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Host Identity Matters—Up to a Point: The Community Context of *Batrachochytrium dendrobatidis* Transmission

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ABSTRACT: The level of detail on host communities needed to understand multihost parasite invasions is an unresolved issue in disease ecology. Coarse community metrics that ignore functional differences between hosts, such as host species richness, can be good predictors of invasion outcomes. Yet if host species vary in the extent to which they maintain and transmit infections, then explicitly accounting for those differences may be important. Through controlled mesocosm experiments and modeling, we show that interspecific differences between host species are important for community-wide infection dynamics of the multihost fungal parasite of amphibians (*Batrachochytrium dendrobatidis* [*Bd*]), but only up to a point. The most abundant host species in our system, fire salamander larvae (*Salamandra salamandra*), did not maintain or transmit infections. Rather, two less abundant "auxiliary" host species, Iberian tree frog (*Hyla molleri*) and spiny toad (*Bufo spinosus*) larvae, maintained and transmitted *Bd*. Frogs had the highest mean rates of *Bd* shedding, giving them the highest contributions to the basic reproduction number, R_0. Toad contributions to R_0 were substantial, however, and when examining community-level patterns of infection and transmission, the effects of frogs and toads were similar. Specifying more than just host species richness to distinguish salamanders from auxiliary host species was critical for predicting community-level *Bd* prevalence and transmission. Distinguishing frogs from toads, however, did not improve predictions. These findings demonstrate limitations to the importance of host species identities in multihost infection dynamics. Host species that exhibit different functional traits, such as susceptibility and infectiousness, may play similar epidemiological roles in the broader community.

Keywords: disease ecology, multihost transmission, community ecology, chytridiomycosis, invasion biology.

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Introduction

Animal communities inevitably get invaded by parasites, and the consequences for hosts range from negligible to catastrophic. Host community ecology is a significant factor affecting the outcomes of parasite invasions because most parasites infect and circulate among multiple host species (Cleaveland et al. 2001). The characteristics of host communities that drive multihost infection dynamics are debated however (Johnson et al. 2015, 2019; Rohr et al. 2020). Well-documented correspondences between infection prevalence and host species richness suggest that crude community measures may explain substantial variation in the outcomes of parasite invasions (Ostfeld and Keesing 2012; Wood and Lafferty 2013; Rohr et al. 2020), despite ignoring differences between host species in their abundance and likelihood of contracting, transmitting, and maintaining infections. Interspecific differences in those basic epidemiological parameters are common however and can result in host species making distinct contributions to the overall maintenance of the parasite (Fenton et al. 2015). Distinguishing the taxonomic identities of host species (hereafter referred to as "host species identities") to account for epidemiologically relevant interspecific differences has led to more precise characterizations of community-level patterns of infection (LoGiudice et al. 2008; Rudge et al. 2013; Venesky et al. 2014; Johnson et al. 2019).

Keeping track of host species identities complicates disease modeling and management and, in certain conditions, may not be necessary to predict invasion outcomes. For instance, one or few "key" host species can largely drive infection dynamics throughout the community (Lloyd-Smith

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et al. 2005; Streicker et al. 2013; Viana et al. 2014; Fenton et al. 2015), suggesting that differentiating the identities of some, but not necessarily all, host species is important for predicting invasion outcomes. Even highly generalist parasites are known to infect certain host species more than others, either because those species are numerically dominant (Johnson et al. 2013; Graystock et al. 2020) or because they have a high capacity to sustain and/or transmit infections (i.e., host competence; Stewart Merrill and Johnson 2020), as exemplified by "super-spreaders" (Lloyd-Smith et al. 2005) and "reservoirs" (Fenton and Pedersen 2005; Reeder et al. 2012; Fenton et al. 2015). Clearly, the identity of those key host species would be critical information for understanding infection dynamics in the host community, but separating the identities of the other hosts may not be essential. It is certainly plausible that some host species could be ignored or grouped as single "nonkey" hosts. Such uncertainties around the importance of host species identities in multihost infection dynamics remain to be resolved empirically.

This study sought to determine the extent to which host species identities matter to multihost dynamics of the generalist fungal parasite of amphibians, *Batrachochytrium dendrobatidis* (*Bd*). *Bd* infects keratinized skin of myriad amphibian species as aquatic zoospores, and host species' responses to *Bd* exposure vary widely (Gervasi et al. 2013; Bielby et al. 2015; Han et al. 2015). Infections in some species can lead to the disease chytridiomycosis, leading eventually to cardiac arrest of individuals (Voyles et al. 2009) and severe declines of populations (Bosch et al. 2001; Briggs et al. 2010). Many amphibian species contract infections without developing chytridiomycosis however, allowing *Bd* to persist endemically (Scheele et al. 2017; Spitzen-van der Sluijs et al. 2017). Certain species can clear infections as well (Daversa et al. 2018), potentially precluding *Bd* establishment following invasions.

Interspecific variation in amphibian responses to *Bd* permits the hypothesis that host species identity is a key factor in community-level *Bd* persistence following an invasion. We tested this hypothesis by experimentally mimicking *Bd* invasions across a range of host communities that varied in relative abundances of constituent host species. We used the experimental data to examine infection dynamics at both the level of species and the level of communities, using metrics with different levels of detail on host communities. First, we examined infection dynamics in the most abundant (i.e., dominant) host species alone, ignoring co-occurring hosts, to determine whether *Bd* maintenance was explained solely by the numerically dominant host. Second, we considered all of the host species and fully incorporated host species identities in an analysis of how *Bd* was maintained in host communities during experimental invasions. Third, we examined how species-specific roles in *Bd* dynamics translated into variation in community-level infection prevalence and the overall basic reproduction number ($R_{0,TOT}$) of the parasite (Fenton et al. 2015). The study demonstrates limitations of host species richness and identity as predictors of the course of *Bd* invasions.

Methods

Study System

Our mesocosm experiments were based on amphibian assemblages seen in a network of 242 ponds in the Peñalara Massif, part of the Guadarrama National Park near Madrid, Spain. *Bd* was first detected at the site in the late 1990s (Bosch et al. 2001) and has persisted in the amphibian communities ever since (Bosch et al. 2018, 2020). Nine amphibian species occupy the ponds during the summer months for breeding and larval development. We chose three species that are competent hosts of *Bd* and vary in overall abundance at the site: larval fire salamanders (*Salamandra salamandra*; hereafter called "salamanders"), spiny common toads (*Bufo spinosus*; hereafter called "toads"), and Iberian tree frogs (*Hyla molleri;* hereafter called "frogs"). Salamanders are the most widespread species in these sites and have the highest overall abundance (Bosch et al. 2018). We therefore used salamanders as the dominant host species in our experimental systems. Local abundances of frog and toad larvae can reach high levels in certain ponds, but their distribution in the network is constrained to a smaller subset of ponds (Bosch et al. 2018). We therefore used frogs and toads as "auxiliary" host species in the experiment.

Experimental Approach

We designed a mesocosm experiment that mimicked episodic invasions by *Bd* into naive (i.e., yearling) larval communities that had equal total host densities but varied in the presence and relative abundance of the three host species. Episodic invasions are multiple sporadic introductions of a parasite into host systems and may occur, for example, from occasional immigration of infected hosts or from anthropogenic disturbance. We included salamanders in all experimental communities at varying abundances to reflect their widespread distribution in the natural system.

The experiment comprised five treatments: (1) control (24 salamanders); (2) two species with toads (12 salamanders and 12 toads); (3) two species with frogs (12 salamanders and 12 frogs); (4) nonrandom three species (12 salamanders, 6 toads, and 6 frogs); and (5) random three species (presence of salamanders, toads, and frogs with relative abundances chosen at random while maintaining the same overall abundance of individuals [24] as the other treatments). The random three-species treatment was included to mimic the variation in host species abundances that

occurs across natural communities (Bosch et al. 2018); abundances of salamanders and toads for each of these tanks were drawn at random from uniform distributions, with means equal to the mean abundance of those species across all other tanks in the experiment, and the number of frogs was then calculated to round the total number of animals up to 24 per tank (see table S8 for initial salamander, frog, and toad abundances in all random and nonrandom three-species tanks). Note that because all of the communities had the same total number of individuals, we effectively assumed substitutive community assembly, whereby increases in abundance of one species was achieved through a concomitant reduction in abundance of the other species (Wojdak et al. 2014; Johnson et al. 2015). Treatments 1–4 were replicated five times, and the fifth random treatment comprised 16 mesocosms, with a different host composition in each. We performed the experiment in a single room held at a constant 18°C temperature with 12-h light periods, located in the Centre for Captive Breeding of Threatened Amphibians in Rascafria, Spain (fig. S1). Mesocosms were covered with 2 cm of gravel, filled with 80 L of river water free of *Bd* (fig. S1), and randomly assigned to one of the five treatments.

We collected yearling salamander larvae, toad larvae, and frog larvae by dipnetting ponds located in the Peñalara Massif, central Spain (40.8500N, 3.8570W). We defined ponds as either *Bd*-positive or *Bd*-negative according to 20 years of historical data (Bosch et al. 2018). We confirmed the *Bd* status of ponds by swabbing 20 animals per pond. Quantitative polymerase chain reaction (qPCR) of the swabs showed that all swabs from presumed *Bd*-positive sites were positive for *Bd*, and likewise, all swabs from presumed *Bd*-negative ponds were negative for *Bd* (data not shown). Salamander larvae were collected from *Bd*-positive ponds and therefore presumed to have previously been exposed to and possibly infected with *Bd* (Medina et al. 2015). Tree frog and spiny toad tadpoles were captured at *Bd*-negative ponds and presumed to be uninfected and not previously exposed to *Bd*. We transported animals, grouped according to the pond of capture, to the Centre for Amphibian Breeding in Rascafria, Spain, where animals were randomly allocated to experimental tanks according to the preassigned treatments. Salamander larvae occupied the whole volume of the tank and were provided with polyethylene tubes as shelters on the bottom of the tank, which was covered by 2 cm of gravel. To avoid salamander predation, frog and toad tadpoles were housed in 2-L plastic containers placed inside the tank and punctured to be permeable to water and *Bd* zoospores (fig. S1). Salamander larvae were fed chopped earthworms twice a week, and frog and toad larvae were fed fish tablets twice per week. We replaced 10% of the water volume twice per week. The experiment was run for 30 days (July 4 to August 2, 2017). Throughout the experiment, we monitored individuals daily for health and gill retention, removing any individuals showing signs of morbidity or with gills retracted to the point that metamorphosis was imminent (to prevent drowning), and we recorded any resulting changes in species' abundances.

We administered active *Bd* zoospores into tanks on days 1, 11, and 18 of the experiment to mimic episodic invasions. We used a global pandemic lineage (GPL) *Bd* strain isolated from a *Salamandra salamandra* larva at the same sites where experimental animals were collected. We counted zoospores using a hemocytometer and adjusted the total volume of inoculate administered to achieve desired concentrations of 18,000–24,000 zoospores/L. We administered equal concentrations into tanks across all treatments for all three exposures.

We haphazardly selected 10 salamanders (or every individual in tanks with $n < 10$) to sample for infection across three phases of the experiment—day 2 (initial phase), day 15 (intermediate phase), and day 30 (final phase)—by rubbing a sterile swab across the entire body surface and returned them to the tanks. We sampled frogs and toads (larvae and some metamorphs at this point) once at the end of the experiment (~day 30) because larval stages of these species cannot be sampled using nondestructive methods. We collected tissue from the keratinized mouthparts for frogs and toads and either tail or toe clips from postmetamorphic stages, which have keratinized skin on their whole body.

We detected *Bd* from samples using standardized DNA extraction and qPCR procedures (Boyle et al. 2004). Briefly, we quantified *Bd* DNA on swabs in duplicate using qPCR diagnostics, negative controls, and four concentration standards serving as positive controls (Garner et al. 2009; Luquet et al. 2012; Bielby et al. 2015). A sample was considered positive when both duplicates amplified or when rerunning single amplifications generated a clear positive. *Bd* loads are reported here in genomic equivalents (GEs), where one GE is equivalent to a single zoospore. We considered GE values of at least 0.01 GE to be positive for infection.

Data Analysis

We used infection prevalence (proportion of animals infected) at the end of the experiment as our main measure of invasion outcomes. When calculating infection prevalence for whole communities, we extrapolated infection data from the 10 sampled individuals of each species to the total final abundance for that species. We also calculated the mean infection loads in communities at the end of the experiment as a measure of infection intensity. We report infection loads as GEs, which we log transformed (+1 to allow for transformation of zero values, as we did not have enough power to analyze infection loads of infected individuals

exclusively) to achieve normal distributions. Because yearling salamanders potentially tested positive for *Bd* at the start of the experiment, we also considered the role of these hosts in seeding infections in communities by calculating their infection prevalence and mean infection loads during the initial phase (day 2) of the experiment. Swabs collected from salamanders during the intermediate phase of the experiment (day 15) were correlated with the final samples collected at the end of the experiment. Given this and that we were most interested in infection outcomes, we omitted intermediate phase swabs from our analyses.

For all statistical modeling, we used an information theoretic approach involving comparison of the performances of multiple model subsets (multimodel inference) in explaining infection data, using Akaike's information criterion for small sample sizes (AICc) as the metric for comparison (Burnham and Anderson 2002; Harrison et al. 2018). The modeling was performed in R (R Core Team 2019) using packages specified below.

Infection Dynamics in the Numerically Dominant Host Species. We first characterized temporal infection dynamics in salamander larvae alone, ignoring the community context, to determine whether *Bd* dynamics could be characterized solely from the numerically dominant host. We examined changes in salamander infection over time using generalized linear mixed models. We used the lme4 package in R (R Core Team 2019) to run the models. The first model used mesocosm-level infection prevalence in salamanders as the response and a binomial error structure, and the second model used mesocosm-level mean infection loads in salamanders (log-transformed GE + 1) as the response and a Gaussian error structure (see table S2 for model formulas). Both models included the phase of the experiment (initial or final) as a fixed effect to capture temporal variation and mesocosm as a random intercept term to account for repeated sampling.

Multihost Infection Dynamics When Distinguishing All Host Species. We next characterized infection prevalence and intensity among all host species. Doing so allowed us to assess whether specific host species drove infections in co-occurring host species, thus acting as key hosts in the community. We performed multimodel inference as a preliminary examination of associations between the numbers of infected hosts for a given host species and the attributes of co-occurring host species in communities (see the supplemental PDF for detailed methodology). The analysis indicated positive associations based on the number of infected co-occurring hosts, specifically between infected frogs and toads (see "Results" for further details). We used this information to outline five possible pathways by which *Bd* infections circulated between host species (table 1).

Table 1: Drivers of *Batrachochytrium dendrobatidis* (*Bd*) dynamics in communities comprising salamanders, frogs, and toads

Scenario	Verbal explanation of models	Model components	Supported
1. Frogs drive infection dynamics	Infected frogs facilitate infection establishment in toads and salamanders	Toads $\text{infected}_{\text{FINAL}}$ ~ frogs $\text{infected}_{\text{FINAL}}$ Salamanders $\text{infected}_{\text{FINAL}}$ ~ frogs $\text{infected}_{\text{FINAL}}$	✓
2. Toads drive infection dynamics	Infected toads facilitate infection establishment in frogs and salamanders	Frogs $\text{infected}_{\text{FINAL}}$ ~ toads $\text{infected}_{\text{FINAL}}$ Salamanders $\text{infected}_{\text{FINAL}}$ ~ toads $\text{infected}_{\text{FINAL}}$	✓
3. Salamanders drive infection dynamics	Infected salamanders facilitate infection establishment in frogs and toads	Frogs $\text{infected}_{\text{FINAL}}$ ~ salamanders $\text{infected}_{\text{FINAL}}$ Toads $\text{infected}_{\text{FINAL}}$ ~ salamanders $\text{infected}_{\text{FINAL}}$	
4. Salamanders seed infections, and frogs drive infection dynamics	Initially infected salamanders facilitate infections in frogs, which then facilitate further infections in frogs and salamanders	Frogs $\text{infected}_{\text{FINAL}}$ ~ salamanders $\text{infected}_{\text{INITIAL}}$ Toads $\text{infected}_{\text{FINAL}}$ ~ frogs $\text{infected}_{\text{FINAL}}$ Salamanders $\text{infected}_{\text{FINAL}}$ ~ frogs $\text{infected}_{\text{FINAL}}$	
5. Salamanders seed infections, and toads drive infection dynamics	Initially infected salamanders facilitate infections in toads, which then facilitate further infections in frogs and salamanders	Toads $\text{infected}_{\text{FINAL}}$ ~ salamanders $\text{infected}_{\text{INITIAL}}$ Frogs $\text{infected}_{\text{FINAL}}$ ~ toads $\text{infected}_{\text{FINAL}}$ Salamanders $\text{infected}_{\text{FINAL}}$ ~ frogs $\text{infected}_{\text{FINAL}}$	

Note: Shown are five scenarios for *Bd* circulation between hosts. The scenarios were informed by results from multimodel inference and assessed using structural equation models. The "supported" column denotes models that were supported initially by multimodel inference and subsequently by structural equation models.

We compared support for the different pathways of infection using piecewise structural equation models (SEMs). Unlike traditional SEMs, piecewise SEMs permit model fitting with smaller data sets and with responses with nonnormal distributions (Lefcheck 2016). Piecewise SEMs integrate multiple linear models with distinct responses into a network of interlinked variables and allow for the direction of each link to be estimated (Lefcheck 2016). Our network comprised final numbers of infected individuals in the three focal hosts, as well as a fourth variable for initially infected salamanders (fig. S2). We considered only mesocosms containing all three host species to allow fitting of all model sets ($N = 21$) and because we were interested in how *Bd* circulated when all host species were present. We constructed SEMs using the piecewiseSEM package in R (Lefcheck 2016) and used the psem() function to estimate their AICc values and standardized regression coefficients.

Variation in Community-Level Infection Prevalence and Intensity. We next examined how the observed routes of infection between host species translated to the importance of host species identities in explaining community-level patterns of infection. Specifically, we examined how different levels of detail describing the host community affected our ability to predict community-level infection prevalence, comparing the following scenarios: (1) community-level infection prevalence varies randomly and is not influenced by host species richness or composition, (2) community-level infection prevalence and intensity are predicted by host species richness alone (least detail; i.e., host species identity does not matter), (3) community-level infection prevalence and intensity are predicted by the proportion of auxiliary hosts in the community, irrespective of their identity (intermediate detail; i.e., identities of salamanders vs. "others" matters), and (4) community-level infection prevalence and intensity are predicted by the relative proportion of frogs, toads, and salamanders in the community (most detail; i.e., identities of all host species matters)

We ran generalized linear models (GLMs) in R to assess support for the above scenarios, running separate model sets for community-wide infection prevalence (overall proportion of hosts infected, regardless of species identity) and mean infection loads (again, averaged over all hosts, regardless of species). We used a binomial error structure for the former model set and a Gaussian error structure for the latter model set. For scenario 1 we ran a GLM including only the intercept term, as a null model. Models for scenarios 2–4 contained host species richness as a fixed effect. For scenario 2 we ran a GLM that included only host species richness as a fixed effect. We expanded this model for scenario 3 to include the proportion of auxiliary hosts (frogs and toads) in communities as a second fixed effect in addition to host species richness. For scenario 4, we added two fixed effects—the proportion of toads and the proportion of frogs in communities—to fully distinguish host species identities in the communities (proportion of salamanders was implicit). We compared which models, and therefore which level of detail about host communities, provided the most accurate yet parsimonious fit to the data according to AICc values.

Species-Specific Contributions to Transmission. To gain deeper insight into the relative contributions each host species made to *Bd* transmission dynamics within our assembled communities, we fitted a dynamic transmission model to the data across all three-species mesocosms (63 data points, 21 tanks × 3 species final infection data) and estimated the key epidemiological parameters for each species. We assumed that the dynamics of transmission within each tank j could be described by the following equations:

$$\frac{dH_i^j}{dt} = -\mu_i^j H_i^j,$$

$$\frac{dI_i^j}{dt} = \beta_i (H_i^j - I_i^j) Z^j - I_i^j (\mu_i^j + \sigma_i),$$

$$\frac{dZ^j}{dt} = \sum_{k=\{\mathrm{S,T,F}\}} \lambda_k I_k^j + \Phi_{(t)} - Z^j \left(\gamma + \sum_{k=\{\mathrm{S,T,F}\}} H_k^j \beta_k \right),$$

where H_i^j is the total abundance of host species i (i = S [salamanders], T [toads], F [frogs]), I_i^j is the number infected of each of those species in tank j, and Z^j is the number of zoospores in tank j.

The parameters β_i, λ_i, and σ_i are the species-specific transmission rate, zoospore shedding rate, and host recovery rate, respectively, for host species i, and γ is the mortality rate of spores. Note that we allow for additional loss of zoospores as a result of removal through contact with hosts, as a potential dilution mechanism. Furthermore, $\Phi_{(t)}$ is a time-dependent function representing the input of zoospores into each tank during the experiment; if the time t is a day in which zoospores were administered, then $\Phi_{(t)}$ is set to the number of spores released at that time point, otherwise $\Phi_{(t)} = 0$. Note that all of the above parameters are assumed to be the same across all tanks j. In addition, μ_i^j is the tank-specific loss rate of host species i in tank j, which we estimate directly from the observed counts of the initial ($H_{i(0)}^j$) and final ($H_{i(\tau)}^j$, where τ is the end point of the experiment) number of individuals, assuming constant exponential loss of hosts throughout the experiment (i.e., $\mu_i^j = -\ln(H_{i(0)}^j / H_{i(\tau)}^j)$). We also assume that zoospores last on average 1 day (Longcore et al. 1999), so $\gamma = 1\ \mathrm{day}^{-1}$. That leaves β_i, λ_i, and σ_i to estimate for each of the three host species (nine parameters in total), again

assuming that these parameters have the same values across all tanks.

The above model predicts the change in total abundance of each species, H_i^j; the number infected of each species, I_i^j; and the number of zoospores, Z^j, in each tank, throughout the experiment. The unknown parameters (β_i, λ_i, and σ_i) were estimated by fitting these simulated dynamics to the observed data of the final numbers of infected salamanders, frogs, and toads across all tanks simultaneously (total of 63 data points across the 21 three-species tanks). Model fitting was carried out by Metropolis-Hastings mcmc using the BayesianTools R package (Hartig et al. 2019), assuming a binomial likelihood function to describe the number of infected hosts of each species in each tank, summed across all tanks. We used uninformative priors for each parameter, and three chains of 100,000 iterations were run with a burn-in time of 40,000 iterations with thinning every 50 iterations. Convergence was assessed using the Gelman-Rubin statistic (which was less than 1.05 for all parameters, so convergence was assumed to have occurred).

Having estimated the relevant epidemiological parameters, the contribution of each host species i to *Bd*'s basic reproduction number, R_0, in each tank j was calculated as

$$R_{0,i}^j = \frac{\beta_i \lambda_i H_i^j}{\mu_i^j(\gamma + \sum_k H_k^j \beta_k)},$$

and the total R_0 of *Bd* in tank j was calculated as

$$R_{0,\mathrm{TOT}}^j = \sum_i R_{0,i}^j, \quad i = \{\mathrm{S}, \mathrm{T}, \mathrm{F}\}.$$

These were calculated for each of 3,000 samples drawn from the posterior parameter distribution sets, and results are expressed as the median and 95% credible intervals from those calculated values. Data and code for all analyses and figures are stored in the Dryad Digital Repository (https://doi.org/10.5061/dryad.2v6wwpznk; Daversa et al. 2022).

Results

Infection Dynamics in the Numerically Dominant Host Species

Bd did not thrive in the dominant host species. Although 31% of salamanders (166 of 525) spanning all 36 mesocosms exhibited *Bd* infections in the initial phase of the experiment, many salamanders cleared infections throughout the course of the experiment (fig. 1*a*). As a result, infection prevalence in salamanders was greatly reduced in the final phase (13% prevalence on average), compared with the initial phase, irrespective of the host community composition (fig. S3). In addition, many salamanders metamorphosed during the experiment (fig. S4; table S1), and there was no indication that infection status influenced likelihood of salamander metamorphosis. There was no clear pattern in how mean *Bd* loads of infected salamanders changed over the course of the experiment (fig. 1*b*).

Multihost Infection Dynamics When Distinguishing All Host Species

Multimodel inference indicated that the final abundances of host species were poor predictors of *Bd* infections. Rather, distinguishing the number of infected co-occurring hosts was important. There was also evidence that the final number of infected frogs in communities was positively associated with the final number of infected toads in communities, and vice versa (see the supplemental PDF for detailed results), partially supporting scenarios 1 and 2 (table 1) for *Bd* dynamics in multihost communities. Neither the number of initially infected salamanders nor the number of infected salamanders at the end of the experiment predicted the final number of toad or frog infections, providing initial evidence against scenarios 3, 4, and 5 for *Bd* dynamics. The SEMs corroborated both lines of evidence and clarified the pathways by which *Bd* circulated between different host species. In the best-performing SEM, infected frogs facilitated infections in toads, in terms of both the number infected and the mean infection loads (fig. S2*a*; table S7, pt. a, scenario 1). The reciprocal pathway from infected toads to infected frogs was also significant in a closely ranked model (fig. S2*b*; table S7, pt. a, scenario 2). Therefore, infections circulated between frogs and toads with no clear directionality, but there was clear agreement that salamanders did not play a significant role in driving infection levels in either species (fig. 2).

Variation in Community-Level Infection Prevalence and Intensity

The null model for community-level infection prevalence was the worst-performing model examined (table 2; ΔAICc scenarios 3 vs. 1 = 48.2), confirming that community-wide infection prevalence was influenced by some aspect of host species richness (fig. 3*a*; table 2; ΔAICc scenarios 2 vs. 1 = 16.7). However, distinguishing the proportion of auxiliary host species better predicted community-wide infection prevalence than host species richness alone (table 2; ΔAICc scenarios 3 vs. 2 = 31.52). Further distinguishing between frogs and toads did not improve predictions for community-wide infection prevalence (table 2; ΔAICc scenarios 4 vs. 3 = 1.16). Community-level mean infection loads also increased with more host species in communities (fig. 3*b*), and there was no evidence that distinguishing auxiliary species from salamanders predicted community-level mean infection loads at the end of the experiment better than host species richness (table 2; ΔAICc scenarios 3 vs. 2 = 0.04).

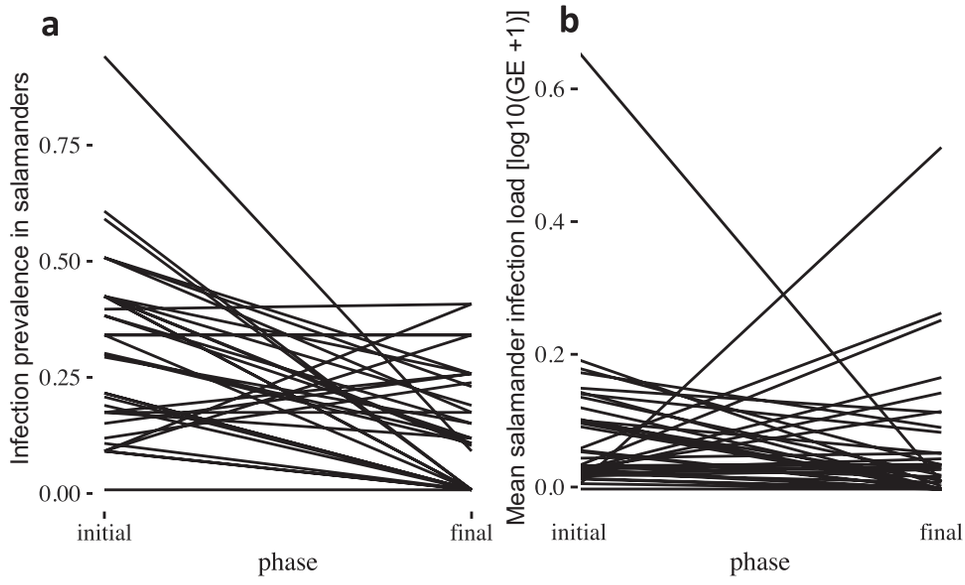

Figure 1: *Batrachochytrium dendrobatidis* (*Bd*) did not thrive in the dominant host species. Temporal dynamics in the mean number of infected salamanders in experimental communities (*a*) and the mean *Bd* loads of infected salamanders in experimental communities (*b*). Lines denote individual host community replicates (i.e., mesocosms). The initial phase denotes samples for *Bd* collected on day 2, and the final phase denotes samples for *Bd* collected on the last day of the experiment. GE = genomic equivalent, which is equivalent to a single zoospore.

Species-Specific Contributions to Transmission

The epidemiological model provided a reasonable fit to the observed data from the three-species tanks (correlation between observed and median predicted numbers infected = 0.70; $R^2 = 0.50$; fig. S7). Examining the posterior parameter distributions for the fitted model suggested that median estimated transmission rates for salamanders were considerably lower (~80%) than those for frogs and toads (fig. 4*a*). Median estimated shedding rates of frogs were ~4 times higher than salamanders, and recovery rates were roughly equal for all species. Together these effects translated into salamanders contributing much less to the overall R_0 of *Bd* compared with the other two species (fig. 4*b*). As such, there was a general negative relationship between the proportion of salamanders in each tank and the overall $R_{0,TOT}$ value for that tank (fig. 4*c*). However, although frogs had the highest shedding rates overall, varying the initial ratio of frog and toad abundances had little consequence for the overall $R_{0,TOT}$ values across the different three-species tanks (fig. 4*d*), suggesting that frogs and toads were largely interchangeable and nondifferentiable in their contributions to overall transmission.

Discussion

Our mesocosm experiment uncovered evidence that host species exhibiting different epidemiologically functional traits—transmission, shedding, and recovery—may play similar epidemiological roles in community-level *Bd* dynamics. Interspecific differences in epidemiologically functional traits are well documented in other amphibian-*Bd* systems (Reeder et al. 2012; Gervasi et al. 2013; Venesky et al. 2014; Han et al. 2015; Fernández-Beaskoetxea et al.

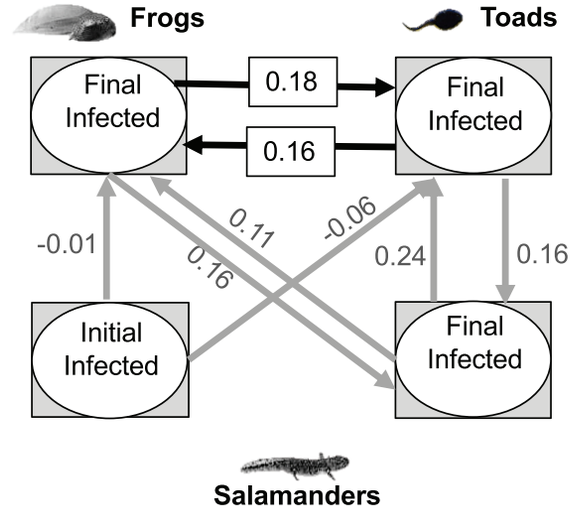

Figure 2: Frogs and toads facilitated infections in each other. The number of infected toads increased with more infected frogs in communities, and vice versa, as shown by the black arrows. Nonsignificant relationships ($P \geq .05$) are denoted by gray arrows, and values denote the standardized regression coefficients.

Table 2: Community-level infection prevalence and mean infection loads

Model term(s)	Infection prevalence			Infection loads		
	Coefficient	SE	ΔAICc	Coefficient	SE	ΔAICc
	Scenario 1: host community characteristics do not predict invasion outcomes					
—	—	—	48.22	—	—	10.00
	Scenario 2: host species richness best predicts invasion outcomes					
Species richness	.61	.15	31.52	.50	.14	.04
	Scenario 3: distinguishing dominant vs. auxiliary hosts best predicts invasion outcomes					
Species richness	.26	.18		.37	.16	
Proportion of auxiliary hosts (frogs and toads)	2.93	.54	.00	.65	.47	.00
	Scenario 4: distinguishing all host species best predicts invasion outcomes					
Species richness	.27	.18		.37	.17	
Proportion of frogs	3.14	.58	1.16	.68	.53	1.99
Proportion of toads	2.68	.61		.62	.56	

Note: Shown are summaries of generalized linear model outputs testing our scenarios for how the level of detail describing host communities (ignoring host species identities, partially specifying host species identities, fully specifying host species identities) affected predictions for community-level infection prevalence. Models of infection prevalence used a binomial error structure, and models of infection loads used a Gaussian error structure. Scenario 3 had the best-performing model according to ranking of Akaike's information criterion for small sample sizes (AICc); ΔAICc indicates the difference in AICc units between the relevant model and the best-performing model. Dashes signify that no fixed effects were included in the null model for scenario 1.

2016), leading some to posit that host species identity is critical for understanding multihost *Bd* dynamics (Gervasi et al. 2013). Our findings challenge this argument by showing that sometimes interspecific differences in host functional traits scale up to influence community-level infection dynamics (exemplified here by the differences between salamanders and the other species), but sometimes they do not (exemplified here by frogs and toads).

Similar epidemiological roles exhibited by frogs and toads resulted in an intermediate level of detail on host communities being optimal for predicting the outcomes of *Bd* invasions. Distinguishing between salamanders and the other host species (frogs and toads) was important for explaining variation in infection prevalence and R_0 of invaded host communities. Distinguishing frogs and toads was not necessary, however, because their contribution to *Bd* transmission overlapped. The best predictor of invasion outcomes was the proportion of salamanders versus other host species in communities. More detail on host communities is not always better in terms of characterizing infection dynamics.

Salamanders consistently exhibited vastly different traits from frogs and toads, resulting in consistently negligible contributions to R_0. The distinctly low rates of shedding and, in particular, transmission exhibited by salamanders scaled up to impact community R_0 and infection prevalence negatively, such that overall $R_{0,TOT}$ was estimated to decrease with increasing salamander abundance (fig. 4*c*). Hence, salamanders played a dilution role in our system, making their taxonomic identities important to distinguish from the other species. As for the frogs and toads in our experiments, our fitted mechanistic model suggested that these two host species showed differences in their median estimated shedding rates, which translated into different species-specific contributions to R_0. However, in the context of overall community transmission dynamics, the variation in abundances and community compositions across our experiment resulted in those species-specific differences having only marginal effects on overall $R_{0,TOT}$ values, as the relative abundance of frogs and toads varied across tanks (fig. 4*d*). These findings of different functional traits (shedding rates), yet similar epidemiological roles exhibited by frogs and toads, raise the question of when differences in host functional traits make host identity relevant to community-level infection dynamics. Definitively answering this question would require further testing, but our experiments hint that the degree of difference in mean trait values, combined with the amount of trait variation that a species exhibits, is an important determinant. In our system, frogs may have been predicted to contribute the most to R_0 on average, but there was substantial variation in their estimated R_0 contributions that overlapped with the R_0 contributions of toads. The wide trait variation of frogs, together with variation in abundances and community compositions, likely moderated the epidemiological differences between frogs and toads when scaling up to community-level *Bd* dynamics.

Documented within-species variation in functional traits of *Bd* hosts (Briggs et al. 2010; Raffel et al. 2015; Daversa

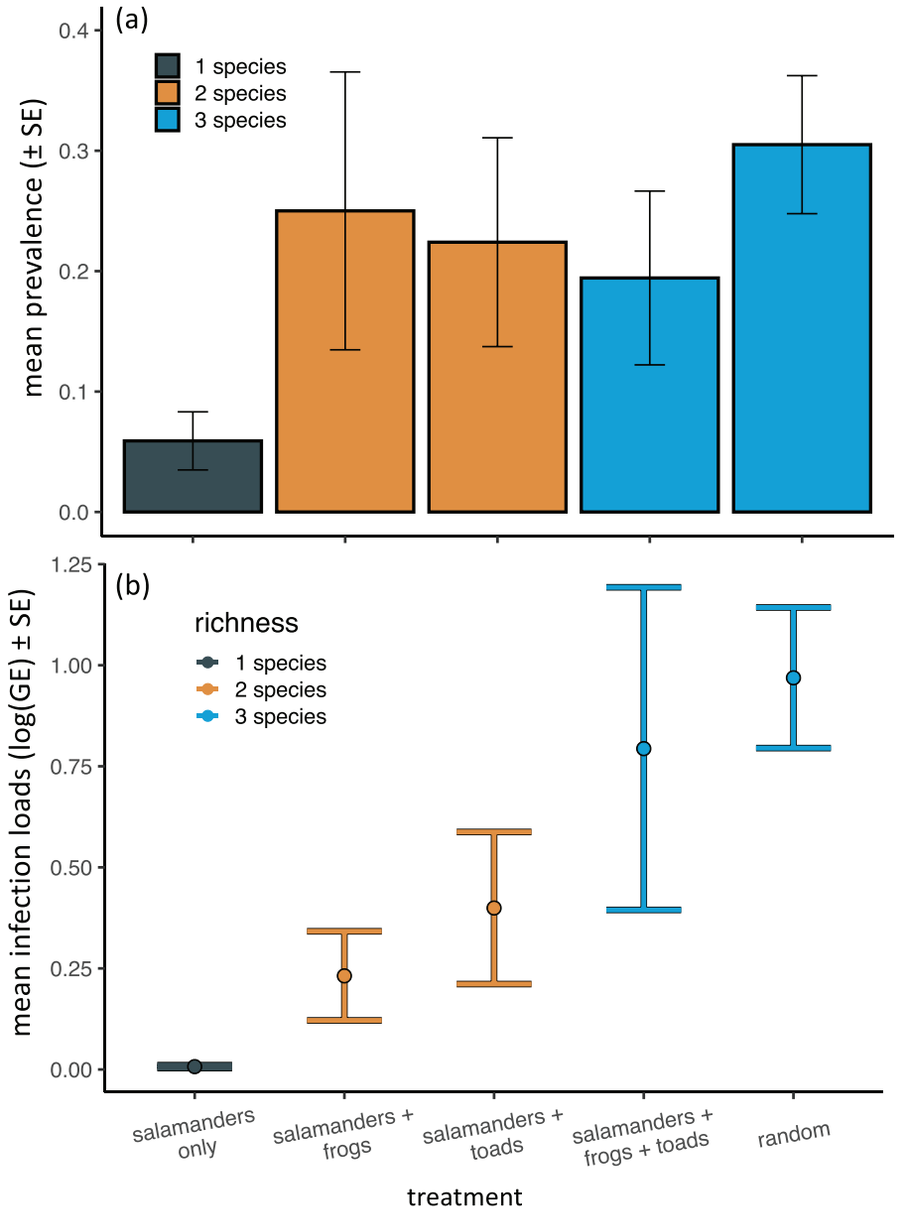

Figure 3: Community-level *Batrachochytrium dendrobatidis* (*Bd*) prevalence and intensity varied by host community richness and composition. *a*, Mean *Bd* prevalence at the end of experiments. *b*, Mean infection loads exhibited by infected individuals in the experimental host communities that varied in species richness and composition. Data were pooled across all host species. In both panels, error bars denote the standard error of the mean values among replicate communities. GE = genomic equivalent, which is equivalent to a single zoospore.

et al. 2018; McMillan et al. 2020) suggests that overlaps in species contributions to *Bd* transmission, like those we observed between frogs and toads, may be common in other host assemblages. We therefore expect functional similarities among host species to occur in other systems as well. Overlapping host traits across species may also produce functional similarities as more species are incorporated into systems. Whereas we focused here on experimental three-species systems, many *Bd* systems in the wild comprise higher levels of host species diversity. Our findings point out that overlaps in rates of transmission and shedding of different host species can result in diverse host species communities exhibiting reduced functional diversity in terms of *Bd* circulation and maintenance.

Host species richness was a strong predictor of the mean infection loads in host communities. Although challenges

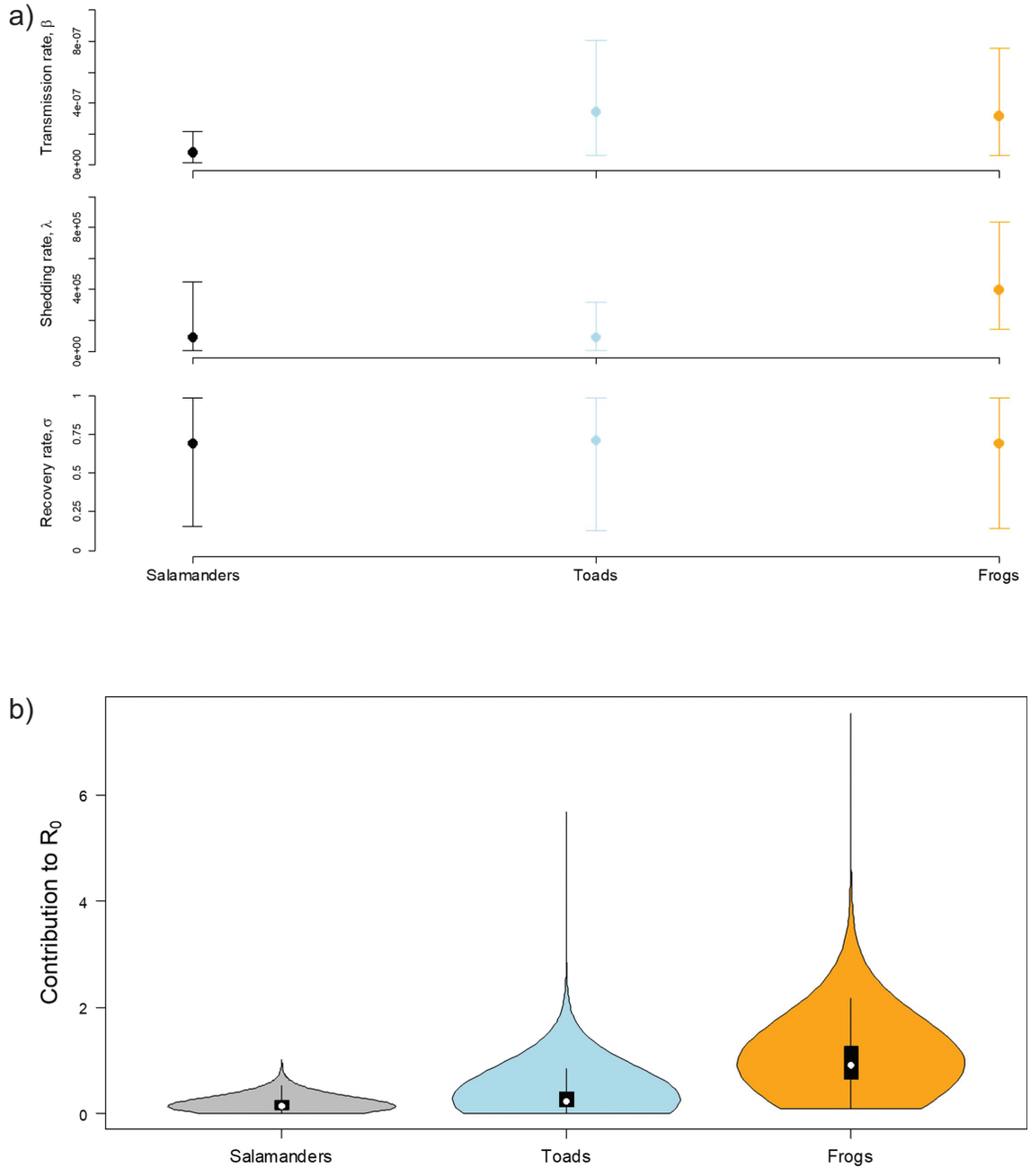

Figure 4: Fitting of a mechanistic epidemiological model suggests that salamanders played a much smaller role in *Batrachochytrium dendrobatidis* (*Bd*) transmission compared with frogs and toads and that frogs and toads make similar contributions to the overall basic reproduction number, R_0, of *Bd*. *a*, Parameter estimates of transmission rates (β_i), zoospore shedding rates (λ_i), and recovery rates (σ_i) for salamanders, toads, and frogs, showing low estimates of salamander transmission rates relative to the other species. Points indicate medians, and bars indicate 95% credible intervals (CIs) from 3,000 draws from posterior estimated parameter distributions. *b*, Estimated species-specific contributions by salamanders, toads, and frogs to R_0, generated from 3,000 draws from the posterior parameter distributions (violin plot shows a kernel density plot over the range of the data; the white point indicates the median, the black box indicates the interquartile range, and the whiskers indicate the lower/upper adjacent values). Salamanders contribute very little to the R_0 of *Bd* in each tank.

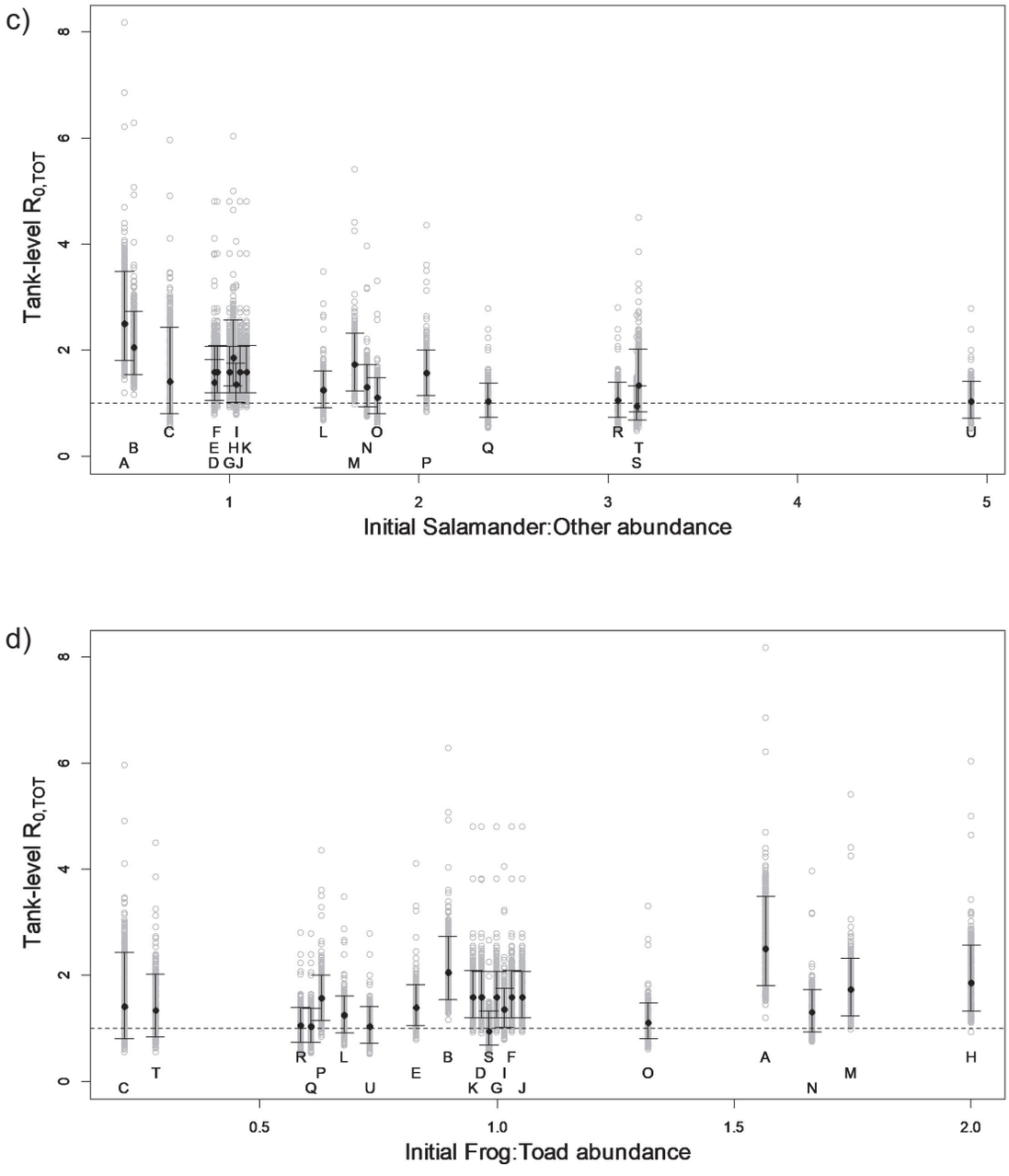

Figure 4: (*Continued*) *c*, Relationship between estimated tank-level $R_{0,TOT}$ values and the ratio between the initial number of salamanders to the other species (frogs and toads combined) from 3,000 draws from posterior estimated parameter distributions (gray points) and median and 95% CIs (black points and bars) for each tank. Overall, there is a strong negative correlation, such that increasing proportional abundance of salamanders results in a reduction in overall R_0. *d*, As in *c*, but with the ratio between initial number of frogs to toads on the *x*-axis (high values indicate increasing abundance of frogs relative to toads in the tanks) showing negligible effect on tank-level $R_{0,TOT}$, indicating that frogs and toads are largely epidemiologically interchangeable across these communities. The uppercase letters in *c* and *d* denote the same tanks in each figure.

in obtaining reliable infection load data from qPCR should be taken into account when interpreting patterns in infection loads (Clare et al. 2016), our infection load data provide evidence that host species richness can influence infections loads. In terms of effects of host species richness on *Bd* prevalence, we found clear differences between single-species (salamander only) and multispecies (containing either frogs or toads or both) communities, whereas two- and three-species communities exhibited similar levels of *Bd* prevalence. Hence, increasing from one species to multiple species actually amplified community-level infection prevalence, in contrast to reported dilution effects (Venesky et al. 2014). This is likely due to the design of our experiment; single-species communities were always comprised of salamanders, whereas multispecies communities always contained frogs or toads. Now knowing the epidemiological roles of the hosts, it makes sense that *Bd* prevalence in single-species (i.e., salamander only) communities was always lower than that observed in multispecies communities. Expanding our experimental design to include single-species communities of frogs and toads would likely change the relationship between host species richness and *Bd* prevalence observed here. It is therefore unlikely that there is a general rule, even in our simplified communities, that increasing host species richness inevitably increases or decreases transmission; the outcome would depend at least to some extent on which species are present in the lower-richness communities and on which species are added to create new communities.

Although salamanders were not the drivers of *Bd* persistence in our mesocosm experiments, their population in the field site at Guadarrama continues a decline that began with the discovery of *Bd* at the site nearly two decades ago (Bosch et al. 2018). To the extent that *Bd* is driving these declines, our findings suggest that management strategies for counteracting salamander declines will need to broaden interventions to co-occurring amphibian species, such as spiny toads and tree frogs, that may actually be responsible for *Bd* maintenance in the communities, with spillover into salamanders potentially driving their decline. More generally, our findings provide promise that tailoring management interventions to each host species may not be necessary when, as we observed in frogs and toads, the epidemiologically functional traits of species are similar.

The trivial epidemiological role that yearling salamander larvae played in our experiment does not imply that the species as a whole is inconsequential to *Bd* dynamics in natural communities. Fire salamanders exhibit multiple life stages, including an overwintering larval stage. *Bd* prevalence in overwintered salamander larvae can reach near 100% early in breeding seasons (Bosch et al. 2018, 2020). Furthermore, overwintering salamander larvae are one of the few hosts that remain in ponds during winter months, making them an important seasonal reservoir of *Bd* that reactivates transmission within ponds in the springtime (Medina et al. 2015). Salamanders therefore clearly impact *Bd* dynamics at specific life stages, but our experiment indicates that *Bd* cannot persist in salamanders alone, as hypothesized previously (Medina et al. 2015), at least not during latter stages of breeding seasons when overwintered larval stages are absent. Collectively, studies of salamanders emphasize that the role a host species plays in *Bd* dynamics may change dramatically across different stages of ontogeny. In the multitude of systems that exhibit distinct life stages like amphibians, host diversity may be a function of both the number of host species and the number of different susceptible life stages of those species.

Because host ontogeny in our system is intertwined with seasonality, our data on new cohorts of hosts lay groundwork for bridging the community ecology of infectious diseases with the seasonality of infectious diseases. Amphibians exhibit distinct phenologies that create dynamic compositions of host species for *Bd* to infect throughout the year. Extending our approach to multiple seasons could assess how the host community context of *Bd* varies across seasons to drive longer-term *Bd* dynamics. Amid increasingly dynamic and changing environmental conditions, accounting for seasonal fluctuations in host community characteristics is likely to be critical for mitigating the harmful consequences of future parasite invasions.

Conclusion

Asking what level of detail is needed to understand the outcomes of invasions by generalist parasites revealed new insights into multihost transmission dynamics. First, host species that exhibit different functional traits (e.g., shedding rates, as seen with the frogs in this study) may make similar contributions to the overall maintenance of parasites in larger ecological communities. Second, the identities of host species with overlapping contributions to R_0 may be interchangeable in models of multihost infection dynamics. Teasing apart species-specific contributions to pathogen transmission and maintenance is both important and a major logistical challenge, and experimental data are vital to clarifying understanding of transmission dynamics in such potentially complex systems. In particular, this work builds on findings from related studies (Gervasi et al. 2013; Venesky et al. 2014; Han et al. 2015) to show that there can be limits to the importance of host species identities in multihost infection dynamics.

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Statement of Authorship

All authors contributed to the original idea and design for the study. J.B. led animal collection and husbandry and ran the experiments. D.R.D., A.F., and A.M. executed the data analyses. A.F. completed the predictive disease modeling. D.R.D. wrote the original draft of the manuscript, which was improved through revision by all coauthors.

Data and Code Availability

Raw data and R scripts are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.2v6wwpznk; Daversa et al. 2022).

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