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ARTICLE
Disease Ecology

Pathogenic fungus causes density- and trait-mediated trophic cascades in an aquatic community

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Abstract

Pathogens can alter species composition and ecosystem function by causing direct and indirect effects on communities. Zoospores of the chytrid fungus *Batrachochytrium dendrobatidis* (hereafter, Bd), a pathogen implicated in worldwide amphibian declines, can be consumed by filter-feeding zooplankton and can damage mouthparts of infected amphibian larvae. Consequently, we hypothesized that this pathogen would affect the abundance of zooplankton and survival and feeding abilities of larval amphibian hosts. In turn, this could affect the algal food resources of zooplankton and tadpoles, which can include phytoplankton and periphyton. We tested these hypotheses by manipulating the presence of western toad (*Anaxyrus boreas*) larvae and Bd in outdoor mesocosms and quantifying the densities of amphibians, zooplankton, phytoplankton, and periphyton. Bd infections reduced amphibian larval densities, but this only weakly benefitted periphyton (a density-mediated indirect effect). After controlling for larval densities, mesocosms with Bd-exposed larvae had significantly more periphyton biomass than mesocosms with larvae but no Bd, consistent with infection-induced mouthpart damage reducing larval feeding rates on attached algae (a trait-mediated indirect effect). In fact, the estimated trait-mediated effect of Bd on periphyton biomass was larger than the density-mediated effect. However, we did not find evidence that Bd exposure triggered a switch to filter-feeding phytoplankton. The presence of Bd was associated with increased copepod abundance, consistent with zooplankton consuming chytrid zoospores. These results suggest that Bd has the potential to cause both trait- and density-mediated indirect effects that can alter community composition and perhaps the primary productivity of freshwater ecosystems.

KEYWORDS
Batrachochytrium dendrobatidis, chytrid fungus, disease-mediated, pathogen, trophic cascade

INTRODUCTION

Parasitism as a consumer strategy is ubiquitous. Recent estimates suggest that parasites comprise over 30% of all species, although this is likely an underestimate (de Meeûs & Renaud, 2002; Dobson et al., 2008). Due to their abundance in natural systems, parasites play critical roles in food web dynamics and trophic interactions (Dobson et al., 2008; Lafferty et al., 2008). However, until recently, research has focused predominately on the direct effects of parasites on their hosts and has neglected indirect effects caused by parasites (Buck & Ripple, 2017). One of the most compelling examples of how infectious agents (i.e., parasitoids, pathogens, parasitic castrators, macroparasites, and trophically transmitted parasites) shape ecosystem structure and function in a density-mediated fashion is the trophic cascade caused by the viral pathogen rinderpest. Rinderpest outbreaks reduced wildebeest population density and herbivory, allowing grass to flourish. This, in turn promoted fire, suppressing tree populations in the Serengeti (Holdo et al., 2009; Sinclair, 1995). Similarly, sea star wasting disease, which is likely caused by an unidentified densovirus, reduced sea star population density on the US Pacific coast causing cascading effects on sea urchin density and kelp cover in the rocky intertidal zone (Schultz et al., 2016). Infectious agents also can trigger trait-mediated indirect effects. For example, the digenean trematode *Cryptocotyle lingua*, reduced algal grazing by infected snails by impairing their digestive system, triggering cascading effects on macroalgal communities on the US Atlantic coast (Wood et al., 2007). Clearly, infectious agents can have cascading effects on ecosystem function via a variety of effects on hosts.

Density- and trait-mediated indirect effects have been illustrated numerous times in the predator–prey literature. More specifically, predators that capture and kill their prey cause numerical reductions in prey populations, which can benefit primary producers (Schmitz et al., 2004). Alternatively, the presence of natural enemies can trigger behavioral changes in prey, reducing herbivory, and indirectly benefitting primary producers (Schmitz et al., 2004). However, trophic cascades triggered by infectious agents are unique because unlike predators, infectious agents (and micropredators) can consume prey with sublethal effects (Lafferty & Kuris, 2002). Therefore, they can cause trait-mediated indirect effects through their consumptive (in addition to nonconsumptive) effects (Buck, 2019; Raffel et al., 2008).

The chytrid fungal pathogen *Batrachochytrium dendrobatidis* (Bd), which causes the disease chytridiomycosis, is linked to amphibian population declines and extinctions worldwide (Stuart et al., 2004; Skerratt et al., 2007; Venesky et al., 2014). Bd has a global distribution and infects a variety of amphibian hosts (Liu et al., 2012; Olson et al., 2021; Xie et al., 2016). Motile Bd zoospores can encyst in the keratinized tissues of metamorphosed amphibians (McMahon & Rohr, 2015), which can impair osmoregulation, ultimately leading to cardiac arrest (Voyles et al., 2009). However, in larval amphibians, infection is isolated to keratinized mouthparts and can cause decreased growth and development, reduced feeding and smaller size at metamorphosis, in addition to reduced survival (Garner et al., 2009; Kilpatrick et al., 2010; McMahon et al., 2013; Parris et al., 2004; Parris & Cornelius, 2004; Rachowicz & Vredenburg, 2004). Larval infection with Bd can also cause oral deformities and influence feeding kinematics (Blaustein et al., 2005; Rachowicz & Vredenburg, 2004; Venesky et al., 2010).

Research on the amphibian-chytrid system has primarily focused on occurrence patterns geographically or taxonomically, while few studies have tested for cascading effects of Bd on aquatic communities (Blaustein et al., 2012; but see Connelly et al., 2008; Smith et al., 2016), and no study has tested for a trait-mediated trophic cascade triggered by Bd even though it has been hypothesized (Buck et al., 2016). Given that Bd infections are well-documented to cause oral deformities (a morphological trait change) in amphibian larvae that reduce feeding rates (Blaustein et al., 2005; Fellers et al., 2001; Rachowicz & Vredenburg, 2004; Venesky et al., 2009, 2010), we hypothesized that Bd exposure would indirectly increase periphyton biomass through a consumptive trait-mediated indirect effect, as *Anaxyrus* tadpoles have been shown to consume and thus reduce periphyton biomass (Preston et al., 2018; Raffel et al., 2010). Furthermore, Bd could reduce larval densities, indirectly increasing periphyton biomass through a consumptive density-mediated effect. Additionally, because Bd is well-documented to reduce keratin in the mouthparts of amphibian larvae, which are necessary to scrape periphyton but not necessary to filter-feed phytoplankton (Fellers et al., 2001; Rachowicz & Vredenburg, 2004; Wassersug & Yamashita, 2001), we hypothesized that Bd might induce a switch from larvae scraping periphyton to filter-feeding phytoplankton.

Many species consume parasites (e.g., Rohr et al., 2015) and thus, we also hypothesized that Bd might directly and indirectly affect other members of the community that might be capable of consuming Bd. Bd zoospores are between 3 and 5 μm in diameter (Longcore et al., 1999), thus within the preferred food particle size of some cladocerans, such as Daphnia (Geller & Müller, 1981). The consumption of Bd zoospores by zooplankton, specifically cladocerans, has been demonstrated on numerous occasions. Daphnia have been documented to consume Bd zoospores (Buck et al., 2011; Searle et al., 2013), to reduce the density of Bd zoospores in the water (Woodhams et al., 2011), and subsequently to reduce Bd infections in

amphibian larvae (Searle et al., 2013). Other aquatic filter-feeding predators, including amphibian larvae, also have been observed consuming Bd zoospores, which can reduce Bd transmission (Venesky et al., 2014). In wetlands, Bd zoospores can be as dense as three million zoospores per liter (Chestnut et al., 2014), thus possibly serving as an important food item for filter-feeding predators. Hence, we hypothesized that Bd would increase zooplankton densities by serving as an additional prey resource and that zooplankton might affect tadpole infection loads. Conversely, Bd exposure may reduce zooplankton densities if amphibian larvae exposed to Bd switch from scraping periphyton to filter-feeding periphyton, thereby reducing the amount of phytoplankton available. Changes to zooplankton densities might also have cascading effects on phytoplankton, their primary food source. For example, we hypothesized that zooplankton would indirectly benefit amphibian larvae by reducing phytoplankton and its shading effect on periphyton, the primary food source of amphibian larvae (Halstead et al., 2018; Hansson, 1988, 1992; Rohr & Crumrine, 2005; Stevenson et al., 1985). Additionally, because cladocerans, copepods, and amphibian larvae compete for algal resources, we also hypothesized that they might negatively affect one another's abundances via competition (Buck et al., 2015). To address all of these hypotheses, we conducted an experiment that manipulated Bd and amphibian larvae to test the direct and indirect effects of Bd on members of the aquatic community. The full conceptual model of interactions studied herein includes seven distinct taxa (Figure 1).

MATERIALS AND METHODS

Experiment

To test for cascading indirect effects of Bd infection on members of the aquatic community, we conducted a 2×2 fully factorial randomized block experiment. We crossed the presence or absence of Bd with the presence or absence of 40 western toad (*Anaxyrus boreas*) larvae in outdoor mesocosms at the Oregon State University Lewis-Brown Horticulture Farm near Corvallis, Oregon, USA. Each treatment was replicated eight times for a total of 32 mesocosms. Experimental units consisted of 120-L mesocosms. On 25 July 2016, we mounted eight standard microscope slides to the inside of each mesocosm for removal during community sampling to monitor periphyton growth. On 28 July 2016, we added well water, 30-g sterile leaf-litter, and 1 L of water containing zooplankton, phytoplankton, and periphyton from laboratory stocks, then covered each with mesh lids.

Animal husbandry

Partial clutches of western toad eggs were collected on 8 June 2016 from Todd Lake, Oregon (44.0298° N, 121.6853° W). Western toads were ideal for this study for three reasons. First, members of the genus primarily scrape surfaces to feed on periphyton but have also been documented switching from feeding on periphyton to phytoplankton (Beiswenger, 1977; Seale & Beckvar, 1980). Second, western toads are highly susceptible to Bd infection (Gervasi et al., 2013, Gervasi et al., 2017; but see Adams et al., 2017). Additionally, western toads are experiencing Bd-related population declines in some parts of their range (Carey, 1993; Drost & Fellers, 1996; Muths et al., 2003). Eggs were reared in 40-L aquaria and larvae were fed a 3:1 ratio of rabbit chow and Tetramin fish flakes (Tetra, Melle, Germany) every other day until reaching Gosner stage 25–27 (determined by the initial development of the limb bud; Gosner, 1960**)**. On 11 August 2016, larvae were weighed and measured then randomly assigned to half of 32 10-L aquaria (one per mesocosm) filled with 9 L of water and allowed to acclimate for 24 h prior to the exposure of a sham or actual inoculation of Bd (see below) on 12 August 2016. On 25 August 2016, aquaria contents and larvae were poured into 120-L mesocosms. At the end of the experiment, all surviving amphibian larvae were removed from the mesocosms, weighed and measured, euthanized using an overdose of MS-222, and then preserved in 10% formalin solution.

Bd culture and inoculation

Bd strain JEL 274, originally isolated from a western toad in Colorado was plated on 1% tryptone-agar plates and incubated at 20°C (Longcore et al., 1999) for 11 days. On 12 August 2016, two plates were flooded with 10 ml of dechlorinated water and the number of motile zoospores was counted using a hemocytometer following the established protocols (Searle et al., 2011). The broth was diluted with dechlorinated water to obtain a concentration of 1.0×10^4 zoospores/ml. We added 68 ml of inoculum to 9 L Bd-treated aquaria for a total dose of 6.75×10^5 zoospores/ml, which, once diluted in 9 L of water, had a final concentration of 75 zoospores/ml. Larvae in the control aquaria were treated with a broth made from flooding sterile agar plates.

Community

Zooplankton, phytoplankton, and periphyton measurements were taken from mesocosms on 24 August 2016 and every two weeks thereafter for the duration of the 60-day experiment. Sampling methodology followed Buck et al. (2015). Water containing zooplankton and

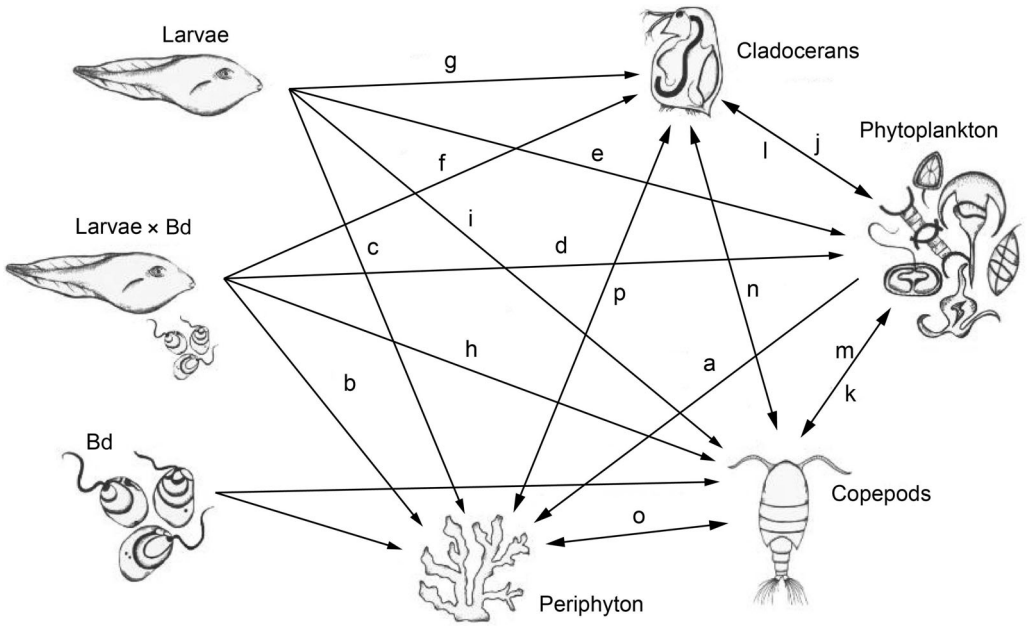

FIGURE 1 The conceptual full path model detailing all hypothesized interrelationships between members of the aquatic community. These include the effects of (a) phytoplankton shading periphyton; toad larvae ((b) Bd-exposed and (c) Bd-unexposed) reducing periphyton biomass through grazing; toad larvae ((d) exposed and (e) unexposed) reducing phytoplankton through grazing; toad larvae ((f) exposed and (g) unexposed) reducing cladocerans through possible competition for algal resources or via passive consumption; toad larvae ((h) exposed and (i) unexposed) reducing copepods through possible competition for algal resources or via passive consumption; zooplankton ((j) cladocerans and (k) copepods) reducing phytoplankton through grazing; phytoplankton concentration driving zooplankton ((l) cladocerans and (m) copepods) abundances; and (n) cladocerans and copepods driving one another's densities through competition. Double-headed arrows represent covariances, whereas single-headed arrows indicate predictors. See Figure 5 for the direct effects of Bd on tadpoles and the hypothesized consequential effects on periphyton. Bd, *Batrachochytrium dendrobatidis*; toad larvae, western toad, *Anaxyrus boreas*

phytoplankton was collected from mesocosms using a 30-ml tube sampler; it was first filtered through a 150-μm mesh to remove zooplankton, and then filtered through a 25-mm Whatman GF/F glass microfiber filter. Zooplankton were then stored in 30% ethanol until being sorted and identified to order using a microscope.

Chlorophyll-*a* extractions were conducted using 10 ml of 90% acetone. Samples were agitated then incubated for 24 h at −20°C following the methods of Welschmeyer (1994). Fluorescence was determined using a Td-700 Turner Designs fluorometer (Sunnyvale, CA) to quantify chlorophyll-*a* concentration as a proxy for phytoplankton abundance. Periphyton biomass was measured by removing and scraping previously mounted standard microscope slides from the sides of each mesocosm, filtering the material through a previously dried and weighed 25-mm Whatman glass microfiber GF/F filter, and then weighing the dried filter paper plus the periphyton.

Infection confirmation

Prior to preservation of tadpoles in 10% formalin solution, larval mouthparts of 10 haphazardly selected tadpoles from each Bd-exposed mesocosm and two haphazardly selected tadpoles from each Bd-unexposed mesocosm were swabbed 25 times each using sterile fine-tip swabs (Medical Wire and Equipment, Corsham, England), and the swabs were stored in the freezer for later analysis. Quantification of Bd load using quantitative polymerase chain reaction (qPCR) followed established protocols (Boyle et al., 2004) with the exception that DNA extractions employed 60 μl of Prepman Ultra (Applied Biosystems, Foster City, CA) instead of 40 μl. Each sample was run in triplicate against Bd standard titrations from 10^{-1} to 10^{2}.

Statistical analyses

Response variables from amphibian larvae included final survival, final mass, and final stage. We used a Welch two-sample *t* test to determine the effects of Bd exposure on larval survival and final mass. Community response variables included chlorophyll *a* concentration, periphyton biomass, cladoceran abundance, and copepod abundance measured on the final day of the experiment. Because we hypothesized a trophic cascade associated with changes in amphibian abundance and traits and

amphibian survival and mass were only measured at the end of the experiment, we focused most of our analyses on measurements taken at the end of the experiment despite several response variables being measured through time. Prior to analyses, all community response variables were log transformed to meet parametric assumptions. Amphibian response variables included proportion surviving and were mass measured on the final day of the experiment. We used path analysis to estimate the significance of hypothesized interrelationships between members of the aquatic community. Using the *Lavaan* package in R version 0.5-23.1097 (2017), we generated a full model that specified all predicted relationships. These included the effects of the following: phytoplankton shading periphyton; toad larvae (exposed and unexposed) reducing periphyton biomass and phytoplankton abundance through grazing (e.g., trait-mediated effect); toad larvae (exposed and unexposed) reducing zooplankton through possible competition for algal resources or via passive consumption; zooplankton reducing phytoplankton through grazing; phytoplankton concentration driving zooplankton abundances and cladocerans; and copepods driving one another's densities through competition (Figure 1). The independent variables in the model (exposure to toad larvae and Bd) were binary as the same number of larvae and zoospores were added to mesocosms and were not measured during the experiment. The interaction between Bd and larvae was coded using dummy variables for Bd, larvae, and their interaction and by observing the principle of marginality (i.e., main effects were always included in models with interactions). Starting with the full model, we removed nonsignificant factors and then compared and ranked each nested model using Akaike information criterion (AIC). We only present the final model, which was fit with maximum likelihood and was selected using AIC (Appendix S1: Table S1). Our model selection procedures considered several hypothesized models, which are provided in Appendix S1: Table S1. We examined modification indices to ensure that we were not missing any important pathways.

Primary producers might exhibit variation in densities because of differences in nutrients due to the decomposition of dead larvae or zoospores or differences in total host nutrient excretion of toad larvae. To test these hypotheses, we constructed two path models fit only using the mesocosms containing amphibian larvae. Each path model had copepods, cladocerans, and phytoplankton and periphyton both covarying with copepods and cladocerans. To test the hypothesis that the decomposition of dead larvae might contribute to primary productivity, the first path model had phytoplankton, cladocerans, and copepods predicted by tadpole survival (i.e., tadpole densities at the end of the experiment) controlling for the Bd presence. To test the hypothesis that greater biomass of amphibian larvae might contribute to primary productivity through greater nutrient excretions, the other path model was identical to the one just mentioned but replaced amphibian larval survival with final mass.

The goal of our final path analysis was to compare the strength of the density- and trait-mediated indirect effects of Bd on periphyton biomass. Similar to the previously described path model, this path model was fit only using the mesocosms containing amphibian larvae. The density-mediated indirect effect was modeled by including two paths, one from Bd to larval densities at the end of the experiment and the other from larval densities to periphyton biomass at the end of the experiment. The trait-mediated indirect effect of Bd on periphyton biomass was assumed to be the remaining effect of Bd on periphyton after controlling for larval density (i.e., an inferred trait-mediated effect). This effect is presumed to be a product of Bd reducing the foraging capacities of amphibian larvae. To increase the chances that we were isolating these density- and trait-mediated effects, we controlled for potential cofounding variables, which included incorporating into the model covariates for any shading effects of phytoplankton on periphyton and covariances between zooplankton taxa and periphyton biomass. To determine the significance of the density- and trait-mediated effects, we conducted a mediation analysis in *Lavaan* (Rosseel, 2012).

RESULTS

Bd-exposed toad larvae experienced lower survival than larvae exposed to the sham inoculate ($t = -2.47$, df $= 13.7$, $p = 0.02$, Welch two-sample t test). On average, 75% of larvae survived in Bd-unexposed mesocosms, but only 60% survived in Bd-exposed mesocosms. At the end of the experiment, mesocosms that were not exposed to Bd had an average of 30.12 ± 1.55 surviving animals out of 40, whereas mesocosms that were exposed had an average of 24.25 ± 1.80 surviving animals out of 40. Bd exposure did not affect the mean final mass of surviving amphibian larvae ($t = 0.26$, df $= 11.5$, $p = 0.79$, Welch two-sample t test). Individual Bd-exposed larvae had an average final mass of 0.55 ± 0.02 g, and individual Bd-nonexposed larvae had an average final mass of 0.52 ± 0.02 g. Bd was not detected on the mouthparts of nonexposed larvae. Of the 80 total larvae tested for Bd infection, 36 (45%) were infected with an average infection load of 4.77 ± 0.50 Bd genome equivalents, as determined by qPCR. However, given that animals harboring heavy infections were unlikely to survive the full length of the experiment to be swabbed, this likely underestimates both prevalence and average load of individuals exposed

to Bd. Thus, examining tadpole mouthparts for Bd-induced depigmentation would also be a biased estimate of depigmentation. For these reasons, we focus strictly on the Bd exposure treatment rather than Bd prevalence, load, or mouthpart depigmentation and encourage future studies to conduct more controlled laboratory studies to better quantify effects on these endpoints on tadpoles that both do and do not die.

Path and mediation analyses revealed that the decline in periphyton biomass was less when the larvae were Bd-exposed, estimated as 0.53, in comparison to when they were not exposed to Bd, estimated as −0.69 ($p = 0.04$; Figures 2 and 3a). The density-mediated indirect effect of Bd on periphyton biomass was only −0.03 (multiplying the two standardized coefficients -0.55×0.05; $p = 0.77$; Figure 4). In contrast, the effect of Bd on periphyton, consistent with a trait-mediated indirect effect, was estimated as 0.36 ($p < 0.04$; Figure 4). Thus, the inferred trait-mediated indirect effect of Bd on periphyton was >13 times larger than the density-mediated indirect effect that was in the opposite direction. Despite the two effects being in the opposite directions, the net or total effect was positive and significant (standardized estimate = 0.33, $p = 0.02$).

Although Bd-exposed larvae seemed to consume less periphyton, we did not find support for the hypothesis that Bd exposure triggered a switch to filter-feeding phytoplankton because Bd-exposed larvae did not reduce phytoplankton abundance more than sham-exposed larvae (path not included in Figure 2; $p = 0.459$). Additionally, the ancillary path analyses we conducted did not provide support for the hypothesis that decomposing tadpoles fueled algal growth (pathways from tadpole survival to phytoplankton and periphyton abundance: $p = 0.355$, standardized coefficient = −0.268 and $p = 0.621$, standardized coefficient = 0.141, respectively) or that the amount of tadpole biomass and thus greater tadpole excretions fueled algal growth (pathways from tadpole biomass to phytoplankton and periphyton abundance: $p = 0.479$, standardized coefficient = 0.173 and $p = 0.757$, standardized coefficient = 0.074, respectively). In our final path model, the presence of amphibian larvae was associated with a reduction in cladoceran abundance ($p = 0.003$; Figures 2 and 5a), copepod abundance increased with Bd ($p = 0.04$; Figures 2 and 3b) and decreased with phytoplankton abundance ($p = 0.002$; Figures 2 and 5b), and copepod and cladoceran abundances negatively covaried ($p = 0.02$; Figures 2 and 5c).

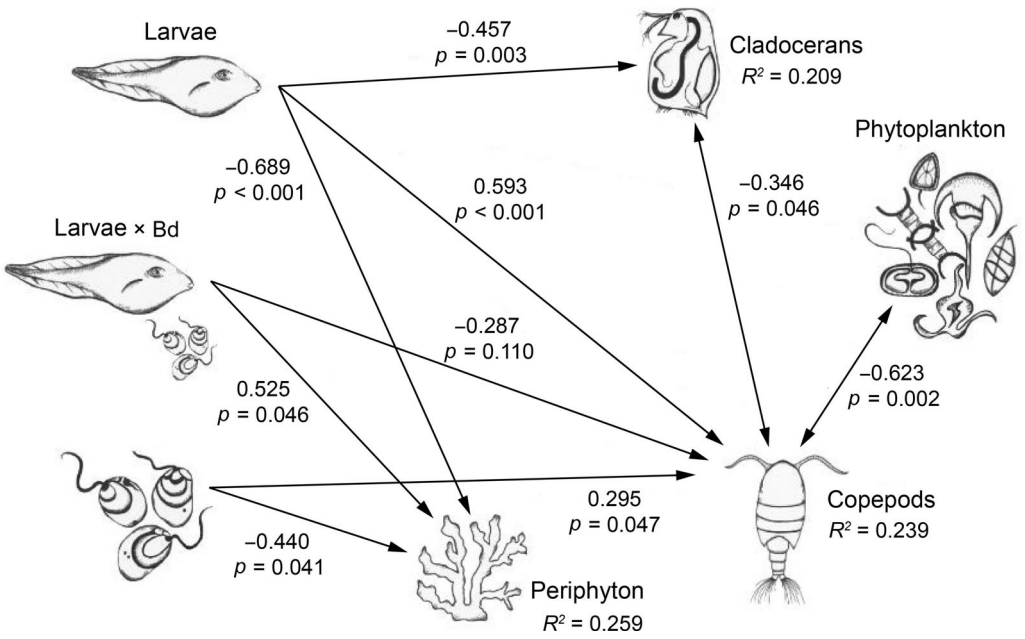

FIGURE 2 The final path model fit with maximum likelihood and selected by AIC and associated standardized coefficients and probability values from mesocosm experimental results. Double-headed arrows represent covariances, whereas single-headed arrows were treated as predictors. Bd, toad larvae and the Bd-by-larvae interactions were modeled as dummy variables based on the presence and absence of each independent variable. The exception was that the final biomass of amphibian larvae in a mesocosm at the end of the experiment better predicted copepod abundance than the presence or absence of larvae. The data fit the model well (chi-squared p value = 0.431, comparative fit index = 0.994, root mean square error of approximation (RMSEA) = 0.023, RMSEA p value = 0.509), and investigation of the modification indices did not suggest that any paths were missing. Standardized coefficients and p values are shown next to each path. R^2 values are only available for response variables receiving unidirectional arrows (they are not available for independent variables or covariances). Bd, *Batrachochytrium dendrobatidis*; toad larvae, western toad, *Anaxyrus boreas*

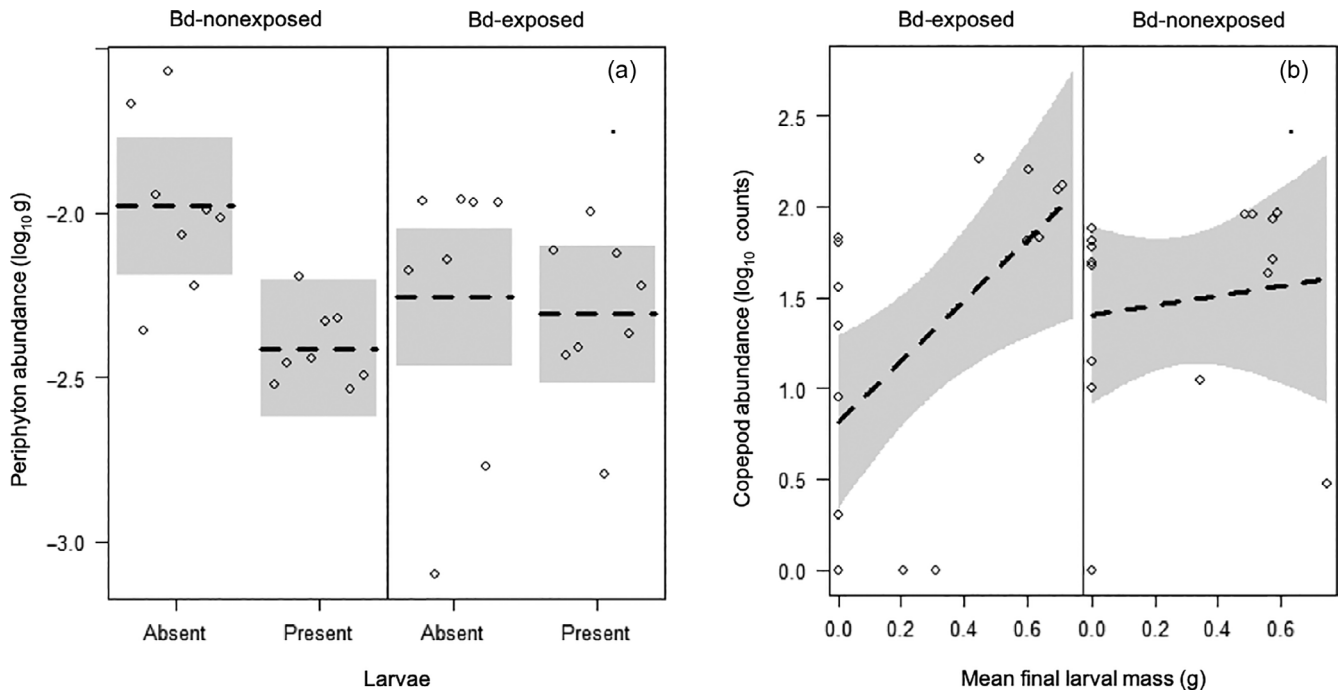

FIGURE 3 Interactions between western toad (*Anaxyrus boreas*) larvae and *Batrachochytrium dendrobatidis* (Bd) exposure on periphyton (a) and copepod abundance (b). The interaction was significant for periphyton abundance ($z = 1.993$, $p = 0.046$) and nonsignificant for copepod abundance ($z = -1.599$, $p = 0.110$) in the final structural equation model. Values plotted are means ±1 SD ($n = 32$ tanks)

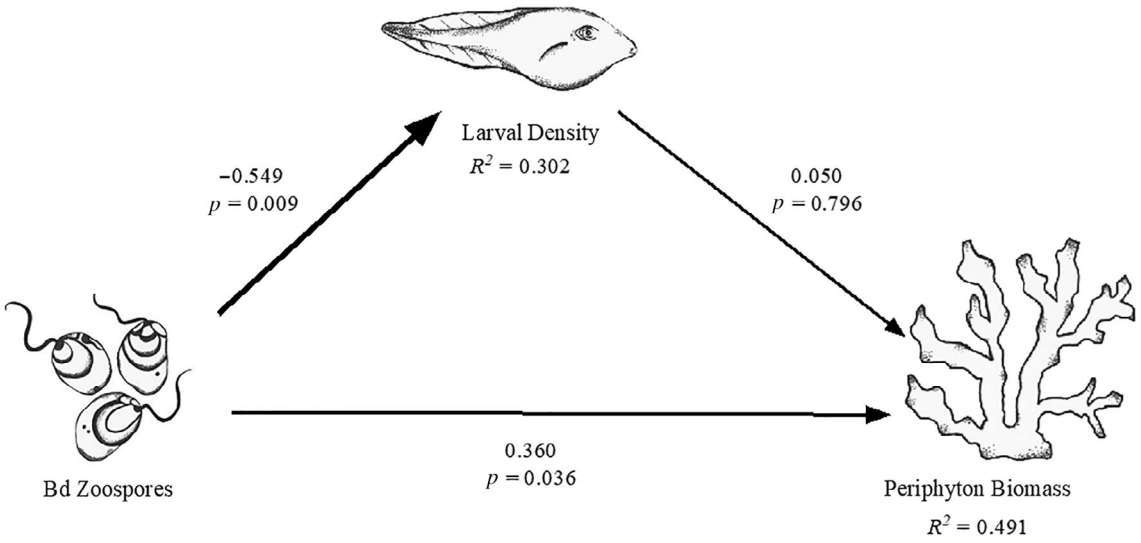

FIGURE 4 Path model testing for the density- and trait-mediated indirect effects of *Batrachochytrium dendrobatidis* (Bd) on periphyton abundance. This path model was fit only using the mesocosms containing western toad (*Anaxyrus boreas*) larvae (unlike the model in Figure 2), and controlled for potential cofounders, such as any shading effects of phytoplankton on periphyton and any covariance between zooplankton taxa and periphyton (not shown in diagram). The density-mediated indirect effect of Bd on periphyton biomass is −0.027, which was estimated by multiplying the standardized coefficient for the effect of Bd on larval densities (Bd reduced survival from 75% to 60%) by the standardized coefficient for the effect of larval densities on periphyton abundance (−0.549 × 0.050). The trait-mediated indirect effect of Bd on periphyton biomass, presumably mediated by the effects of Bd on larval foraging abilities, was estimated as the standardized path coefficient from Bd to periphyton biomass controlling for larval densities, which was 0.360. Hence, the trait-mediated indirect effect is considerably larger than the density-mediated indirect effect

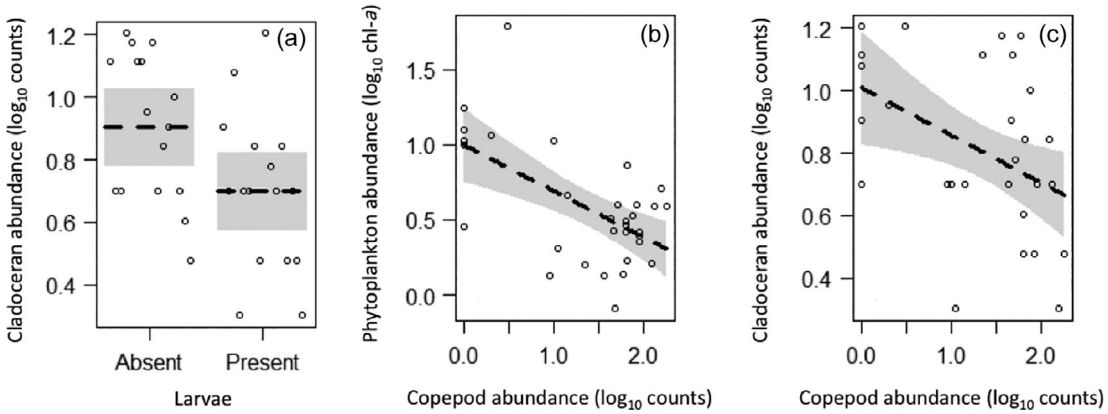

FIGURE 5 Relationships between western toad (*Anaxyrus boreas*) larvae and cladoceran abundance (a) and between copepod abundance and both phytoplankton (b) and cladoceran abundance (c). All relationships were significant in the final model. Values plotted are means ±1 SD ($n = 32$ tanks)

DISCUSSION

We investigated the potential for the amphibian chytrid fungus, Bd, to trigger both density- and trait-mediated indirect effects on aquatic community composition. First, we hypothesized that Bd would indirectly increase periphyton biomass because Bd (1) can be deadly to amphibian larvae that consume periphyton (density-mediated indirect effect) and (2) is well-documented to affect the feeding abilities of surviving larval hosts by causing mouthpart damage (trait-mediated indirect effect) (Blaustein et al., 2005; Fellers et al., 2001; McMahon & Rohr, 2015; Rachowicz & Vredenburg, 2004; Venesky et al., 2009; Venesky et al., 2010). As predicted, our results support trait-mediated indirect effects of Bd on members of the aquatic community. After controlling for larval densities, mesocosms with Bd-exposed larvae had significantly more periphyton biomass than mesocosms with larvae but no Bd, consistent with infection-induced mouthpart damage reducing larval feeding rates on attached algae (Figure 2). Mesocosms without larvae had significantly higher periphyton biomass than tanks with larvae, clearly indicating that larvae can reduce their algal resources. Bd-exposed mesocosms had lower amphibian densities at the end of the experiment than mesocosms without Bd. Bd-induced reduction in larval survival from 75% to 60% did not detectably increase periphyton biomass. Consequently, there was no measurable density-mediated indirect effect of Bd on periphyton biomass. However, the interaction between larvae and periphyton biomass may be confounded by the unknown direct effects of Bd on periphyton biomass or an indirect effect of Bd on zooplankton abundances and subsequent consumption and reduction of periphyton biomass (Figure 2). When compared, the inferred trait-mediated indirect effect of Bd on periphyton biomass was estimated to be >13 times stronger than the density-mediated effect. Importantly, the strength and type of the trait-mediated indirect effect may depend on infection prevalence and disease dynamics. For example, in this study, we observed a relatively moderate infection prevalence (45%), which only weakly reduced amphibian larval densities (from 75% survival to 60%), potentially contributing to the detection of a trait-mediated indirect effect. Conversely, imagine a scenario where Bd enters a highly susceptible host population or species and causes rapid and high parasite-induced host mortality. At least initially, most of the observed effects might be density-mediated because of the extremely rapid disease progression and high mortality, although one could imagine that parasite avoidance responses would evolve rapidly if extirpation or extinction does not occur.

Our second hypothesis was that Bd would increase zooplankton densities by serving as an additional prey resource. Filter-feeding cladocerans opportunistically feed on Bd zoospores (Buck et al., 2011), reducing the amount of Bd in the water and amphibian larval infection load (Buck et al., 2015; Hamilton et al., 2012; Searle et al., 2013). Therefore, we expected zooplankton abundance (specifically cladocerans) to be greater in mesocosms containing Bd because of the additional food source. We did not find evidence that cladoceran abundance increased in the presence of Bd, but copepod abundance did. This might be due to a lack of power, given that cladocerans were relatively rare in mesocosms compared to copepods. Further experimentation and direct measurement of Bd zoospore concentration is needed to fully understand the complexities of this relationship. In addition, these results provide further evidence that copepod and cladoceran abundance can be negatively correlated with one another (Chang & Hanazato, 2003; Gliwiz, 1994; Rumschlag et al., 2020). At last, cladoceran abundance was negatively affected by the presence of amphibian larvae. This suggests that larvae may inadvertently graze on zooplankton while feeding on

algae (Hamilton et al., 2012) or possibly compete with zooplankton for algal resources. Further experimental feeding trials are necessary to fully understand the complex relationships among Bd, its larval amphibian hosts, and algae.

Finally, due to widespread support for Bd-induced mouthpart damage in infected amphibian larvae, we hypothesized that Bd exposure would trigger a switch in surviving larvae from scraping periphyton to filter-feeding phytoplankton. Although we found evidence supporting the hypothesis that Bd-exposed anuran larvae fed less on periphyton than sham-exposed larvae, we did not find evidence that Bd-exposed larvae switched to feeding on phytoplankton because Bd-exposed larvae did not reduce phytoplankton abundance more than sham-exposed larvae. This investigation was prompted by a previous study in which Bd-exposed Cascades frog (*Rana cascadae*) larvae appeared to consume less periphyton and more phytoplankton than unexposed larvae (Buck et al., 2012). We chose to use western toad larvae because of their documented feeding plasticity (Beiswenger, 1977; Seale & Beckvar, 1980). However, they are also highly susceptible to Bd infection (Gervasi et al., 2017). Therefore, animals with high infection loads might have died before achieving late-stage infections with severe mouthpart damage. Future research is warranted to continue investigations of Bd-induced feeding plasticity in other species. Importantly, the fact that zooplankton abundances were significantly greater in mesocosms with than without Bd made it difficult to definitively assess whether Bd-exposed larvae switched from scraping periphyton to filter-feeding phytoplankton. This could be driven by any increase in filter-feeding phytoplankton by Bd-infected larvae being partially counteracted by greater competition for phytoplankton because of the greater abundance of zooplankton. To more cleanly test the hypothesis that larvae switch from scraping to filter-feeding when infected with Bd, a laboratory study could be conducted identical to ours but in the absence of zooplankton.

The results of this study add to the evidence that Bd can alter species composition by causing density- and trait-mediated indirect effects on communities. Although ecologists are increasingly recognizing the potential for pathogens such as Bd to drive community structure (Buck, 2019), we provide the first support for a trait-mediated indirect effect caused by this chytrid fungus and are the first to test the strength of a consumptive trait-mediated indirect effect compared to a consumptive density-mediated indirect effect. These conclusions highlight the direct and cascading effects that infectious agents can have on community structure. However, our experimental design relied on variation in toad density within treatment groups and only posited trait-mediated effects based on variation not attributable to density (traits are only indirectly manipulated), and thus future studies should more directly quantify Bd-induced density- and trait-mediated effects. Although ecologists are increasingly aware that infectious agents can drive community structure via their direct and indirect effects on hosts (Buck, 2019; Buck et al., 2016; Buck & Ripple, 2017; Hatcher et al., 2012; Hatcher & Dunn, 2011; Lafferty et al., 2008; Lafferty & Kuris, 2012; Rohr et al., 2015; Skorping & Högstedt, 2001; Wood et al., 2007), further study of consumptive trait-mediated indirect effects is needed to advance our understanding of the role that infectious agents play in shaping community structure and function.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Carmen C. Harjoe, Julia C. Buck, Andrew R. Blaustein, and Deanna H. Olson conceived and designed the experiment. Carmen C. Harjoe and Claire E. Roberts collected data and performed laboratory analyses. Carmen C. Harjoe and Jason R. Rohr performed statistical analyses. Carmen C. Harjoe, Andrew R. Blaustein, and Deanna H. Olson led the writing of the manuscript. Julia C. Buck, Claire E. Roberts, Jason R. Rohr, Andrew R. Blaustein, and Deanna H. Olson contributed critically to the drafts and gave final approval for publication. Jason R. Rohr handled the manuscript submission and revision process, and responses to reviews.

DATA AVAILABILITY STATEMENT

Community response and amphibian morphological data measurements (Rohr, 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.19127081.

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