BIODIVERSITY LOSS

# Tropical snake diversity collapses after widespread amphibian loss

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**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*).

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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 Torríjos 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



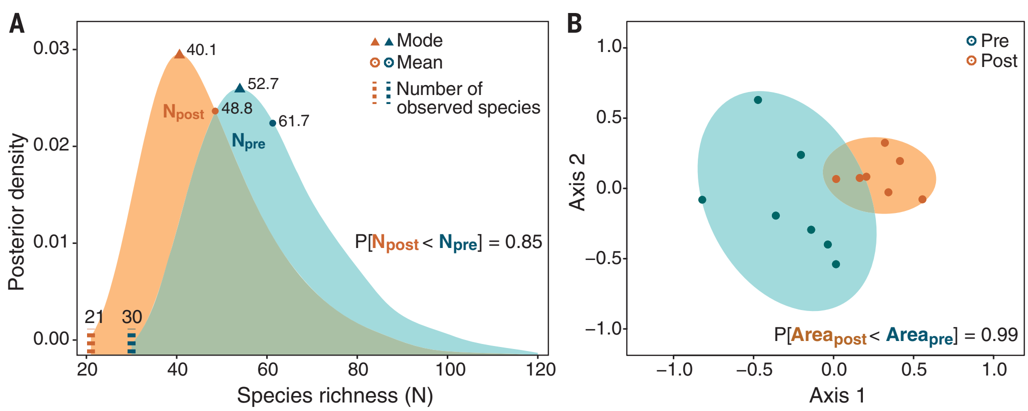


**Fig. 1. Snake species richness and composition before and after the epizootic that led to amphibian loss.** (**A**) Observed (dashed lines) and estimated snake species richness (posterior density plots with mean and mode) pre-epizootic ($N_{pre}$, blue) and post-epizootic ($N_{post}$, orange). (**B**) 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

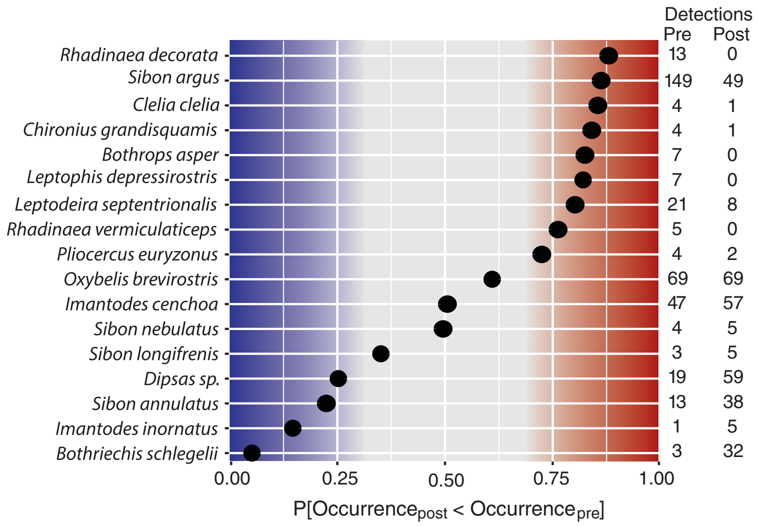


**Fig. 2. Changes in snake species occurrence rates after the epizootic that led to amphibian loss.** Probabilities (black circles) that occurrence rates were lower post-epizootic than pre-epizootic for the 17 snake species with at least five total detections across both time periods. High values (red-shaded 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.

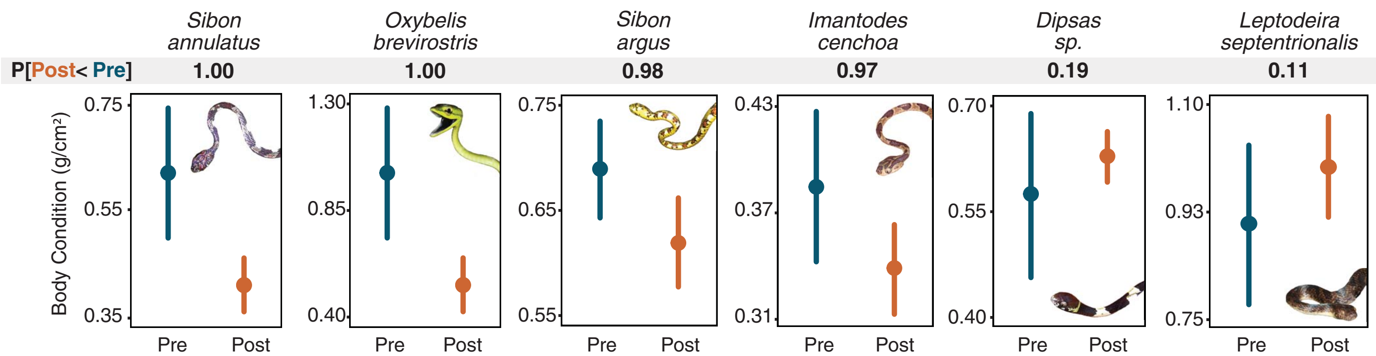


**Fig. 3. Average body condition for snake species before and after the epizootic that led to amphibian loss.** Body condition for the six snake species with at least five samples available both pre-epizootic (blue) and post-epizootic (orange). Mean values (circles) and 95% credible intervals (lines)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

## REFERENCES AND NOTES


1. G. Ceballos *et al*., *Sci. Adv.* **1**, e1400253 (2015).
2. R. K. Colwell, R. R. Dunn, N. C. Harris, *Annu. Rev. Ecol. Evol. Syst.* **43**, 183–203 (2012).
3. R. Dirzo *et al*., *Science* **345**, 401–406 (2014).
4. F. Isbell *et al*., *Nature* **526**, 574–577 (2015).
5. H. M. Pereira *et al*., *Science* **330**, 1496–1501 (2010).
6. C. J. Bradshaw, N. S. Sodhi, B. W. Brook, *Front. Ecol. Environ.* **7**, 79–87 (2009).
7. International Union for Conservation of Nature (IUCN), The IUCN Red List of Threatened Species, version 2019-2 (IUCN, 2019); www.iucnredlist.org [accessed 4 November 2019].
8. C. Hof, M. B. Araújo, W. Jetz, C. Rahbek, *Nature* **480**, 516–519 (2011).
9. B. C. Scheele *et al*., *Science* **363**, 1459–1463 (2019).
10. M. R. Whiles *et al*., *Front. Ecol. Environ.* **4**, 27–34 (2006).
11. A. J. Crawford, K. R. Lips, E. Bermingham, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 13777–13782 (2010).
12. K. R. Lips *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **103**, 3165–3170 (2006).
13. M. Böhm *et al*., *Biol. Conserv.* **157**, 372–385 (2013).
14. E. F. Zipkin, J. A. Royle, D. K. Dawson, S. Bates, *Biol. Conserv.* **143**, 479–484 (2010).
15. J. M. Ray, C. E. Montgomery, H. K. Mahon, A. H. Savitzky, K. R. Lips, *Copeia* **2012**, 197–202 (2012).
16. M. L. McKinney, J. L. Lockwood, *Trends Ecol. Evol.* **14**, 450–453 (1999).
17. H. W. Greene, *Mem. Cali. Acad. Sci.* **12**, 259–280 (1988).
18. M. R. Whiles *et al*., *Ecosystems (N. Y.)* **16**, 146–157 (2013).
19. C. N. Johnson *et al*., *Science* **356**, 270–275 (2017).
20. E. F. Zipkin, G. V. DiRenzo, J. M. Ray, S. Rossman, K. R. Lips, Code and data for Tropical snake diversity collapses after widespread amphibian loss. Zenodo (2020); doi:10.5281/zenodo.3628038.



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## SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/367/6479/814/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 and S2
Tables S1 to S4
References (*21*–*81*)

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**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 after amphibians were decimated by chytridiomycosis. They found that the snake community was less diverse and most species were in decline, except for a few "winning" species.

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