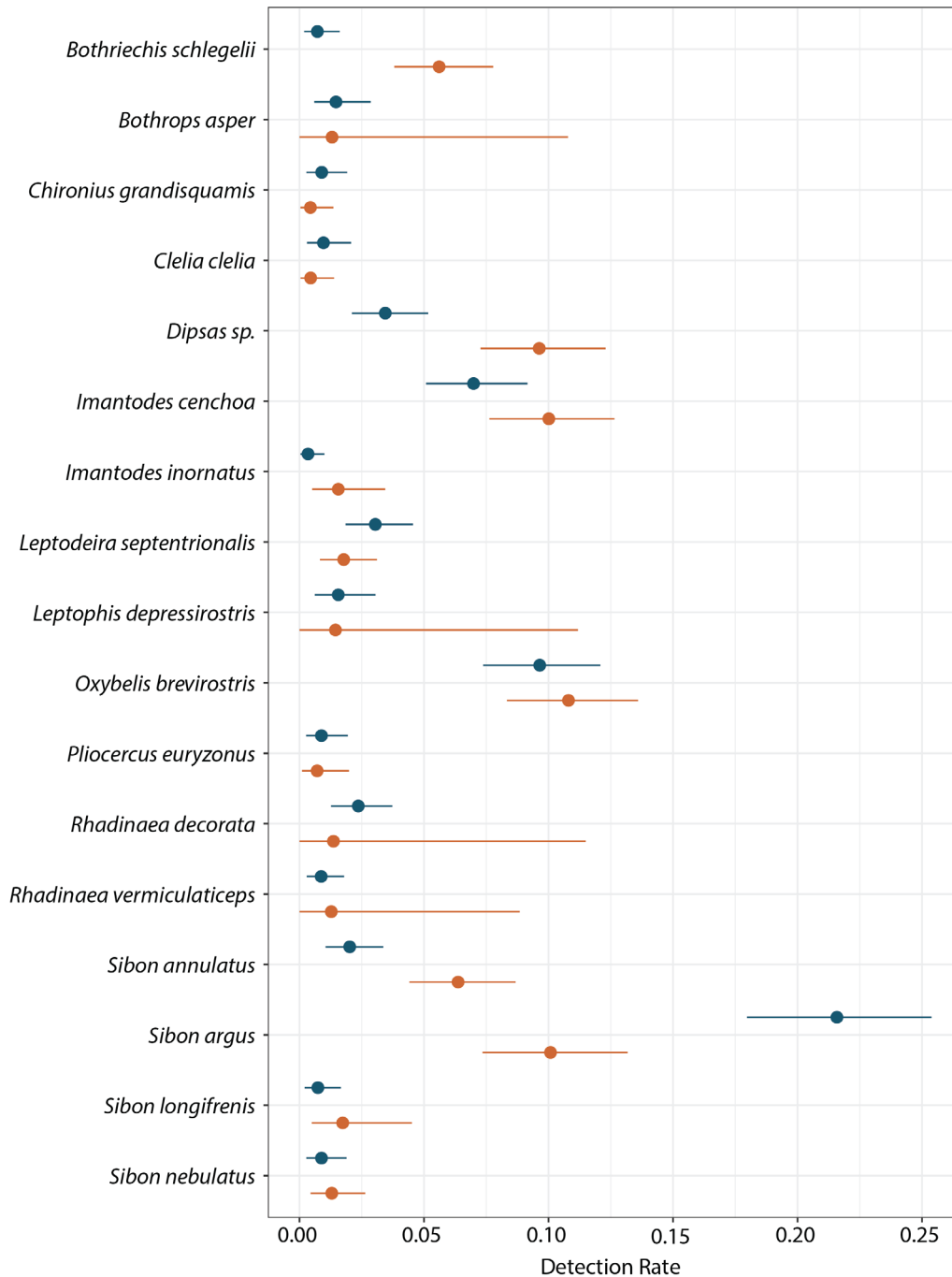


Fig. S2.

Detection rates for the 17 snake species with at least five total detections before and after the epizootic that led to amphibian mass mortality (listed alphabetically). Detection rates are calculated as the probability that a species is observed on a transect (conditional on its use of the transect) during a single sampling event pre-epizootic (blue) and post-epizootic (orange). Mean estimates (points) with 95% credible intervals (lines) shown.

Table S1.

Life history and diet characteristics of the 17 snake species with at least five detections across both time periods (i.e., all species listed in Fig. 2), ordered by the probability that their occurrence rate was lower post-epizootic (2006-2012) compared to pre-epizootic (1997-2004). The species with asterisks (*) belong to Viperidae while the others come from the two closely related Colubridae and Dipsadidae. For each species, we include: relative body size (s = small, m = medium, or l = large), preferred habitat (t = terrestrial, a = arboreal), active period (d = diurnal, n = nocturnal), and known diet items. The diet items are categorized as follows: amphibian adults (A), amphibian eggs (E), invertebrates (i.e., small invertebrates, oligochaetes, and mollusks; I), lizards and lizard eggs (L), snakes (S), birds (B), and mammals (M). We report an X for prey items that have been recorded in the literature with light gray shading (X) denoting that the prey item has been reported only rarely. A bold (X) indicates that the species has been documented feeding on the diet item specifically in our study region within Central Panama. We included peer-reviewed literature that reports the feeding behaviors of our focal snake species. We also included three books (38, 44, 48) because of their comprehensive natural history on snake species in Central America including one by J.M.R. that focuses specifically on Panama and contains extensive information on the El Copé snake community. The varying number of articles cited on species highlights the true variation in what is known about each species.

Species	P[post <pre]	Body size	Habitat	Active	Diet							Sources
					A	E	I	L	S	B	M	
<i>Rhadinaea decorata</i>	0.88	s	t	d	X	X	X	X				49, 50, 51, 52
<i>Sibon argus</i>	0.86	s	a	n		X	X					15, 44, 53, 54, 55, 56
<i>Clelia clelia</i>	0.85	l	t	d				X	X	X	X	57, 58, 59, 60, 61
<i>Chironius grandisquamis</i>	0.84	l	t	d	X			X		X	X	44, 62
<i>Bothrops asper</i> *	0.82	l	t	n	X		X	X	X	X	X	38, 63, 64, 65, 66, 67
<i>Leptophis depressirostris</i>	0.82	m	a	d	X			X				48, 68
<i>Leptodeira septentrionalis</i>	0.80	m	a	n	X	X		X	X			66, 69, 70, 71, 72, 73
<i>Rhadinaea vermiculaticeps</i>	0.76	s	t	d	X			X				44
<i>Pliocercus euryzonus</i>	0.72	m	t	d	X							48, 74

<i>Oxybelis brevirostris</i>	0.61	m	a	d	X	X	44, 75
<i>Imantodes cenchoa</i>	0.51	m	a	n	X	X	44, 76
<i>Sibon nebulatus</i>	0.50	m	a	n	X	X	15, 44, 55
<i>Sibon longifrenis</i>	0.35	s	a	n	X	X	15, 55, 77
<i>Dipsas sp.</i>	0.25	s	a	n		X	15, 44
<i>Sibon annulatus</i>	0.22	s	a	n		X	15, 44, 55
<i>Imantodes inornatus</i>	0.15	m	a	n	X	X	44, 48
<i>Bothriechis schlegelli</i> *	0.05	m	a	n	X	X X X X	10, 44, 78, 79, 80, 81

Table S2.

Number of detections and occurrence rates for the 36 observed snake species before and after the epizootic that led to amphibian mass mortality (ordered alphabetically). All species observed on at least one occasion are listed in the table, including the total number of detections pre- and post-epizootic. Occurrence rates per transect (mean and 95% credible intervals [CI] of posterior distributions), or the probability that a species used a survey transect in the time periods pre- and post-epizootic, are reported for species with at least five total observations over the 13-year study period (i.e., all species listed in Fig. 2 and Table S1). Occurrence estimates for species with less than five detections in a particular time period are shadowed in gray to highlight data deficiencies.

Species	<i>Pre-epizootic</i>			<i>Post-epizootic</i>		
	Detections	Occurrence rate		Detections	Occurrence rate	
		Mean	95% CI		Mean	95% CI
<i>Atropoides mexicanus</i>	1	-	-	0	-	-
<i>Bothriechis schlegelii</i>	3	0.66	0.38-0.87	32	0.88	0.75-0.97
<i>Bothrops asper</i>	7	0.77	0.56-0.91	0	0.45	0.01-0.95
<i>Chironius grandisquamis</i>	4	0.70	0.43-0.88	1	0.49	0.12-0.85
<i>Clelia clelia</i>	4	0.71	0.46-0.89	1	0.49	0.12-0.85
<i>Clelia equitoriana</i>	0	-	-	1	-	-
<i>Dendrophidion clarkii</i>	1	-	-	0	-	-
<i>Dipsas sp.</i>	19	0.87	0.74-0.96	59	0.92	0.82-0.98
<i>Drymobius rhombifer</i>	1	-	-	0	-	-
<i>Erythrolamprus epinephalus</i>	1	-	-	0	-	-
<i>Geophis bellus</i>	3	-	-	0	-	-
<i>Geophis brachycephalus</i>	0	-	-	2	-	-
<i>Geophis hoffmanni</i>	1	-	-	0	-	-
<i>Hydromorphus concolor</i>	1	-	-	0	-	-
<i>Imantodes cenchoa</i>	47	0.92	0.82-0.98	57	0.92	0.82-0.98
<i>Imantodes inornatus</i>	1	0.52	0.16-0.81	5	0.72	0.45-0.93
<i>Lachesis stenophrys</i>	0	-	-	1	-	-
<i>Leptodeira septentrionalis</i>	21	0.86	0.72-0.95	8	0.74	0.51-0.94
<i>Leptophis ahaetulla</i>	2	-	-	0	-	-
<i>Leptophis depressirostris</i>	7	0.78	0.58-0.92	0	0.45	0.01-0.95
<i>Leptophis nebulosus</i>	0	-	-	2	-	-
<i>Mastigodryas alternatus</i>	1	-	-	0	-	-
<i>Micrurus multifasciatus</i>	1	-	-	0	-	-
<i>Micrurus stewarti</i>	1	-	-	1	-	-
<i>Ninia maculata</i>	3	-	-	0	-	-

<i>Nothopsis rugosus</i>	1	-	-	1	-	-
<i>Oxybelis brevirostris</i>	69	0.94	0.85-0.99	69	0.92	0.83-0.98
<i>Oxyrhopus petolarius</i>	0	-	-	1	-	-
<i>Pliocercus euryzonus</i>	4	0.69	0.42-0.88	2	0.58	0.21-0.88
<i>Rhadinaea decorata</i>	13	0.83	0.67-0.94	0	0.45	0.01-0.95
<i>Rhadinaea vermiculatriceps</i>	5	0.70	0.44-0.88	0	0.44	0.01-0.94
<i>Rhinobothrium bovallii</i>	0	-	-	1	-	-
<i>Sibon annulatus</i>	13	0.82	0.64-0.93	38	0.89	0.77-0.98
<i>Sibon argus</i>	149	0.96	0.90-1.00	49	0.92	0.82-0.98
<i>Sibon longifrenis</i>	3	0.67	0.39-0.87	5	0.72	0.42-0.93
<i>Sibon nebulatus</i>	4	0.70	0.42-0.88	5	0.69	0.40-0.92

Table S3.

Values for the community-level parameters estimated in the occurrence model. Posterior distributions for each community-level parameter (see *Community occurrence model* section of the Materials and Methods for detailed descriptions) are summarized by their means and standard deviations (SD).

Parameter	Parameter description	Mean	SD
Ω_{pre}	Probability that a species is a true member of the pre-epizootic community	0.26	0.08
Ω_{post}	Probability that a species is a true member of the post-epizootic community	0.21	0.07
μ_{pre}	Mean community-level snake occurrence rate pre-epizootic (logit scale)	0.00	0.77
μ_{post}	Mean community-level snake occurrence rate post-epizootic (logit scale)	-0.30	1.00
σ	Community-level standard deviation	1.49	0.47
v	Detection probability for a snake species with average occurrence (logit scale)	-6.02	0.65
ρ	Correlation parameter estimating species detection based on species occurrence	1.46	0.51

Table S4.

Sample sizes and summary statistics for the six species with at least five body condition samples (i.e., captures) within each time period, pre- and post-epizootic. Data for the body condition analyses came from both the standardized transect surveys and opportunistic surveys. Note that efforts to capture individual snakes to measure body condition increased post-epizootic (see *Body condition analysis* section of the Materials and Methods). Mean and standard deviations of the body condition data for each species are shown pre- and post-epizootic. Estimated population-level values are plotted in Fig. 3 (Main Text).

Species	<i>Pre-epizootic</i>			<i>Post-epizootic</i>		
	Samples	Mean	SD	Samples	Mean	SD
<i>Dipsas sp.</i>	13	0.58	0.09	142	0.63	0.22
<i>Imantodes cenchoa</i>	30	0.38	0.10	84	0.34	0.12
<i>Leptodeira septentrionalis</i>	12	0.91	0.29	29	1.00	0.18
<i>Oxybelis brevirostris</i>	26	1.01	1.85	148	0.53	0.10
<i>Sibon annulatus</i>	8	0.63	0.32	73	0.41	0.10
<i>Sibon argus</i>	65	0.69	0.17	84	0.62	0.21

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