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Research Letters

Climatic driver of chytrid prevalence in the Critically Endangered Admirable Redbelly Toad

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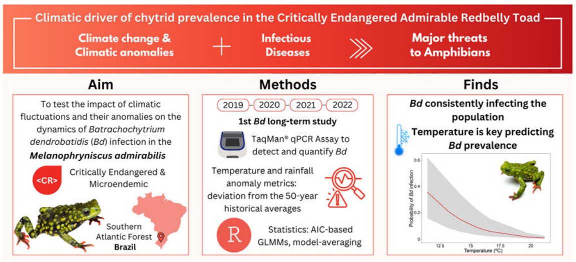
HIGHLIGHTS

- First record of chytrid in the micro-endemic *Melanophryniscus admirabilis;*
- Chytrid was consistently infecting the only known *M. admirabilis* population;
- Temperature influences chytrid dynamics in a threatened toad population;
- Chytrid had no effect on the body condition of *M. admirabilis.*

GRAPHICAL ABSTRACT


Climatic driver of chytrid prevalence in the Critically Endangered Admirable Redbelly Toad

Climate change & Climatic anomalies + Infectious Diseases » Major threats to Amphibians

Aim

To test the impact of climatic fluctuations and their anomalies on the dynamics of *Batrachochytrium dendrobatidis* (*Bd*) infection in the ***Melanophryniscus admirabilis***

Critically Endangered & Microendemic

Southern Atlantic Forest **Brazil**

Methods

2019 – 2020 – 2021 – 2022

1st *Bd* long-term study

TaqMan® qPCR Assay to detect and quantify *Bd*

Temperature and rainfall anomaly metrics: deviation from the 50-year historical averages

Statistics: AIC-based GLMMs, model-averaging

Finds

***Bd* consistently infecting the population**

Temperature is key predicting *Bd* prevalence

ARTICLE INFO

Keywords:
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Melanophryniscus admirabilis
Temperature

ABSTRACT

Global warming is driving shifts in rainfall and temperature patterns, and projections indicate an increase in frequency and intensity of climate anomalies. These changes influence wildlife disease dynamics, affecting pathogen development, host behavior, physiology, and disease susceptibility. Understanding the intricate interplay between climatic anomalies and emerging pathogens in amphibians is essential to inform conservation efforts targeted towards this highly threatened vertebrate group. We therefore investigated the dynamics of the waterborne chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) in the microendemic and Critically Endangered amphibian *Melanophryniscus admirabilis* under climatic anomalies and seasonal climatic fluctuations. Additionally, considering the sublethal effects of *Bd* in our focal host species, we tested whether *Bd* infection explains the variation in host body condition. We found that *Bd* was consistently infecting Admirable Redbelly Toad population for more than three years. Our results point to links between *Bd* prevalence and seasonal temperatures,

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indicating that temperature plays a crucial role in *Bd* transmission among toads. However, we failed to find an effect of *Bd* infection on host body condition. The insights gained from this study can improve conservation efforts and help elucidate the links between climatic factors and chytrid infection, informing management plans for threatened amphibian populations.

Introduction

The modifications resulting from the expansion of human populations have led to an increased frequency and intensity of climatic extremes (Seneviratne et al., 2021). Rainfall and temperature patterns have globally shifted in response to global warming, and climatic anomalies are projected to increase in frequency and intensity (Seneviratne et al., 2021). Climatic anomalies can alter entire ecosystems, extending their impact also over wildlife disease dynamics (Greenspan et al., 2020; Rohr and Raffel, 2010). This intricate interplay occurs through a wide range of mechanisms, encompassing shifts in pathogen development (Nnadi and Carter, 2021), and alterations in host behavior and physiological traits (Bozinovic and Pörtner, 2015) that often lead to increased susceptibility to diseases (Bradley et al., 2019).

Wildlife disease dynamics are influenced by micro and macroclimatic variables often involving synergistic interactions between pathogens and their hosts (Altizer et al., 2013). Chytridiomycosis is among the most devastating wildlife diseases, driving amphibian population declines worldwide and causing catastrophic, ongoing biodiversity losses (Scheele et al., 2019). Caused by the waterborne fungal pathogen *Batrachochytrium dendrobatidis* (hereafter *Bd*), chytridiomycosis dynamics is influenced by climatic variables (Ruggeri et al., 2018). Climatic extremes, such as deficit in rainfall, can intensify seasonal pathogen amplification and trigger localized pathogen clusters (e.g., Moura-Campos et al., 2021), consequently, increasing host disease susceptibility. Simultaneously, these extremes have been linked to significant declines in amphibian populations by increasing desiccating breeding sites and causing recruitment failure (Scheele et al., 2012). Consequently, accelerated climate variability could synergistically intensify these impacts and drive amphibians to the extinction path, as amphibians are already the most threatened vertebrate taxon (IUCN, 2023). The *Bd*-amphibian system thus provides an opportunity to investigate the impact of climate anomalies on disease dynamics in formally threatened species, such as Admirable Redbelly Toad, *Melanophryniscus admirabilis* (Bufonidae), from southern Brazil, a region with widespread occurrence of *Bd*. This microendemic Neotropical species (range size of 1.6 km^2, IUCN, 2023) is classified as Critically Endangered (CR) by the IUCN Red List of Threatened Species (IUCN, 2023) and in the Brazilian Red List (Brasil, 2022), further highlighting the urgency of understanding and addressing the *Bd* infection dynamics and the intricate interplay between climate, *Bd*, and the conservation of this species (IUCN, 2023).

Melanophryniscus admirabilis uses temporary small pools (0.4–22 cm deep) formed on flat rock outcrops as vocalization and breeding aggregation sites. While evidence of breeding activity has been recorded in nearly every month of the year, the breeding season is concentrated from mid-August to mid-October (Abadie et al., unpublished results). Similarly, *Bd* depends on water for its growth, survival, and dispersion, although it can be transported by other non-amphibian vectors (e.g., Pontes et al., 2018; Prado et al., 2023). Therefore, rainfall and its anomalies could significantly impact the reproductive biology of *M. admirabilis* and pathogen infection dynamics (Moura-Campos et al., 2021; Ruggeri et al., 2018). Temperature also plays an important role in the reproductive success of Admirable Redbelly Toad because this species depends on the duration and availability of deepest pools (Bordignon et al., unpublished results), which can quickly evaporate under high temperatures. Additionally, despite *Bd* exhibiting varying thermal tolerance, temperature can induce alterations in *Bd* life history (Stevenson et al., 2013) and plays a major role in determining the *Bd* infection loads in hosts (Bielby et al., 2022). Some amphibians can demonstrate increased susceptibility to chytridiomycosis in the presence of anomalies in environmental temperatures (Cohen et al., 2019). For example, transitions from warm El Niño years to cooler La Niña triggered *Bd* outbreaks in a Neotropical Bufonidae toad (Rohr and Raffel, 2010), as temperature-induced stress can significantly impair the ability of hosts to mount effective innate immune defenses against *Bd* (Grogan et al., 2018). Hence, seasonal and historical variations in temperature and rainfall are recognized as relevant environmental variables likely influencing *Bd* infection dynamics in *M. admirabilis.*

Alternatively, the environmental context can benefit amphibians in mitigating *Bd* infections (Karavlan and Venesky, 2016). For instance, *Bd* growth is significantly suppressed at temperatures above 25 °C (Stevenson et al., 2013), thus, predicted increases in average global temperatures could suppress pathogen growth in amphibians' skin. However, the interaction of *Bd* and warming could lead to an increase in mortality of cool-adapted host species at higher temperatures, despite lower infection loads (Neely et al., 2020). This suggests that even when temperatures approach the upper thermal limit of the pathogen, *Bd* infection may cause declines in cool-adapted toads due to the combined pressures of pathogen infection and warming-related stress (Neely et al., 2020). Specifically, *Bd* infection can lead to host stress, with downstream impacts on host body condition and fitness (Bosch et al., 2023). *Bd* infection has also been linked to population declines in wild amphibians through sublethal effects that reduce host fitness, extending beyond immediate consequences to affect long-term population dynamics and persistence (Palomar et al., 2023; Valenzuela-Sánchez et al., 2017). Understanding these broader consequences and *Bd* dynamics is vital for effective conservation strategies for the Critically Endangered *M. admirabilis*, particularly in light of its higher vulnerability to extinction due to stochastic events (Fonte et al., 2022).

Considering the importance of *Bd* on amphibian population declines and pivotal role of climatic variables in predicting amphibian host-pathogen dynamics, we aimed to test whether local monthly climatic fluctuations and climatic anomalies would be associated with changes in *Bd* dynamics in Admirable Redbelly Toad. Given the fact that our focal amphibian species depends on temporary pools to breed and that *Bd* is a waterborne pathogen prone to desiccation in dry, warm environments, we hypothesized that seasonal fluctuations in temperature and rainfall impact *Bd* dynamics. Specifically, due to the preference for reproduction and aggregation at deeper pools (Bordignon et al., unpublished results), we expect that periods with lower temperatures and high rainfall will result in higher *Bd* prevalence and infections load. Additionally, we hypothesized that the *M. admirabilis* population will experience higher *Bd* prevalence and infections load in periods when rainfall exceeds the historical average and when temperatures are below the historical average. Finally, considering *Bd* sublethal effects (Palomar et al., 2023; Valenzuela-Sánchez et al., 2017; Wu, 2023), we expect that *Bd* infection status has negative consequences on host body condition. Combined, our goals will allow us to elucidate the *Bd* dynamics of a critically endangered Neotropical species, representing the first long-term study of *Bd* dynamics in Admirable Redbelly Toad.

Methods

Study site and field sampling

The only known site for *M. admirabilis* is located in the municipality of Arvorezinha, State of Rio Grande do Sul, Brazil (52°18'W, 28°51'S), in the Atlantic Forest. The climate is humid subtropical, and seasons (autumn, winter, spring, and summer) are differentiated by temperature, with well-distributed rainfall year-round. We sampled along $\sim$ 400 m on the Forqueta river's bank, where toads concentrate to breed. We surveyed the site at least twice a year, from September 2019 to December 2022 (exclusively between August and December), totaling nine field campaigns (Table 1). This period maximizes detection and captures seasonal temperature variation relevant to *Bd* dynamics. We captured each toad using new disposable latex gloves and swabbed the skin using MedicalWire MW113 swabs, totaling 30 strokes. We measured the snout-vent length (SVL; mm) and the body mass (g) of each toad.

We applied a photo-identification standardized procedure as a mark-recapture method (Fig. S1). A detailed description of these methods can be found in the supplementary material.

Pathogen detection and quantification

We determined the sensitivity performance for *Bd* diagnostics in our qPCR equipment (QuantStudio™ 6 Flex, Thermo Fisher Scientific) through a series of replicate standard curves. These assays revealed that the amount of target DNA sequence that can be detected with 95 % probability (LOD) is 0.1 copies per reaction (Table S1, Fig. S2). Thus, we considered samples to be *Bd*-positive (*Bd*$^{+}$) when the infection loads were $\geq$ 0.1 genomic equivalents of zoospores (hereafter GE). A detailed description of these assays can be found in the supplementary material.

To determine the *Bd* presence and infection loads in each toad, we extracted DNA from skin swabs using PrepMan ULTRA®. To quantify *Bd* infection loads, we used a Taqman® qPCR Assay with standards ranging from 10^{-1} to 10^{3} GE (Boyle et al., 2004).

Abiotic data

We obtained the mean temperature (ºC) for the 15 days leading up to the sampling from two automated weather stations located approximately 23 and 37 km from the study site (*Instituto Nacional de Meteorologia do Brasil*). To assess temperature anomaly metrics, we used the TerraClimate dataset (Abatzoglou et al., 2018). We calculated temperature deviation (ºC) by subtracting the historical mean temperature for the 30 days preceding sampling period over the past 50 years from the mean temperature of the 30 days preceding sampling. The resulting deviation values could be negative for colder-than-average months, and positive for warmer-than-average months. Additionally, we recorded the accumulated rainfall (mm), for each month prior to sampling using data from a hydrometeorological station located 5.5 km from the study site (*Agência Nacional de Águas e Saneamento Básico*). To assess rainfall anomaly metrics (mm), we calculated the rainfall deviation by subtracting the historical mean of the 30 days preceding sampling period over the past 50 years from the accumulated rainfall of the 30 days prior to sampling day (Abatzoglou et al., 2018). Like our temperature anomaly metrics, we extracted rainfall deviations (mm) for one, two, and three months prior to the sampled month. This analysis provided us with negative values for dryer-than-average months and positive values for wetter-than-average months.

Table 1
Variation of *Batrachochytrium dendrobatidis* (*Bd*) prevalence and infection loads in *Melanophryniscus admirabilis* between 2019 and 2022. *Bd* prevalence is the proportion of infected toads out of the total number of toads sampled. *Bd* infection load is represented by the mean and standard deviation (SD) of zoospore genomic equivalents (GE) by year and month (only *Bd*$^{+}$ toads). Total refers to the general *Bd* prevalence and mean of infection load and SD.

Year	Season	Month	*Bd* prevalence (*Bd*$^{+}$/n)	New/ recaptures	Mean *Bd* infection load
2019	Cold	September	13.33 % (2/15)	15/0	0.35 ± 0.33
2019	Warm	December	26.28 % (11/41)	40/1	23.20 ± 48.47
2020	Cold	August	13.63 % (6/44)	42/2	3.19 ± 3.84
2020	Warm	November	1.40 % (1/71)	61/10	16.67
2021	Cold	August	34.78 % (16/46)	39/7	155.05 ± 523.53
2021	Cold	September	11.10 % (1/9)	9/0	0.78
2021	Warm	December	4.65 % (2/43)	40/3	81.88 ± 114.69
2022	Cold	August	18 % (9/50)	37/13	78.74 ± 151.76
2022	Warm	November	30 % (6/20)	14/6	54.64 ± 93.24
		Total	15.92 % (54/339)	297/42	73.58 ± 293.36

Data analyses and modelling

To assess the potential effects of monthly climatic fluctuations and climatic deviations (anomalies) on *Bd* prevalence and infection loads, we removed highly correlated variables based on a Spearman rank to prevent multicollinearity between predictors. We employed a model selection approach based on Akaike Information Criterion (AIC). For *Bd* prevalence, we fit a Generalized Linear Mixed Model (GLMM) with binomial distribution and logit link function. We also fit a gaussian GLMM with log link function, with *Bd* infection loads (log10-transformed GE; only *Bd*$^{+}$ samples) as the response variable. The explanatory variables in both global models were: season (warm or cold), temperature, accumulated rainfall, and climatic anomaly metrics depicting temperature deviation. For both GLMMs, we included year as a random factor. We ran models with all possible combinations of explanatory variables and selected the best-fitting ones based on ΔAIC < 2 (Table 2). A detailed description of these models can be found in the supplementary material (Table S2). To account for model uncertainty, we performed model averaging, calculating averaged coefficient estimates (slopes) and standard deviations for each variable. These final estimates used to predict the influence of climatic variables on *Bd* prevalence and infection load were derived from this model-averaging procedure.

To investigate any significant differences in body condition between *Bd*$^{+}$ and *Bd*$^{-}$ toads (explanatory categorical variable), we performed a Student's *t*-test, including body condition data from non-recaptured adults males sampled until August 2021 (n = 140). We performed a linear regression analysis to test for the potential effect of *Bd* infection loads on body condition of *Bd*$^{+}$ non-recaptured males (n = 29). The body condition metric utilized the Scaled Mass Index (SMI) approach, based on standardized major axis regression between mass and snout − vent length (Peig and Green, 2009). Finally, we also applied an exact binomial test to assess if *Bd* infection gains were higher than expected by

Table 2
Model-averaged coefficient estimates for climatic variables influencing *Batrachochytrium dendrobatidis* (*Bd*) prevalence and infection load in *Melanophryniscus admirabilis* from Brazil. Model averaging was performed using all models within ΔAIC $\leq$ 2 of the top-ranked models, incorporating their relative weights. Significant predictors ($p < 0.05$) are in bold.

Model	Estimate	Std error	*z* value	*P*
Prevalence				
Warm Season	2.049	1.051	1.940	0.052
Temperature	−1.510	0.551	2.729	**<0.01**
Dev. Temp.	0.062	0.225	0.278	0.781
Rainfall	0.501	0.268	1.860	0.062
Infection load				
Warm Season	0.584	0.728	0.793	0.427
Temperature	−0.204	0.314	0.644	0.520
Dev. Temp.	0.134	0.127	1.024	0.306
Rainfall	−0.177	0.117	1.466	0.143

Warm Season: November, December; Cold Season: August, September. Temperature: mean temperature of the 15 days prior to sampling date. Dev. Temp.: temperature deviation subtracting the historical temperature monthly mean from the mean of the month prior to sampling date. Rainfall: accumulated monthly rainfall from the month prior to sampling date.

chance. All statistical analyses were performed using R Statistical Software, version 2023.3.

Results

We collected 339 skin swab samples from 297 individuals, and overall *Bd* prevalence was 15.9 % (54/339; Table 1), and the mean infection load in Bd^+ toads was 73.58 GE (± 293.36 SD), ranging from 0.1 to 2,112.45 GE (Table 1). *Bd* was detected in all nine field campaigns, with the lowest prevalence (1.40 %, 1/71) recorded in November 2020 (Table 1, Fig. 1) and the highest (34.78 %, 16/46) in August 2021 (Table 1, Fig. 1).

Our most parsimonious GLMM models retained two models within $\Delta AIC \leq 2$ for *Bd* prevalence and seven models for *Bd* infection load (Table S2). Model averaging for *Bd* prevalence identified temperature as the only significant negative predictor ($z = 2.729$, $P < 0.01$; Fig. 2, Table 2). Model averaging explaining *Bd* infection load did not identify any statistically significant predictors (Table 2).

We did not observe a significant difference in SMI between Bd^+ and Bd^- toads (*t-value* $= -0.405$, $df = 39.537$, $P = 0.687$). Additionally, we did not find a significant association between SMI and infection loads of Bd^+ individuals ($\beta = 0.059$, $r = -0.007$, $P = 0.383$; Fig. S3). A total of 262 toads were captured once, 29 captured twice, five captured three times, and one was captured four times. Regarding *Bd* infection status over time, a total of seven recaptured toads were found infected with *Bd* at least once (Fig. 3). Despite toads gained infection seven times, while they cleared *Bd* infection only three times (Fig. 3), this difference was not statistically significant ($P = 0.171$).

Discussion

Our study revealed that *Bd* was consistently infecting the Admirable Redbelly Toad population across all sampling periods spanning more than three years, with some periods showing higher prevalence than the expected 20 % for the Atlantic Forest amphibians (Carvalho et al., 2017). Given that this is the only known population of *M. admirabilis*, the consistent *Bd* detection, combined with other interacting stressors, could affect population persistence.

Contrary to our predictions, only one climatic variable predicted *Bd* prevalence in Admirable Redbelly Toads. Our findings suggest that lower temperatures were key in predicting *Bd* prevalence in this species. One of the main breeding site selection criteria for *M. admirabilis* is pool depth and size, with deeper pools being more likely to be used as breeding sites (Bordignon et al., unpublished results). During colder periods, reduced evaporation helps maintain water levels in these pools, ensuring their availability for breeding. Peaks of explosive breeding events occur in periods with mild temperatures, and the highest recorded aggregation – over 300 toads – occurred in August (austral winter) (Abadie et al., unpublished results). Toad aggregations serve as significant reservoirs of infective *Bd* zoospores (Longo et al., 2010), increasing the likelihood of *Bd* transmission when toads interact and shed zoospores into water pools (Moura-Campos et al., 2021). Additionally, population density and contact rates among toads have also been linked with higher *Bd* prevalence in other *Melanophryniscus* species (Pontes et al., 2021). Although not measured in this study, it is possible that the higher density of toads at the ponds during breeding periods, combined with the seasonal demography of *M. admirabilis,* may also play a role in *Bd* infection dynamics in the only known population of this species. These results highlight the importance of considering both climatic and ecological factors when assessing *Bd* risk in amphibian populations.

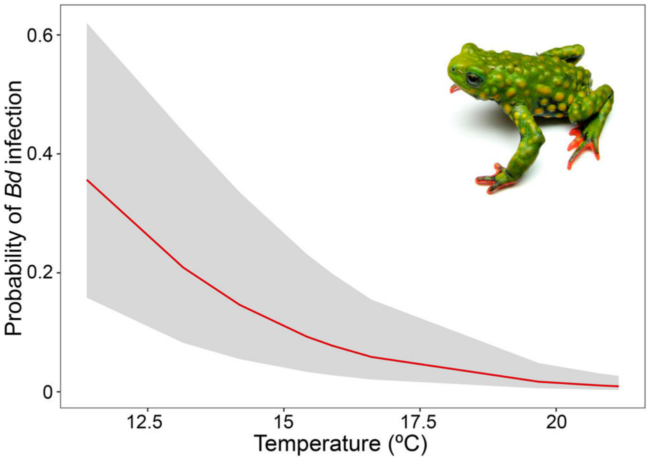

Fig. 2. Visualization of the Generalized Linear Model (GLM) fit for *Batrachochytrium dendrobatidis* (*Bd*) infection risk (prevalence) and temperature (ºC) ($z = 2.729$, $P < 0.001$).

Although climatic variables were not good predictors of *Bd* infection in *M. admirabilis*, the patoghen was consistently detected throughout the study period. Overall, *Bd* infection loads were low, – a pattern also found in *Melanophryniscus montevidensis* species (Pontes et al., 2021) – with the highest load coinciding with the period of prevalence peak.

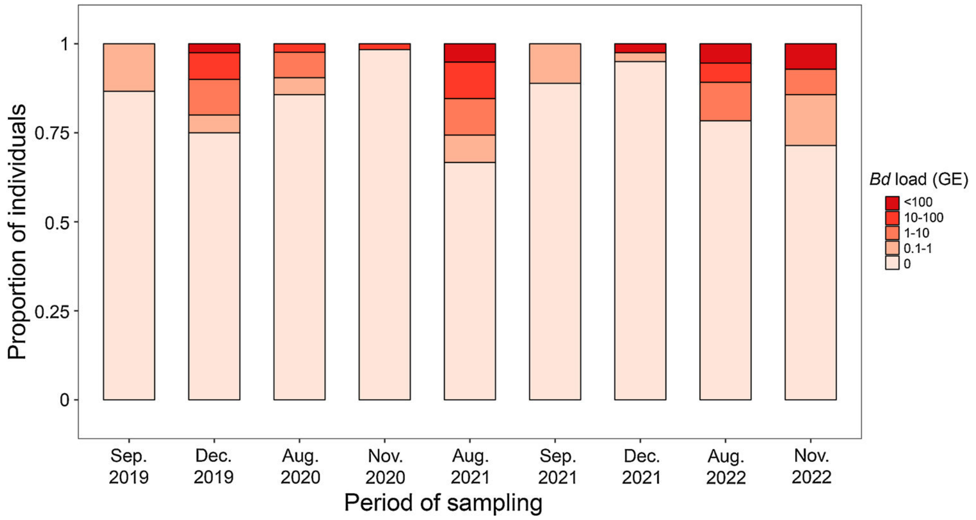

Fig. 1. Proportion of *Melanophryniscus admirabilis* toads infected with *Batrachochytrium dendrobatidis* (*Bd*) and proportion of genomic equivalents of zoospores (GE) by months.

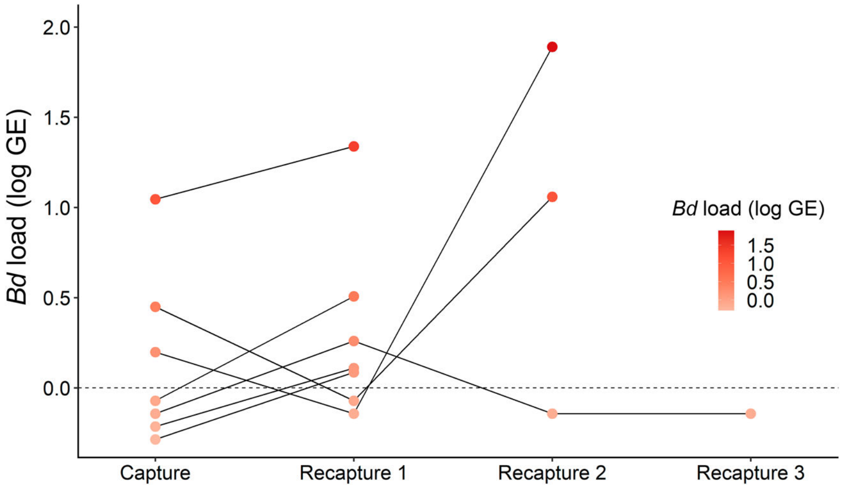

Fig. 3. Individual variation in *Batrachochytrium dendrobatidis* (*Bd*) infection loads (log genomic equivalents of zoospores, GE) in *Melanophryniscus admirabilis* toads (lines connect the same individual). Values below zero indicate an uninfected sample. Recapture intervals varied between individuals, with the minimum being 75 days and the maximum being 3 years and 2 months.

Additionally, even low infection levels can negatively impact bufonids, and Bd^+ toads can exhibit lower survival probabilities, even in populations with some capacity to adapt to chytridiomycosis (Palomar et al., 2016, 2023). This suggests that, despite low infection loads, *Bd* can still impact amphibian persistence and contribute to long-term silent population declines (Palomar et al., 2023; Valenzuela-Sánchez et al., 2017). From a conservation perspective, the Admirable Redbelly Toad population may be facing not only potential impacts from *Bd* infection, but also multiple environmental and anthropogenic threats, including, for example, exposure to antibiotic-resistant bacteria (Ienes-Lima et al., 2023a,b), pesticide contamination from nearby tobacco crops, and competition with invasive species (IUCN, 2023).

Our findings suggest that *Bd* presence and infection load were not linked to host body condition. Evidence of sublethal effects of *Bd* on body condition is rarely observed in wild populations that do not experience chytridiomycosis-related mortality. However, it is worth noting that even at low infection loads, *Bd* could lead to impaired skin physiology (*i.e.,* skin integrity, osmoregulation, and hormone production) (Wu, 2023). Additionally, *Bd* is known to alter the amphibian skin microbiome (Becker et al., 2019) and the presence of the bacteria *Serratia marcescens* could also be playing an important structural role in skin microbiome health in *M. admirabilis* (Ienes-Lima et al., 2023a). Furthermore, while not statistically significant, our capture-mark-recapture analysis showed that although individuals demonstrated the ability to clear *Bd* infection, they more often show an increase in infection likelihood rather than clearance over time. The higher probability of becoming Bd^+ than the probability of clearance is a characteristic of populations on a path of slow decline (Palomar et al., 2023). Therefore, tracking individual *Bd* infection status over time remains essential, especially considering our limited sample size, to better understand long-term infection and support future demographic assessments of the population health.

The species within the genus *Melanophryniscus* could be affected by climate change in different ways, including the reduction of suitable habitats (Zank et al., 2014). This study represents the first long-term investigation into *Bd* infection dynamics in *M. admirabilis* under variable climatic conditions and contributes to the IUCN Red List Assessments by providing *Bd* infection data (IUCN, 2023). While chytridiomycosis may not pose an immediate threat to the Admirable Redbelly Toads, common stressors such as herbicides (da-Silva et al., 2023) and anthropogenic impact (Ienes-Lima et al., 2023b) could amplify the fitness impact of climate change (Greenspan et al., 2017). The results gained from this study underscore the importance of long-term monitoring to assess the impacts of synergistic threats on the *M. admirabilis* population. Future research should investigate the role of host density, seasonal demographic changes, and habitat characteristics to better understand the mechanisms driving *Bd* prevalence in Admirable Redbelly Toad. We advocate for the continuation of disease ecology research on the critically endangered *M. admirabilis* population, including *Bd* and other amphibian pathogens such as *Ranavirus* (Ruggeri et al., 2023).

Ethics and permits

This work was conducted under permits by Instituto Chico Mendes de Conservação da Biodiversidade (SISBio #72718), Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado (SisGen #A3D44D1) and approved by Unicamp animal care and ethics committee (CEUA #5581-1/2020).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pecon.2025.07.001.

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