TITLE PAGE

DISASSEMBLY OF A TADPOLE COMMUNITY BY A MULTI-HOST FUNGAL PATHOGEN WITH LIMITED

EVIDENCE OF RECOVERY

Running title: Community disassembly by pathogen

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ABSTRACT

Emerging infectious diseases can cause host community disassembly, but the mechanisms driving the order of species declines and extirpations following a disease outbreak are unclear. We documented the community disassembly of a Neotropical tadpole community during a chytridiomycosis outbreak, triggered by the generalist fungal pathogen, *Batrachochytrium dendrobatidis* (*Bd*). Within the first 11 months of *Bd* arrival, tadpole density and occupancy rapidly declined. Rarity, in terms of tadpole occupancy and adult relative abundance, did not predict the odds of tadpole species occupancy declines. But species losses were taxonomically selective, with glassfrogs (Family: Centrolenidae) disappearing the fastest and tree frogs (Family: Hylidae) and dart-poison frogs (Family: Dendrobatidae) remaining the longest. We detected biotic homogenization of tadpole communities, with post-decline communities resembling one another more strongly than pre-decline communities. The entire tadpole community was extirpated within 22 months following *Bd* arrival, and we found limited signs of recovery within 10 years post-outbreak. Because of imperfect species detection inherent to sampling species rich tropical communities and the difficulty of devising a single study design protocol to sample physically complex tropical habitats, we used simulations to provide recommendations for future surveys to adequately sample diverse Neotropical communities. Our unique dataset on tadpole community composition before and after *Bd* arrival is a valuable baseline for assessing amphibian recovery. Our results are of direct relevance to conservation managers and community ecologists interested in understanding the timing, magnitude, and consequences of disease outbreaks as emerging infectious diseases spread globally.

Keywords: *Amphibians, Batrachochytrium dendrobatidis, disease, extinction, site-occupancy model, Neotropics, Panama.*

INTRODUCTION

Emerging infectious diseases can cause community disassembly (Zavaleta et al. 2009, Fisher et al. 2012), defined as the predictable loss of species and population declines. During community disassembly, the first species extirpated are generally rare species– species with small geographic ranges, small population size, or a narrow habitat tolerance (Rabinowitz 1981, Larsen et al. 2005, Gehring et al. 2014, Rader et al. 2014). Subsequent losses tend to include common, generalist species that have declined since the initial disturbance (e.g., Wright et al. 2007, Larsen et al. 2008). The last remaining species reduce patterns of community turnover across the study area, increasing biotic homogenization (McKinney and Lockwood 1999).

In the case of tropical amphibian declines and extirpations caused by the fungal pathogen *Batrachochytrium dendrobatidis* (hereafter *Bd*), many amphibian communities experience rapid, widespread population declines and species extirpations following pathogen arrival (Berger et al. 1998, Lips et al. 1998, 1999, 2006). A species susceptibility to *Bd* is correlated with several host characteristics (Lips et al. 2003). First, phylogeny can predict species susceptibility to *Bd*. For example, family-level amphibian phylogenies suggest that families with similar traits share the same vulnerabilities to threats (Corey and Waite 2008), but a species-level phylogenetic analysis on the amphibian fauna of El Copé, Panama showed no evidence that species with similar traits shared the same susceptibility to *Bd* (Crawford et al. 2010). The discrepancy between the results in each study are likely caused by differences in taxonomic, spatial, and temporal scales used– where rapid, widespread amphibian losses produced no species-level phylogenetic variation to *Bd* susceptibility in El Copé, Panama. Secondly, species ecology (i.e., traits) and rarity (i.e., abundance, geographic distribution, and habitat specialization; Rabinowitz 1981) affects a host's vulnerability to disturbance-related declines (Lips et al. 2003, Rachowicz and Briggs 2007, Briggs et al. 2010). For example,

species with small geographic distributions experience larger *Bd*-related occupancy declines than widespread species (Smith et al. 2009). A species' vulnerability to *Bd*-related declines can be a product of either environmental or demographic stochasticity (Lande 1993) or species-specific traits that pre-dispose them to disease (Lips et al. 2003). Host density can have the opposite effect, where higher host densities increase the number of infections, making population declines worse (e.g., Rachowicz and Briggs 2007, Briggs et al. 2010). For example, density-dependent *Bd* pathogen transmission of *Rana muscosa* has led to species extirpations and population declines across its range. Given that species' *Bd* susceptibility is correlated to these variables, we expect that the community disassembly of tadpoles may be correlated to phylogeny, ecological traits, and/or rarity.

Distinguishing between ecological rarity (i.e., low density, low occupancy, habitat specialization) and observational rarity (i.e., cryptic, fossorial, secretive) of hard to find species is largely overlooked in community disassembly studies. For instance, in a Neotropical forest, colorful dendrobatid amphibians are much easier to find than cryptic species of the genus *Eleutherodactylus* (Duellman and Trueb 1986). If imperfect detection is not accounted for, species occupancy (i.e., the proportion of sites where the species is present) will be under-estimated (i.e., MacKenzie et al. 2006, Kéry 2010). By underestimating species occupancy pre- and post- outbreaks, population occupancy declines will be overestimated and extirpations will be biased towards difficult to find species, leading to false inference with regards to the drivers of occupancy declines.

Here, we describe the disassembly of a stream-dwelling tadpole community in response to a *Bd* outbreak, while taking into account imperfect species detection. In this system, stream tadpoles occupy semi-isolated microhabitats (e.g., leaf packs, isolated pools, and in-stream pools and riffles) that allow for the consistent quantification of tadpole occupancy, density, and species richness. Prior to the introduction of *Bd*, these tadpole

assemblages were diverse (McDiarmid and Altig 1999, Crawford et al. 2010), abundant

(McDiarmid and Altig 1999) and structured spatially (Inger et al. 1986) and temporally

(Heyer 1976), creating an opportunity to compare several species characteristics

simultaneously that have been shown to contribute to species losses caused by disease. We

address the following specific questions in this study: (1) What are the patterns of community

disassembly following an outbreak? (2) What factors correlate to the order of species losses?

(3) And how can we improve the sampling of species rich communities when species'

detection is variable and imperfect?

We expected that tadpole occupancy would decline following the mass mortality of

adult amphibians in El Copé, Panama (Lips et al. 2006), and that the magnitude of tadpole

occupancy declines would depend on their microhabitat use and season. Like most other

multi-host pathogens, we predicted that rare species and relatives that share similar traits

would be extirpated first. We predicted that the tadpole communities that remained following

the *Bd* outbreak would be more similar in species composition, and would be mainly

comprised of common, generalist species. Finally, we expected that *Bd* arrival would cause

rapid changes to the tadpole community that would persist several years post-invasion. Our

results are relevant to conservation managers trying to understand and predict community

disassembly following outbreaks, especially as generalist fungal pathogens spread globally.

MATERIALS AND METHODS

STUDY SITE

The study site was located within Parque Nacional G. D. Omar Torríjos Herrera in

Coclé Province, approximately 8 km north of the town of El Copé, Panama (8° 40' N, 80°

37' 17'' W, Lips et al. 2003). The park spans elevations between 500 and 1000 m, and our

study sites are located at ~775 m elevation. This site experiences both a dry (December to

April) and wet (May to November) season. Mean annual air temperature at the park during 2003–2005 ranged from 16–23°C, and mean annual rainfall was ~3709 mm (McCaffery and Lips 2013; *unpublished data*).

STUDY SYSTEM

Starting in 1998, we started monitoring adult amphibian populations in El Copé, Panama (Lips et al. 2006), and we were consistently capturing amphibians until September 2004 when *Bd* was first detected in El Copé. We started monitoring tadpole populations starting July 2003, 15 months prior to the September 2004 die-off. The El Copé amphibian fauna experienced rapid species losses and declines. We, therefore, expect minimal compensatory or evolutionary dynamics interfering with community disassembly inference. This project is part of the larger Tropical Amphibians Declines in Streams (TADS) project to quantify the consequences of amphibian losses on ecosystem structure and function.

The original El Copé amphibian community consisted of 74 species (Lips et al. 2003, Crawford et al. 2010), of which ~22 had stream-dwelling tadpoles. The amphibian community was diverse with respect to life history (e.g., habitat use, reproductive mode), demography (e.g., survivorship, longevity), and ecology (e.g., clutch size, body size, dispersal distance). By 2008, only 44 species remained at low population densities (Crawford et al. 2010).

FIELD SURVEYS

We surveyed tadpole communities in four 200 m stream transects: Loop, Silenciosa, Cascada, and Guabal (see map in McCaffery and Lips 2013; Angeli et al. 2014). We mapped and measured the area covered by each of four microhabitats (riffle, pool, isolated pool, and leaf pack) at the beginning of the wet and dry seasons. We defined riffles as fast-flowing,

shallow sections with gravel and cobble substrates, pools as areas of calm water deeper than 20 cm in the main channel, isolated pools as small, shallow pools spatially separated from the main stream channel, and leaf packs as detritus accumulations at the bottom of pools. We used a *k*-means clustering analysis to divide streams into segments that were repeatedly visited each month throughout the study. To determine the appropriate number of stream segments, we calculated the within group sum of squares by the number of clusters extracted and examined this plot for a bend, similar to a scree plot in factor analysis, indicating the minimum number of clusters. The *k*-means analysis divided each stream transect into four segments for a total of 16 stream sites per microhabitat. Each segment was sampled either once, twice, or three times per month using the random sampling method described below.

To sample riffles, we used 250 μm D-nets and disturbed substrate with our feet while holding nets immediately downstream (Barbour et al. 1999). To sample leaf packs, we used a modified stovepipe benthic corer (22 cm diameter) with a base of rubberized flaps that kept the sampler sealed against rough and uneven substrates. We drove the corer into the substrate and searched through the contents for tadpoles (Colón-Gaud et al. 2010). We used a dip net to exhaustively sample pools and isolated pools until three consecutive scoops produced no tadpoles (Heyer et al. 1994, Ranvestel et al. 2004). We also measured the length, width, and depths of all microhabitats across each 200 m transect to account for variability in survey area.

We expected minimal differences in individual- and species-level detection probabilities within microhabitats because each microhabitat was searched until no new tadpoles were found. This guaranteed that within a given microhabitat although tadpole species vary in size and coloration (e.g., *Lithobates warszewitschii* = 115 mm, dark and heavily molted, Villa 1990; *Espadarana prosoblepon* = 12.3 mm, bright red dorsal, and pale brown ventral, Savage 2002), species detection probability is close to 1.0; but overall, tadpole

detection probability is less than 1.0 because, within a stream segment, tadpoles are present in some microhabitat sites and not others. The variables that caused the largest difference in detection probability among species were likely to be differences in abundance and distribution across microhabitats, rather than within microhabitat differences.

For leaf packs, isolated pools, and riffles, we randomly sampled three microhabitat sites per stream each month for 15 months before (June 2003–August 2004) and 11 months following (October 2004–August 2005) *Bd* arrival in September 2004. For pools, we randomly sampled between four and eight pool sites per stream each month before *Bd* arrived. We re-sampled all microhabitats in at least one stream annually between 2006 and 2011 and again in 2014 (Appendix S1: Table S1). All our analyses are based on the first two years of intensive sampling (2003–2005) of leaf pack, isolated pools, and riffles because no individuals were found in the majority of subsequent annual surveys.

We excluded pools from all analyses because logistical difficulties prevented the sampling of pools post-decline (2004–2005) and the sampling of leaf packs from September to December 2003. We report data of pools pre-decline to provide baseline data of these understudied communities. We also did not include September 2004 in analyses to limit biases between pre- and post- *Bd* samples because *Bd* arrived mid-September 2004 (Lips et al. 2006).

STATISTICAL ANALYSES

I. Patterns of community disassembly

Tadpole density

To determine if the magnitude of tadpole density declines differed among microhabitats or between seasons, we calculated tadpole habitat-weighted density (HWD) before and after *Bd* arrival in each microhabitat and stream by pooling monthly tadpole

abundances across species. We used HWD to adjust for spatiotemporal variations in microhabitat availability caused by differences among streams and between seasons. HWD was calculated by dividing total tadpole abundance per microhabitat in each stream each month by the total area sampled and multiplying by the percent area each microhabitat covered in each stream that season. Our reformatted data consisted of tadpole HWD per microhabitat per stream per month from 2003−2005.

To determine if tadpole HWD differed among microhabitats or between seasons following *Bd* arrival, we used a generalized linear mixed effects model, with monthly tadpole HWD as the response variable and microhabitat, season, disease state (*Bd* present or absent), all two-way interactions, and the three-way interaction as the explanatory variables. We included month as a fixed effect to account for repeated measures of density across months and included stream as a random effect to account for pseudo-replication of microhabitats within streams (Gillies et al. 2006). We used a negative binomial distribution to account for over dispersion of the response variable, and we accessed model fit by visually inspecting the residuals. We fit this model using package glmmADMB (Fournier et al. 2012, Skaug et al. 2014) in R version 3.2.1 (R Core Team 2015).

We could not account for biases in tadpole abundance caused by imperfect detection because the parameters of the species-specific hierarchical *N*-mixture models we tried to fit did not converge. We used stream segments as sites and monthly repeated visits to stream segments as replicate surveys. The lack of parameter convergence was likely caused by large differences in tadpole densities between the replicate surveys at each site. These differences could be caused by variations in species microhabitat use within a given stream segment and not necessarily a violation of the closure assumption (i.e., no births, deaths, immigration, or emigration). Density estimates that are not adjusted for imperfect detection are often underestimates of the true abundance (e.g., Banks-Leite et al. 2014) and inappropriately using

N-mixture models causes abundance overestimates (i.e., Dail and Madsen 2011).

Species occupancy

   To determine if species occupancy differed before and after *Bd* arrival, we used a hierarchical occupancy model to quantify changes in species-specific occupancy. In this analysis, we were able to account for imperfect detection, by estimating microhabitat specific detection rates. We define occupancy as the probability a species occupied a stream segment, and we define detection probability as the probability we detect a species in a given stream segment, given that the species is present. We included data for all species that were detected in three or more microhabitat samples within a season (Ferraz et al. 2007, Ruiz-Gutiérrez et al. 2010; Appendix S1: Table S2). We had sufficient data to estimate occupancy for eight of the 13 species identified to species level.

   We used different microhabitat samples as repeated surveys for stream segments (Hines et al. 2010). Since we did not know *a priori* species microhabitat use or breeding season, we ran each species occupancy model with the full set of microhabitat and season covariates.

   For a selected species, we estimated the occupancy probability (ψ) of tadpoles as,

$$z_{i,m} \sim Bernoulli(\psi_{i,m}),$$

where $z = 1$ when the m_{th} species occupies the i_{th} stream segment, and $z = 0$ otherwise. We investigated the association between species tadpole occupancy and the covariates microhabitat, season, disease state, and their interactions using an effects-parameterized generalized linear mixed model where,

$$logit(\psi_{i,m}) = \alpha_{0,n,m} + \beta_{0,m}Wet_i + \beta_{1,m}LeafPack_i + \beta_{2,m}Riffle_i + \beta_{3,m}Wet_iLeafPack_i +$$

$$\beta_{4,m}Wet_iRiffle_i + \beta_{5,m}Post_i + \beta_{6,m}Post_iWet_i + \beta_{7,m}Post_iLeafPack_i + \beta_{8,m}Post_iRiffle_i +$$

$$\beta_{9,m}Post_iWet_iLeafPack_i + \beta_{10,m}Post_iWet_iRiffle_i + \gamma_{i,m} + \eta_{d,m}.$$

We included $\alpha_{0,n,m}$ to account for spatial variations of the n_{th} stream for the m_{th} species, $\gamma_{i,m} \sim$

$normal(0, \sigma_\gamma^2)$ was included as a random effect to account for variation among stream

segments for the m_{th} species, and $\eta_{d,m} \sim normal(0, \sigma_\eta^2)$ was included as a random effect to

account for pseudo-replication of stream segments across months.

We estimated detection probability as,

$$y_{i,j,m} \sim Bernoulli(p_i z_{i,m}),$$

where,

$$logit(p_i) = \alpha1 + \beta Hab_i.$$

When tadpoles of the m_{th} species were observed during the j_{th} survey at the i_{th} stream

segment site then $y = 1$, and $y = 0$, otherwise. Detection was modeled as the product of p_i, the

probability of detecting a species, given that it is present at the i_{th} stream segment site (i.e., z

$= 1$).

To reduce the number of parameters estimated and to increase precision, we

combined the detection probability of leaf packs and isolated pools as the intercept of the

model and riffles as the covariate Hab, since previous runs of the model showed very similar

detection probability estimates between leaf packs and isolated pools (*unpublished*). We

assumed that tadpole detection probability was constant between seasons and years because

sparse post-decline data prevented us from estimating detection probability.

We fit all models using Bayesian methods and estimated the posterior distributions for

all parameters using Markov chain Monte Carlo (MCMC) methods implemented in JAGS

3.4.0 in R version 3.2.1 (R Core Team 2015) using the rjags package (Plummer 2015). For all

parameters, we used priors following the recommendation of Lunn et al. (2012; i.e.,

normal(0, 0.368), gamma(0.01, 0.01), uniform(0, 1)). We ran three chains for each parameter,

and ran each chain for 100,000 iterations with a burn-in period of 5,000 iterations. We

evaluated convergence of chains by visual inspecting trace plots and using the diagnostics of

Gelman (Brooks and Gelman 1998). We also assessed model fits using posterior predictive checks (Appendix S1: Fig. S1; Gelman et al. 2014).

To determine how much more likely a species was to successfully occupy a microhabitat before *Bd* than after *Bd* arrival, we calculated the odds ratio (i.e., OR = $odds_{post}/odds_{pre}$) by dividing the post-*Bd* logit output of the occupancy model by the pre-*Bd* logit output of the occupancy model. If the OR is close to one, then it suggests that there is no change in occupancy. If the OR is below one, then it suggests that the odds of occupancy is greater pre-*Bd* than post-*Bd*. And if the OR is above one, then the odds of occupancy is lower pre-*Bd* than post-*Bd*. We considered the effect of *Bd* biologically meaningful if the 95% credible interval fell below or above one– interpreted as a 95% probability that the OR significantly changed.

Community composition

To determine if tadpole communities post-*Bd* invasion were more similar to one another than tadpole communities before *Bd* arrival, we used a permutational analysis of multivariate dispersion (PERMDISP2; Anderson et al. 2006) in R version 3.2.1 (R Core Team 2015). We used the Bray-Curtis metric, which allows dispersion distance to reflect variability in community structure. We visualized the data using non-metric multidimensional scaling (NMDS). We defined communities as the tadpole assemblages sampled in each microhabitat-stream-season-year combination, for a total of 48 communities (3 microhabitats x 4 streams x 2 seasons x 2 years). We only included data between 2003 and 2005.

II. The order of species losses

Species relatedness

To determine if the order of species disappearances was correlated with their phylogenetic relationship, we fit several macro-evolutionary likelihood models to the last Julian day a species was seen in El Copé. We fit Brownian, Ornstein-Uhlenbeck, Lambda, and white noise models using the package 'geiger' in the R version 3.2.1 (Harmon et al. 2008, R Core Team 2015). We used our observational field data to determine the last Julian day each species was detected in El Copé. We did not interpret results as the true date of species extirpations because our data likely reflect the date of last species detection.

We set 01 January 2003 as Julian Day 0, and 31 December 2005 as Julian Day 1095. *Bd* likely arrived between Julian Day 609 and 638 in September 2004 (Lips et al. 2006). We used a rooted, time-calibrated El Copé amphibian tree (Crawford et al. 2010). All species differed from sister lineages by a genetic distance at the COI gene or 16S gene by at least eight or two percent, respectively. We excluded any individuals that were not classified to species level (e.g., *Centrolene* spp. and *Colostethus* spp.). We also did not include any pool samples or pool habitat specialist (i.e., *Atelopus zeteki*) because the last Julian Day those species were seen would have reflected the last day pools were sampled. We included all species that were found pre-*Bd* arrival for a total of 11 species, representing four families (i.e., Ranidae, Centrolenidae, Hylidae, Dendrobatidae), and we compared the fit of each model using AICc. We considered the model with the lowest AICc as the model of best fit.

Rarity

To determine if species ecological rarity was a predictor of occupancy decline, we used two metrics of rarity: (1) tadpole seasonal microhabitat occupancy from the species occupancy model outlined above and (2) raw field data from transects of adult relative

abundance (Crawford et al. 2010). We used both tadpole occupancy and adult relative abundance to reflect species' variations in rarity across life stages. We calculated the species-specific habitat-weighted OR as the product of the odds ratios for each microhabitat in each season from the occupancy model outlined above and the average percent habitat available to adjust for variations in microhabitat cover among streams. To quantify the strength of the relationships between adult relative abundance and OR and between tadpole pre-*Bd* occupancy versus OR, we tested for an association between paired samples by calculating Pearson's correlation coefficient using the function cor.test() in R.

III. Imperfect detection and sampling biases

Not adjusting for imperfect detection in occupancy models

We compared all the results from our detection-adjusted occupancy model (i.e., species occupancy declines and rarity analyses) to the results of a logistic regression, which does not adjust for detection probability, using a slightly modified dataset and the model outlined above. We modified the dataset by collapsing the stream segment site by visit matrix for each species, such that if a species was ever detected at a stream segment site it was considered present. We assigned the detection probability, p, for all microhabitat equal to one. We then used the same statistical approach using Markov chain Monte Carlo (MCMC) methods implemented   in JAGS 3.4.0 in R version 3.2.1. (R Core Team 2015) using the rjags package (Plummer 2015).

Optimizing species sampling

To determine how to improve the sampling of species rich communities when species' detection is variable and imperfect, we used a single-season single-species occupancy model to analyze simulated data under different scenarios (Data S1, Metadata S1).

We simulated occupancy data for a single species under scenarios spanning high to low detection and occupancy probabilities (range = 0.1 to 0.9) and varied the number of sites sampled (range: 5 to 200 sites by 20) and the number of surveys per site (range: 1 to 9 surveys per site by 2). We generated a total of 5,000 unique scenarios to test how variations in occupancy, detection, number of sites sampled, and number of surveys per site affected the precision of occupancy estimates.

We fit all models using Bayesian methods using the same procedure outlined above for species occupancy. For each unique combination of occupancy, detection, sites and surveys, we simulated 25 occupancy datasets and analyzed each dataset under a Bayesian framework. For each analysis, we ran three chains for each parameter, and ran each chain for 10,000 iterations with a burn-in period of 1,000 iterations.

To determine how well models performed under different sampling schemes, we calculated the root mean square error between true and recovered occupancy estimates for each of the 25 datasets per scenario. The root mean square error represents the sample standard deviation of the difference between predicted and true estimates. Based on occupancy and the degree of precision we wanted in model estimates, we decided *a priori* that our maximum acceptable root mean square error was 0.10 (i.e., Guillera-Arroita et al. 2010, Guillera-Arroita 2011).

RESULTS

Field summary

We captured 2,021 individuals of 14 species across four microhabitats 15 months prior to *Bd*'s arrival. Of those, 1,123 individuals were found in pools. We found 11 species during the wet season and 12 species during the dry season, with 9 species common to both (Appendix S1: Table S2).

Before *Bd* arrival, average monthly HWD per microhabitat ranged from 0.00 to 20.08 individuals m^{-2} during the dry season and 0.00 to 6.69 individuals m^{-2} during the wet season (Fig. 1). Species that had >75% of captures during the dry season, included: *Atelopus varius*, *Colostethus panamensis*, *Lithobates warszewitschii*, *Espadarana prosoblepon*, *Sachatamia albomaculata*, *Hyloscirtus colymba,* and *Hyalinobatrachium colymbiphyllum.* Species with >75% of captures in the wet season included: *Colostethus spp.*, *Hyloscirtus palmeri*, *Sachatamia ilex* and *Teratohyla spinosa*. Species with >98% of captures in a single microhabitat included: *Atelopus varius* (pools), *L. warszewitschii* (pools), most centrolenid species (leaf packs), and *Colostethus* spp. (isolated pools; Appendix S1: Table S2).

During the 11 months following *Bd*'s arrival, we captured 249 individuals of eight species across three microhabitats, representing a 72% decrease in captures and a 43% decrease in species richness. Within 11 months of *Bd* arrival, habitat-weighted density decreased from an average HWD of 4.53 ± 1.19 individuals m^{-2} (mean ± SE) to 0.34 ± 0.08 individuals m^{-2} after *Bd* ($z = 4.12$, $p < 0.001$; Fig. 1). The magnitude of density declines did not differ between microhabitats or seasons ($p > 0.05$). Post-decline, the highest densities of tadpoles were found in isolated pools, mostly of the families Dendrobatidae (*Silverstoneia flotator*, *C. panamensis*, *S. nubicola*, *Allobates talamancae, and Colostethus* spp.) or Hylidae (*H. palmeri, H. colymba*). Only two species had >75% of captures in the dry season: *Allobates talamancae* and *L. warszewitschii*, and only *Hyalinobatrachium colymbiphyllum* had >75% of captures during the wet season (Appendix S1: Table S2). Five species were never seen post-decline (*Atelopus varius, E. prosoblepon, S. albomaculata, S. ilex, T. spinosa*; Appendix S1: Table S2).

We did not detect any tadpoles during any of the annual surveys conducted from 2006 to 2011, precluding further analyses. In April 2014, we found several pools and isolated pools with tadpoles of *Silverstoneia nubicola* and an unidentified species, ranging in HWD between 0.95 to 4.49 individuals m^{-2}.

I. Patterns of community disassembly

Species occupancy

Half of the species in any microhabitat and season (24 of 48) declined in occupancy after *Bd* arrival (Fig. 2). Detection probability was significantly higher for tadpoles in leaf packs and isolated pools (0.41±0.20), than for tadpoles found in riffles during the entire study (0.13±0.03; Appendix S1: Table S3).

Community composition

Tadpole communities were homogenized, where post-decline tadpole communities were more similar to one another than the pre-decline tadpole communities were to each other (Fig. 3; PERMDISP2, $F_{1,46}$ = 15.02, $p < 0.001$). Pre-decline tadpole community dissimilarity among microhabitat and between seasons was 65% greater than their post-decline counterparts (Pre-decline average distance to median = 0.35; Post-decline average distance to median = 0.12).

II. The order of species losses

Species relatedness

We found that the Brownian model best fit the timing of species disappearance dates, indicating a taxonomic signal to the order of species losses and taxonomic homogenization (Fig. 4; Appendix S1: Table S4), with centrolenids disappearing first– sometimes without

ever being seen post-*Bd* arrival– and hylids, dendrobatids, and the ranids still seen several months post-*Bd* arrival. All other models increased the AICc score by at least 3 points (Appendix S1: Table S4). No tadpoles were seen during the survey in 2006.

Rarity

Neither tadpole occupancy nor adult relative abundance predicted the odds of occupancy decline among tadpole species (Fig. 2 and 5; Pearson's correlation coefficient = -0.01, t = -0.05, df = 46, p = 0.95; Pearson's correlation coefficient = 0.08, t = 0.20, df = 6, p = 0.84, respectively).

III. Imperfect detection and sampling biases

Not adjusting for imperfect detection in occupancy models

Using the logistic regression, we found that over half (~ 58%) of tadpole species, regardless of microhabitat and season, declined following *Bd* arrival (Appendix S1: Table S5). Similar to the detection-adjusted model results, we found no relationship between adult relative abundance and the odds of species decline (Pearson's correlation coefficient = -0.11, t = -0.27, df = 6, p = 0.78). But, in contrast to the detection-adjusted model, we found that as tadpole pre-*Bd* occupancy increased, then the likelihood of species declined also increased (Pearson's correlation coefficient = 0.96, t = 25.69, df = 46, p < 0.001).

Optimizing species sampling

When sampling a species rich community with variable and imperfect detection, our simulations suggest that the minimum number of sites a surveyor should sample is 25 microhabitat sites at least three times to obtain an occupancy estimate with a maximum error of 0.10 (Appendix S1: Table S6 and Fig. S2).

DISCUSSION

Bd caused rapid, widespread abundance and occupancy declines in the tadpole community that was immediate and persistent. Tadpoles declined in abundance and occupancy rapidly within the first 11 months of the adult outbreak, and by the second year, all tadpoles had been extirpated. Sampling between 2006 and 2011 produced no tadpoles, even for species with adults that persisted post-*Bd* invasion. In 2014, the first tadpoles were detected but at very low densities and in few microhabitats.

Within 11 months of *Bd* invasion, tadpole community disassembly– the order of species declines and losses– was marked by taxonomic and ecologic homogenization with the disappearance of Centrolenid habitat-specialists, resembling the regional pattern of adult community disassembly (Smith et al. 2009). Centrolenids were mainly found in leaf packs and were the first ones that disappeared, likely driving the homogenizing pattern across El Copé, whereas at the regional scale, geographically restricted endemic species drove the homogenizing pattern of adult amphibians (Smith et al. 2009). Homogenization in both adults and tadpoles resulted in higher than expected taxonomic and ecological similarity among communities post-*Bd*.

The biotic homogenization detected in both adults and tadpoles at regional and local scales, respectively, has implications for future ecological and evolutionary processes (Olden et al. 2004). Ecologically, across space, *Bd* has dissolved historical biogeographical patterns, such that increasing distance between sites, even > 500 km, is not correlated with community composition dissimilarity (Smith et al. 2009), essentially erasing information on why species are in their present locations. These species losses also decrease functional stability of communities and ecosystems, where food webs may be re-structured (Barnum et al. 2015) or ecosystem resilience degraded (Petchey and Gaston 2009). Evolutionarily, biotic homogenization can decrease genetic variability within species, compromising individual

fitness by disrupting local adaptation and decreasing the genetic variability of isolated populations and speciation (Olden et al. 2004). Therefore, via the mechanism of biotic homogenization, the world may be losing more species than appreciated when we combine observed species extirpations and decreased speciation rates.

Species rarity, both in terms of adult relative abundance and tadpole occupancy, did not predict the odds of species occupancy declines caused by *Bd*, indicating that *Bd* is so widespread that we see no effect of rarity on community disassembly patterns. Rare and common species experienced comparably large occupancy declines from *Bd* invasion. Rarity is a widely accepted indicator of species vulnerability for many taxa (Zavaleta et al. 2009), but the mechanism (i.e., species ecology versus low numbers) driving species susceptibility can vary by disturbance. In this system, where *Bd* is highly virulent and hosts are naïve to infection, species rarity– of either tadpoles or adults– did not influence vulnerability to *Bd*. Host susceptibility to pathogen-related declines is more complicated than relating them to host population size, where aspects of host ecology may also contribute to species vulnerability (Lips et al. 2003). For example, riparian species are more vulnerable to abundance and occupancy declines than terrestrial species (Lips et al. 2003, Brem and Lips 2008). In our system, we only examined stream-dwelling tadpoles; if we had surveyed the entire landscape for tadpoles (i.e., bromeliads, canopy, refuges, etc.), we may have detected more pronounced variations in susceptibility. Within a single habitat type though, we did not find that rarity of tadpole occupancy or adult relative abundance predicted the odds of species occupancy declines.

For some threats, such as disease, species extinction risk may not be predicted by the usual explanations, such as rarity (i.e., small geographic range size, low abundance, and ecological specialization; Rabinowitz 1981) or species traits (e.g., Lips et al. 2003, Langwig et al. 2012), because of spatial scale. In this study, we focused on stream-dwelling species,

which are among the most susceptible to *Bd* (Brem and Lips, 2008), and we did not find that rarity or species traits correlated to extinction risk because all tadpoles declined and disappeared within 22 months of *Bd* arrival. These results strongly reinforce the hypothesis that for Neotropical amphibian species that live in streams, very little else matters besides whether a species survives the initial *Bd* outbreak or not.

We hypothesize that low adult abundance, low reproductive output, and high metamorph mortality are preventing tadpole community recovery. We found little evidence that tadpole communities were recovering within the decade after *Bd* invasion, although we likely did not sample enough to detect all species of tadpoles. For tadpole abundance to increase, adult abundance and reproductive output needs to increase. It is possible that infected tadpoles have reduced growth rates (Parris and Cornelius 2004, Garner et al. 2009) and higher disease-related mortality, or that metamorphs and subadults have high mortality rates (Berger et al. 1998, Rachowicz et al. 2006, Langhammer et al. 2014) but evidence for the latter is lacking.

Recovery almost certainly does not mean that the tadpole community will return to their pre-*Bd* state. Stochastic (ecological drift) and deterministic (niche-selection) driven processes, as well as priority effects, will likely re-structure the tadpole community as it reassembles, where the relative importance of each process may depend on the harshness of the ecological filter, in this case *Bd* (e.g., Chase 2007). In 2014, we detected a few individuals of *Silverstoneia nubicola*, which were among the last tadpole species detected in 2005. Although there is a parallel between species disassembly and re-assembly order, the tadpole community is unlikely to re-assemble in the reverse disassembly order because community disassembly was triggered by species' pathogen naivety, whereas re-assembly will likely reflect the combined effects of amphibian dispersal and ability to cope with *Bd* infection and persistence. We propose that more reliable metrics to quantify tadpole community resilience

and stream ecosystem function would be to compare algal community composition (Connelly et al. 2008), macroinvertebrate assemblages (Colón-Guad et al. 2010), or nitrogen cycling rates (Whiles et al. 2013) before and after the *Bd* outbreak.

The 100% tadpole abundance declines reported here are larger than the adult abundance declines described at El Copé, Panama (Crawford et al. 2010). The higher tadpole rate of loss is likely driven by both decreased recruitment and lower detection probability than adults. Tadpoles have naturally high mortality rates (Calef 1973, Heyer et al. 1975) and when the additional chytrid-related mortality (Garner et al. 2009) is added to the system, the likelihood of tadpole survival is slim– explaining the discrepancy between tadpole and adult relative abundance declines. It may also be that tadpoles were still present but we did not detect them– especially given that some centrolenid adults are present at El Copé and we did not find their tadpoles (Crawford et al. 2010).

By not sampling pools after *Bd* arrival, we were unable to quantify the impact of *Bd* invasion on that microhabitat. However, our main conclusions would not have changed because amphibian adult mass mortality was widespread across El Copé (Lips et al. 2006). We resampled pools in 2006, and we found no individuals, similar to the patterns in the other microhabitats.

Sampling recommendations

We provide the first estimates of Neotropical tadpole detection probabilities, which could replace vague priors traditionally used in Bayesian analyses to make more precise occupancy estimates. Most Neotropical regions have experienced widespread losses of amphibians from *Bd* (James et al. 2015), making it difficult to estimate unbiased tadpole detection probabilities. Tadpoles are cryptic, secretive, and difficult to detect (Heard et al. 2006, Smith et al. 2007), but monitoring tadpoles may provide a better solution to monitoring

amphibian community dynamics post-*Bd* because stream-dwelling tadpoles are spatially constrained, whereas amphibian adults are not.

Our study was not designed with the intent of using *N*-mixture or occupancy models, but we were able to analyze the majority of species using hierarchical occupancy models. If we had not accounted for imperfect species detection in this analysis, we would have likely overestimated occupancy declines and inaccurately interpreted the correlation between species odds of decline to tadpole pre-*Bd* occupancy (but see Welsh et al. 2013). Observational error, in this case, can lead to misclassifying species as extirpated or having greater odds of decline. We recommend that future researchers survey at least 25 sites, three times each per season, to adequately sample a species rich community for both rare and common species.

Occupancy studies should be designed carefully to ensure efficient use of available resources. To avoid wasted effort, biologists should anticipate the quality of their data (MacKenzie and Royle 2005, Guillera-Arroita et al. 2011). The precision and bias of occupancy estimates will also depend highly on the species biology and the system in general. For example, when working with rare species, the best sampling designs will tend to have more replication than in cases where the precision of occupancy estimates is of interest. Therefore, thought and care should be given to designing sampling schemes before collecting data to prevent loss of time, money, and resources.

Conclusions

Phylogeny, ecological traits, and rarity have been associated with adult amphibian declines (but see Crawford et al. 2010), but we only detected evidence that two of these three characteristics predicted tadpole declines, where closely related species did share susceptibility to *Bd*. The discrepancy between the order of extirpations and declines of adult

and tadpoles may be attributed to when in the life cycle hosts are gaining infection and dying. If hosts are dying before reproduction, the patterns of species abundance and occupancy declines will be greater than after they reproduce. For example, the mountain yellow-legged frog, *Rana muscosa*, develops fatal *Bd* infection post-metamorphosis, creating the illusion of healthy abundant tadpole populations but severely declined juvenile and adult populations.

We found that tadpole communities were taxonomically and ecologically homogenized within 11 months of *Bd* invasion and communities collapsed within 22 months. *Bd* drove hosts to extirpation, and we have not seen signs or evidence of substantial tadpole community recovery within 10 years post outbreak. Our results are directly relevant to researchers interested in improving sampling methods of diverse communities, disease ecologists interested in understanding how multi-host fungal pathogens impact different life stages, community ecologists interested in pathogen-driven community disassembly of vertebrates, and conservation practitioners in charge of culling, vaccinating, and sterilizing wild populations experiencing declines and extirpations caused by multi-host fungal pathogens.

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DATA AVAILABILITY

Data associated with this paper are available in Dryad: http://dx.doi.org/10.5061/dryad.q586c

Figure 1 Effects of *Bd* arrival on habitat weighted density (individuals per meter^2) of tadpoles in each of three microhabitats (leaf pack, isolated pool, riffle) for 15 months before and 11 months after *Bd* arrival in September 2004 (Lips et al. 2006). The solid black line represents the rolling average of tadpole habitat weighted density for the entire tadpole community. The heavy black horizontal lines represent the dry season, and the heavy black vertical line represents the arrival of *Bd* in September 2004.

Figure 2 Patterns of occupancy by species, microhabitat, and season pre- (left) and post- (middle) *Bd* arrival with the odds ratio (i.e., OR = $odds_{post}/odds_{pre}$; right). All points represent the mean ± 95% credible interval. Tadpole pre-*Bd* occupancy rarity was not a significant predictor of decline (Pearson's correlation coefficient = -0.01, t = -0.05, df = 46, p = 0.95). Odds ratios less than one indicate occupancy declines post-*Bd*. Species codes: Hc = *H. colymba*; Hp = *H. palmeri*; Sf = *S. flotator*; Sn = *S. nubicola*; Cp = *C. panamensis*; Lw = *L. warszewitschii*; Hcol = *H. colymbiphyllum*; Ep = *E. prosoblepon*.

Figure 3 Non-metric multidimensional scaling (NMDS) ordination of tadpole communities– tadpole samples from each microhabitat-stream-season combination– pre- and post-*Bd* using Bray-Curtis dissimilarity. After *Bd* arrival, tadpole communities became more similar to one another, represented by the nested circles. Lines connect communities to the centroid of each group (i.e., pre- or post-*Bd*). Ellipses represent 95% confidence intervals around group centroids.

Figure 4 Phylogenetic patterns of order of species losses in stream-dwelling tadpoles with last Julian Day a species was seen mapped onto branches. Our rooted, time-calibrated, and trimmed phylogenetic tree comes from the El Copé amphibian tree (Crawford, Lips, and Bermingham 2010). Julian Day zero corresponds to 01 January 2003, and Julian day 1095 corresponds to 31 December 2005. *Bd* arrived between Julian day 609 and 638, and we mark day 609 on the legend of the image. Most glassfrog species were the first to disappear from El Copé– with many not seen post-*Bd* arrival; while treefrogs and poison-dart frogs remained detectable after *Bd* arrival (model of best fit: Brownian; Appendix S1: Table S4).

Figure 5 Adult relative abundance pre-*Bd* arrival (Crawford et al. 2010) by habitat-weighted odds ratio of tadpole declines. Adult relative abundance was not a significant predictor of the odds of tadpole occupancy decline (Pearson's correlation coefficient = 0.08, $t = 0.20$, $df = 6$, $p = 0.84$).

Julian day

303   855