Effects of climate change and El Niño anomalies on historical declines, extinctions, and disease emergence in Brazilian amphibians

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ABSTRACT

Amphibian declines, linked to climate change and disease, pose a global challenge, yet their primary drivers remain debated. We investigated the historical decline of Brazilian amphibians by assessing the influence of climate change, extreme weather events, and the chytrid fungus *Batrachochytrium dendrobatidis* (Bd). Our analysis encompassed 90 amphibian species more than a century (1900–2014), integrating historical climate data—including El Niño anomalies and Southern Hemisphere temperature records—with documented extreme weather events and amphibian population trends. Using Granger causality tests, we identified gradual climate change and extreme weather events, particularly El Niño-driven temperature anomalies, as the primary drivers of amphibian population declines in Brazil. Structural equation models further supported these findings, demonstrating that climate-driven stressors significantly contribute to population crashes and increase Bd infections. However, Bd infections peaked years after population declines, suggesting that the fungus acts as an opportunistic pathogen rather than a primary driver of amphibian losses in Brazil. These findings challenge the prevailing view that Bd is the main cause of declines, instead highlighting climate anomalies and extreme weather events as the predominant factors.

INTRODUCTION

Amphibians have declined abruptly throughout the world, with the most pronounced impacts observed in populations and species inhabiting tropical forests (IUCN, 2024; Luedtke et al., 2023; Stuart et al., 2008). Anthropogenic threats, including climate change and the spread of disease, have been implicated in these global declines (Luedtke et al., 2023; Stuart et al., 2008). The frog-killing fungus *Batrachochytrium dendrobatidis* (Bd) has been linked to many declines in montane forests, mostly in Central America, the tropical Andes, and Australia (IUCN, 2024). Recent increases in temperature and rainfall variability have also been linked to amphibian declines, especially in cool-adapted, high-elevation amphibians, by reducing their ability to fend off *Bd* infections (Cohen et al., 2017; 2019; Rohr & Raffel, 2010; Sapsford et al., 2013). These factors have contributed to amphibians being among the most threatened groups of vertebrates (IUCN, 2024).

Brazil hosts the largest proportion of amphibian species globally, most of which are endemic (Segalla et al., 2021). Anura, encompassing frogs and toads, constitutes most of this diversity (Segalla et al., 2021). Many population declines and extinctions in the country, which began in the 1970s, are ongoing, and research efforts are actively documenting these worrisome trends (Eterovick et al., 2005; Heyer et al., 1988; Ferrante et al., 2019; 2023a; Toledo et al., 2023; Weygoldt, 1989). These historical declines have been attributed to myriad factors, including habitat loss and fragmentation (Becker et al., 2007; Ferrante et al., 2017), discontinuity between natural aquatic and terrestrial habitats (Becker et al., 2007; 2009), expansion of agricultural crops (Ferrante et al., 2017), pesticides (Ferrante & Fearnside, 2020), climate change (Ferrante et al., 2023a; 2023b), and a combination of these factors (Ferrante et al. 2019; Heyer et al., 1988). In relatively undisturbed natural habitats, *Bd* has been implicated as a likely driver of historical declines (Carvalho et al., 2017). These

declines in montane natural forests targeted mostly cool-adapted, stream-breeding amphibian species (Berger et al., 2005; Lips et al., 2006; Woodhams & Alford, 2005). Despite these observations, the primary causes of these declines and extinctions are yet to be determined (Stuart et al., 2004).

An updated list of threatened species in Brazil, showing an increase in the number of threatened amphibian species in the country, was recently released by Instituto Chico Mendes de Conservação da Biodiversidade (ICMbio, 2022), the Brazilian government agency responsible for the management and conservation of Brazilian biodiversity. Despite the limited information on species distributions and abundances across much of Brazil, two species were confirmed as extinct, 15 species were classified as possibly extinct, 44 species were classified under some threatened status (e.g., endangered torrent frog [*Hylodes sazimai*]), and 27 species were characterized as near threatened (ICMbio, 2022). In light of this, there is a pressing need to delve into the historical factors behind the massive population declines and local extinctions of Brazilian anurans.

The proposition that climate change was the primary driver of historical declines and extinctions in Brazil was initially put forward by Heyer et al. (1988). Instances of extreme weather events, such as frost, droughts, and localized climate changes, have been documented in Brazil as causing population declines and affecting the recruitment of new individuals in frog populations (Heyer et al., 1988; Ferrante et al., 2023a). This includes *H. sazimai*, which was classified as endangered in the most recent list of threatened species (Ferrante et al., 2023a). This phenomenon is not unique to Brazil and poses a threat to amphibian populations globally (Pounds & Crump, 1994; Pounds et al., 1999).

In Brazil gradual climate change and drought events (Getirana, 2016; Getirana et al., 2021) have had a direct impact on frog activity, reproduction rates, and population dynamics (Ferrante et al., 2023a). Although many populations have undergone morphological changes

to adapt to these shifts, the evolutionary time required is much shorter than the speed of climate change (Ferrante et al., 2023a). Reduced reproduction and increased mortality rates have led to lower recruitment and the decline of these frog populations (Ferrante et al., 2023a). Projections based on the most likely Intergovernmental Panel on Climate Change (IPCC) climate scenarios indicate that even common species may disappear in <20 years (Ferrante et al., 2023b).

Drought events have affected the skin microbiota of frogs and caused them to aggregate in remaining water bodies, factors that together have increased the level of pathogens, such as *Bd* (Buttimer et al., 2024). Even though in vitro studies show that *Bd* grows more slowly in culture media at higher temperatures, it proliferates much better on hosts within the same range of higher temperatures (Cohen et al., 2017). This suggests that warming sometimes tips the balance in favor of the pathogen (Cohen et al., 2017). An example of this phenomenon has been observed in some species of high-elevation Atlantic Forest pumpkin toadlets (e.g., *Brachycephalus rotenbergae*), which are adapted to cooler temperatures (Buttimer et al., 2024). When faced with elevated temperatures, these frogs are susceptible to illness and mortality due to chytridiomycosis, even when temperatures surpass the optimal thermal limit for *Bd* (Neely et al., 2020). This makes the investigation of the effects of climate change on historical declines of amphibians in Brazil extremely relevant.

The climate change hypothesis lost some support after the presence of *Bd* in Brazil was confirmed (Carvalho et al., 2017; Toledo et al., 2023), although the influence of *Bd* on global amphibian declines has been questioned due to gaps in the data (Lambert et al., 2019). Unlike in other locations, a massive wave of anuran deaths associated with the presence of *Bd* has never been observed in Brazil (Lips, 2016). In addition, one of the *Bd* strains has been recorded in Brazil over a period of over 100 years (O'Hanlon et al., 2018); thus, through coevolution between parasite and host, native amphibians may have greater resistance to this

pathogen than amphibians in other parts of the world. The lack of declines or extinctions of anurans in areas where animals have been introduced that are considered to be reservoirs for *Bd*, such as the American bullfrog (*Aquarana catesbeiana*), supports the hypothesis that these species may exhibit resistance to Bd due to coevolution with the pathogen (Ferrante et al., 2020).

Due to the uncertain historical record and to gaps in explaining amphibian declines in Brazil, we tested whether *Bd*, climate change, or both synergistically best explain these declines. We sought to improve understanding of past biodiversity loss and to develop better measures for future preservation.

METHODS

By comparing the chronology of *Bd* infection with the occurrence of gradual climate change and extreme weather events in the same locations, we sought to test the roles of these factors in observed declines of amphibians. Establishing a definitive cause-and-effect relationship is inherently challenging. This difficulty arises from the fact that a single effect may stem from multiple causes, either independently or in combination. Additionally, robust correlations between two variables may be due to an intervening third variable. This is especially evident in population decline trends, where multiple causal processes may be in play. An alternative approach involves exploring whether a time series can serve as a predictive tool for another, as proposed by Granger (1969). We used Granger's (1969) causality test to assess the potential of various factors for forecasting anuran population declines and extinctions in Brazil. Specifically, we sought to identify peaks BD infection ; extreme weather events (droughts, floods, frosts, heatwaves, severe cold waves, and wildfires) in the same location and year of the decline; historical El Niño anomalies; and

gradual climate change (comparison of annual rainfall and average temperature before the year of the decline).

Local declines and extinctions were evaluated for 90 anuran species in Brazil, considering all reported declines from 1923 to 2014 (Appendix S1). Historical data on these local declines or extinctions were recently confirmed by Carvalho et al. (2017) and Toledo et al. (2023), and we used newer data on declines recorded in southern Minas Gerais state that are only addressed in the present study. We extracted the *Bd* infection data from Carvalho et al. (2017), who assessed the percentage of *Bd* infections in frogs at the locations of these declines or extinctions in the years when they were recorded.

The data on extreme weather events (droughts, floods, frosts, heatwaves, severe cold waves and wildfires) at the locations of declines were accessed through documentary research (Scott & Marshall, 2015) and converted to presence or absence data. We used this method because the available climate data rasters and shapefiles for Brazil, such as those from WorldClim, which provide data starting only from 1970, are more recent than the historical amphibian declines recorded for Brazil. Lima and Lira (2021) found a synchronicity and statistical significance between historical spatial climatic datasets and documentary evidence in Brazil, which supports our use of documentary evidence.

Data on local climate change patterns in areas of historical decline and extirpation were obtained from the System of Generation and Availability of Climatological Information (ICEA, 2023). We ran regressions of consecutive temperature and precipitation monthly means in the years and locations of historical declines for a five-year period (the year of each decline or extinction event plus the preceding four years). We used a 5-year period to ensure robust statistical analyses based on the parameters established by Green (1991). This approach allowed us to use linear regression to identify significant trends and patterns in climate variations and minimize the influence of seasonal anomalies and short-term

fluctuations. Significant regressions ($p < 0.05$) were interpreted as indicating gradual climate change at the location in the same period as the recorded declines (i.e., an increase or decrease in rainfall or temperature over the five years preceding the decline).

Historical global El Niño Southern Oscillation (ENSO) anomaly data (Mann et al., 2009) were extracted from the Climate Explorer platform (https://climexp.knmi.nl/start.cgi). El Niño Southern Oscillation significantly influences global climate patterns through its contrasting phases, El Niño and La Niña (van Oldenborgh et al., 2021). This warming alters atmospheric circulation patterns, leading to increased precipitation in the western Americas and drought conditions in Australia and Southeast Asia (van Oldenborgh et al., 2021). Conversely, La Niña involves the anomalous cooling of these sea surface temperatures, which enhances precipitation in Australia and Southeast Asia and causes drier conditions in the western Americas (van Oldenborgh et al., 2021). ENSO-induced climate anomalies significantly alter atmospheric circulation, increasing the frequency and intensity of extreme weather events such as droughts, floods, frosts, heatwaves, severe cold waves and wildfires (Grimm & Tedeschi 2009; Silva et al., 2018; Reis et al., 2021; van Oldenborgh et al., 2021). These disruptions amplify deviations from normal climate conditions, resulting in substantial impacts on ecosystems, species, and human activities (Grimm & Tedeschi 2009; Holmgren et al., 2001; Mann et al., 2009; Reis et al., 2021; Silva et al., 2018; van Oldenborgh et al., 2021).

The Granger (1969) causality test is a statistical hypothesis test for determining whether one time series is useful in forecasting another. However, testing for Granger (1969) causality when one or both time series are not stationary can lead to spurious causality (He & Maekawa, 1999). Therefore, we followed the procedure recommended by Toda & Yamamoto (1995). For each time series used, we first confirmed that no other time series was integrated with it before continuing with the Granger (1969) causality test. We then created a vector

autoregression model (VAR) for each time series after determining the most parsimonious lag length based on the Akaike information criterion (AIC). We tested for misspecification in residual serial correlation in each time series VAR model. Finally, we added the maximum order of integration to the number of lags to carry out a Wald test. This procedure ensured that the Granger (1969) causality test was applied with the correct degrees of freedom (Toda & Yamamoto, 1995). We ran all analyses in R (R Core Team, 2024) with forecast (Hyndman et al., 2022) and "vars" (Pfaff, 2008) packages.

We used structural equation models (SEMs) to evaluate the relationships between the variables of interest and the AIC to evaluate goodness of fit. Directed separation tests were conducted to assess the conditional independence between the variables. Given that both gradual climate change and extreme climate events can differentially affect high-elevation and lowland areas, we used SEM with and without altitude data. We obtained the local elevation for each geographic coordinate with the "elevation" function in the rgbif package in R (Chamberlain et al., 2023). This function retrieves specific geographic coordinates from the Global Biodiversity Information Facility. We also used SEMs to assess the impact of Bd, climate change, and extreme weather events on families and genera and to assess the influence of global temperature increase and Southern hemisphere temperature (Morice et al., 2021) as these variables lack oscillatory behavior and are therefore unsuitable for analysis with the Granger (1969) test.

We subjected the SEMs to the Fisher *C* test to evaluate global fit. Through the parameter perturbation analyses and comparison of alternative models, we evaluated the models' efficiency by analyzing different variables. These three sensitivity tests confirmed the robustness and reliability of our models, ensuring that they accurately represented the observed phenomena. All SEMs were run in R Software (R Core Team, 2024).

RESULTS

SID, page 2; do not mix Results and Discussion

We found decline and extinction events for 90 species of Brazilian frogs from 1923 to 2014. Eight species were possibly extinct (*Cycloramphus stejnegeri*, *Holoaden bradei*, *Hylodes glaber*, *Paratelmatobius lutzii*, *Phrynomedusa marginata*, *Phrynomedusa vanzolinii*, *Thoropa lutzii*, *Thoropa petropolitana*), one critically endangered species (*Hylodes mertensi*) and one endangered species (*Hylodes sazimai*) (Appendix S1). We also found, for the first time, a massive decline of 26 frog species in southern Minas Gerais in 2014, attributed to a severe drought event.

Gradual climate change was a strong predictor of historical amphibian declines in Brazil ($p < 0.001$; $F = 7.83$) (Figure 1a). Extreme weather events, such as droughts and frosts, combined with gradual climate change detected at the same locations, were even better predictors of historical declines ($p < 0.001$; $F = 5.643$) (Figure 1b). Extreme weather events alone did not predict historical amphibian declines ($p = 0.115$; $F = 2.008$) (Figure 1c). The climatic anomalies caused by El Niño were also good predictors of historical declines of amphibians in Brazil, although the results were marginally significant ($p = 0.058$; $F = 2.84$) (Figure 1d). The different climatic databases we used showed similar results and corroborated our finding that global and local conditions affected the historical declines of amphibians in Brazil. Peaks of Bd infection showed no Granger causal correlation with historical declines in amphibians ($p = 0.434$; $F = 0.715$) and began 15 and 4 years after the decline waves started, making it an implausible cause of historical population declines and extinctions (Figures 1e).

The results of the SEMs corroborated the Granger (1996) test, showing that climatic anomalies caused by El Niño explained the extreme climatic events that occurred in the locations of the historical declines of amphibians in Brazil and explained increases in *Bd* (Figure 2a, b). The rise in temperature in the Southern Hemisphere further explained the increase in Bd infections in Brazil, accounting for approximately 60% of cases (Figure 2c, d). Extreme weather events resulting from El Niño anomalies and increases in global temperatures or temperatures in the Southern hemisphere accounted for >97% of the historical declines in Brazil (Figure 2). However, the El Niño anomalies and the rise in global or Southern Hemisphere temperatures did not affect the gradual climate change observed in areas of historical declines and extinctions (Figures 2b, d). The SEMs indicated that climate change in areas of declines and extinctions was associated with 66% of these cases (Figure 2b, d) and that these declines and extirpations were driven by changes in climatic variables independent of global temperature rise, such as alterations in rainfall patterns.

As with the Granger (1996) test, the SEMs also did not reveal any effect of Bd on historical declines of amphibians in Brazil. Together, the Granger test (1996) and SEMs indicated that both extreme climatic events driven by rising global temperatures and local climate changes in areas of decline—resulting from alterations in other climatic patterns (Figure 2)—were the primary drivers of the historical declines observed in Brazilian frogs (Figure 1b). These factors often exerted a synergistic impact on regions that had experienced such declines and extinctions (Figure 1b).

The SEMs also did not reveal increased vulnerability to any of the variables when controlling for family, genus, or altitude, although high altitudes were correlated with 30% of amphibian declines in Brazil when added to the model (Figure 3). In these cases, the impact of extreme climatic events was reduced but remained significant, suggesting that anuran

populations at high altitudes may be more vulnerable to extreme climatic events (Figure 3). Neither high-altitude species nor specific families exhibited greater susceptibility to Bd (Figures 2 and 3).

The structural equation model also revealed a negative relationship between the percentage of Bd infection and the number of frog declines or extinctions (i.e., as the percentage of infection increased, the number of deaths declined). The SEMs suggests that increased infection percentages may correlate with reduced mortality, potentially due to natural population immunization (herd immunity) (Figure 3).

Although Bd was not associated with the historical declines of amphibians in Brazil, climatic events, including anomalies caused by El Niño, and an increase in Southern hemisphere temperature were significant predictors of increases in Bd infection (Figures 2 and 3).

DISCUSSION

Extreme climate events driven by El Niño anomalies have been exacerbated by climate change in intensity and frequency (McPhaden et al., 2020; Wang et al., 2019). Our results suggest that historical amphibian declines in Brazil (Carvalho et al., 2017; Toledo et al., 2023) are primarily explained by these extreme climatic events together with gradual climate change (Figure 1b). The extreme events occurred at regional and local scales (e.g., droughts, floods, frosts, and wildfires) and at larger scales (e.g., heatwaves and severe cold). These events exhibit broad spatial magnitudes, which can trigger and intensify extreme climate phenomena at the local scale (Figure 2).

At the global scale, increased temperatures and El Niño climatic anomalies have been a significant driver of climatic events at the landscape level (Figure 2). These anomalies act synergically with other local threats to amphibian populations, exacerbating the overall impact on these species (Ferrante et al., 2019). Heatwaves and droughts can exacerbate local threats at the landscape level, such as habitat fragmentation. Many forest fragments can become dry, which significantly affects local diversity of amphibians (Becker et al., 2007; 2009). For example, in southern Minas Gerais in 2014, forest fragments with water bodies became dry fragments due to the formation of a climate instability cell over southeastern Brazil (Ferrante et al. 2023a).

In fragmented landscapes, different land uses and edge effects generated by agricultural matrices that are seasonal or of low-stature vegetation (e.g., pasture and sugar cane) make forest fragments more vulnerable to climatic factors, such as wind, heatwaves, cold waves, and droughts (Ferrante et al., 2017). These conditions significantly affect the structure of forest fragments, species' diversity and composition, and the abundance of amphibians (Ferrante et al., 2017). Small populations of species with high ecological requirements that are isolated in forest fragments are particularly vulnerable, as extreme climate events can lead to abrupt declines and even local extinctions due to low reproductive rates and individual mortality (Ferrante et al., 2023a).

The synergistic combination of threats at the landscape level, such as livestock in conservation areas and climate change impacts like El Niño anomalies, heatwaves, and droughts, also increase wildfires (Ferrante & Fearnside, 2022; Viegas et al., 2022). This feedback loop exacerbates local and global climate change, leading to direct and indirect biodiversity loss (Ferrante & Fearnside, 2022; Viegas et al., 2022).

We found that extreme climatic events, such as droughts, explain the increase in *Bd* infections in Brazilian amphibians (Figure 3). These findings also point to how climate

change, global temperature increase, El Niño anomalies, and extreme climate events can lead to significant increases in zoonotic disease spillovers in tropical regions. Our results are consistent with other studies that show that climate anomalies caused by El Niño, temperature increase, climate changes, and extreme weather events lead to increases in diseases, including in humans (Anyamba et al., 2019; Ferreira et al., 2022; Hulber et al., 2018). These findings underscore an urgent concern for animal and human health in the Amazon region, where record-high temperatures, severe droughts exacerbated by El Niño, and deforestation exacerbated by the BR-319 highway are driving an increased risk of zoonotic spillover (Ferrante & Becker, 2024; Ferrante, 2024). The spillover events that have occurred highlight the pressing need to address these interconnected environmental and public health threats (Ferrante & Fearnside, 2023; Ferrante, 2024; Naveca et al., 2024).

Our findings about Bd align with those of Buttimer et al. (2024), who observed that drought events affect the skin microbiota of anurans in Brazil's Serra do Japi and lead to an increased Bd load in animals. Buttimer et al.'s (2024) findings support our conclusion that Bd tends to emerge in populations that are weakened and under climate stress, particularly in areas influenced by extreme weather events, including droughts influenced by El Niño climatic anomalies and global temperature increase (Figures 2 and 3). However, our data showed that infections by Bd peaked over a median of 15 years after historical declines in Brazilian amphibian populations (Figure 1e), suggesting that, for Brazilian frogs, Bd is an opportunistic and nonlethal pathogen for most species. This idea is supported by several studies that show population declines and high levels of inbreeding lead to increased susceptibility to diseases, including fungal infections, due to reduced genetic diversity (Abascal et al., 2016; Bannasch et al., 2021; Neaves et al., 2015). This temporal disparity between the peaks of Bd infections and historical declines makes it implausible that Bd caused these declines (Figure 1e).

The lack of effect of Bd on historical declines could not be attributed to poor data quality for two reasons: First, the structural equation models showed a significant effect of El Niño and increased global and Southern hemisphere temperature on the increase in *Bd* . Second, these were the same data used to argue that Bd could cause historical declines because the fungus had been detected in many areas of the Atlantic Forest (Carvalho et al., 2017; Toledo et al., 2023).

The absence of observations of massive deaths caused by Bd in Brazil (Lips, 2016) contrasts with occurrences in other countries, such as Australia, Costa Rica, Ecuador, and Peru (Laurance et al., 1996; Lips et al., 2006; O'Hanlon et al., 2018; Vredenburg et al., 2010), which reinforces the hypothesis that Bd is not responsible for the historical declines or extinctions of amphibians in Brazil. Similar to Europe, Brazil hosts several Bd lineages, records of which span over a century, including non-native variants to the region (Lips, 2016). Brazil is the only country where hybridization between *Bd* variants has been observed (Lips, 2016; O'Hanlon et al., 2018), reinforcing the similarity among variants.

Pathogens are exhibit greater resistance to climate change than their hosts, which also appears to be the case for Bd and amphibian hosts (Cohen et al., 2017). This may explain the rise in Bd infections in postdecline populations made vulnerable by climate change. Perhaps *Bd* is an opportunistic non-lethal pathogen for most Brazilian amphibians as a result of a possible coevolution between host and pathogen, which would be beneficial for both. The co-evolution between Brazilian amphibians and Bd (O'Hanlon et al., 2018) suggests that many Brazilian amphibians are resistant to lethal infections by this pathogen, which is lethal to amphibians in other parts of the world (Ferrante et al., 2020). This hypothesis is supported by our data, which showed an increase in Bd infection rates accompanied by a decrease in frog mortality (Figure 3). Rising pathogen loads in a population accompanied by declining mortality rates is widely recognized in epidemiology as an indication of herd immunity (Fine

et al., 2011; Ferrante et al., 2022; 2024). This phenomenon suggests that as infection rates increase, the population develops a form of collective resistance, mitigating the pathogen's impacts on survival rates (Fine et al., 2011).

If Brazilian amphibians exhibit a greater resistance to Bd infections due to co-evolution with the Bd strain recorded in Brazil over 100 years ago, this resistance may extend to other strains. Additional evidence supporting this hypothesis comes from the non-native American bullfrog, which is a natural reservoir for *Bd* (O'Hanlon et al., 2018). The introduction of this species to southern Minas Gerais 15 years ago did not affect the richness or composition of native anuran species (Ferrante et al., 2020). This suggests that the anuran community of the Atlantic Forest may be resistant to lethal *Bd* infections (Ferrante et al., 2020). Monitoring of the American bullfrog in southern Brazil further supports these findings. No noticeable impacts on native species richness were observed, and bullfrogs are abundant in some of the most species-rich amphibian communities (Both et al., 2014).

The results of an analysis of the temporal progression of the Bd epidemic in three landscapes in the United States (Vredenburg et al. 2010) showed that the number of *Bd*-infected frogs increases prior to population declines (Appendix S2). This pattern contrasts sharply with our findings for Brazil, where Bd prevalence tended to increase predominantly after population declines and extinctions had already occurred (Figure 1e). These observations strongly support the hypothesis that Brazilian amphibians exhibit a greater resistance to Bd infections. Moreover, they suggest that, in Brazil, Bd functions primarily as an opportunistic pathogen, exploiting amphibian populations that have already undergone declines caused by other stressors (Figure 1 and 2).

In Australia, by contrast, the declines reported by Laurance et al., (1996) overlap with regions experiencing rising temperatures and coincide with years of historical temperature increases (Appendix S3). This suggests that rising temperatures in the Southern Hemisphere

may have played a significant role in triggering amphibian declines in other regions of the world, a pattern reflected in our data for Brazil (Figure 2c, d). Recent studies show that Bd was present in Costa Rica prior to the widespread population declines observed in the 1980s; infections increased significantly after this period (De León et al., 2019). These trends coincided with climatic changes that may have facilitated the fungus's spread (De León et al., 2019). These findings suggest that Bd epidemiological dynamics vary across different regions of the globe and are influenced by distinct climatic patterns and prior exposure to the fungus.

Our hypothesis that high temperatures, droughts, and historical decline of frogs in Brazil are associated with increased rates of Bd infections is corroborated by mathematical modeling, which shows that Bd exhibits higher population growth at high temperatures than at low temperatures (Voyles et al., 2012). This finding provides additional support for our conclusion regarding the impact of El Niño and temperature increase in explaining the peaks in Bd growth in Brazil. Our data support the hypothesis that historical declines and extinctions of amphibians in Brazil are associated with extreme weather events and gradual climate change (Figures 1 and 2). This threat may have acted synergistically with other threats, including habitat loss and fragmentation, the disruption of connections between aquatic and terrestrial ecosystems (Becker et al., 2007; 2009), the expansion of agricultural crops in the landscape (Ferrante et al., 2017), and the intensive use of pesticides (Ferrante & Fearnside, 2020). Changes in rainfall patterns and climate change are significant factors contributing to population declines of frogs in the Atlantic Forest (Ferrante et al., 2023a), a region that has witnessed most of the historical amphibian declines in Brazil (Carvalho et al., 2017; Eterovick et al., 2005; Ferrante et al., 2019; 2023a; Heyer et al., 1988; Toledo et al., 2023; Weygoldt, 1989). The extent of drought events could exacerbate the effects of habitat fragmentation (Becker et al., 2007; 2009), which reduces recruitment, and result in fewer frog populations (Ferrante et al., 2023a).

We identified key drivers of amphibian declines in Brazil, corroborating Heyer et al.'s (1998) hypothesis that climatic events are major contributors to this decline. Some well-documented events also support this hypothesis (Getirana, 2016; Ferrante et al., 2023a). For instance, in 2014, the formation of a climate instability cell over southeastern Brazil severely disrupted the rainfall regime, negatively impacting anuran populations (Ferrante et al., 2023a). Heyer et al. (1998) suggest frosts as the cause of extinctions in Boracéia, in the state of São Paulo, a hypothesis also supported by some extreme climate events we considered here.

Our results also highlight the urgent need for large-scale investigations into biodiversity loss and the rise of pathogens in undersampled biomes that are experiencing severe effects from climate change and El Niño, such as the Amazon region. Furthermore, investigating the synergistic effects of increasing disease prevalence, population declines, and rising inbreeding levels is essential for developing effective conservation strategies and mitigating the impacts of climate change on biodiversity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

AUTHOR CONTRIBUTIONS

LF conceived of the idea; LF and FBB designed the research and conducted statistical analyses; LF, FBB, ILK, LMD, AG, CFBH, LCS and PMF wrote and revised the manuscript.

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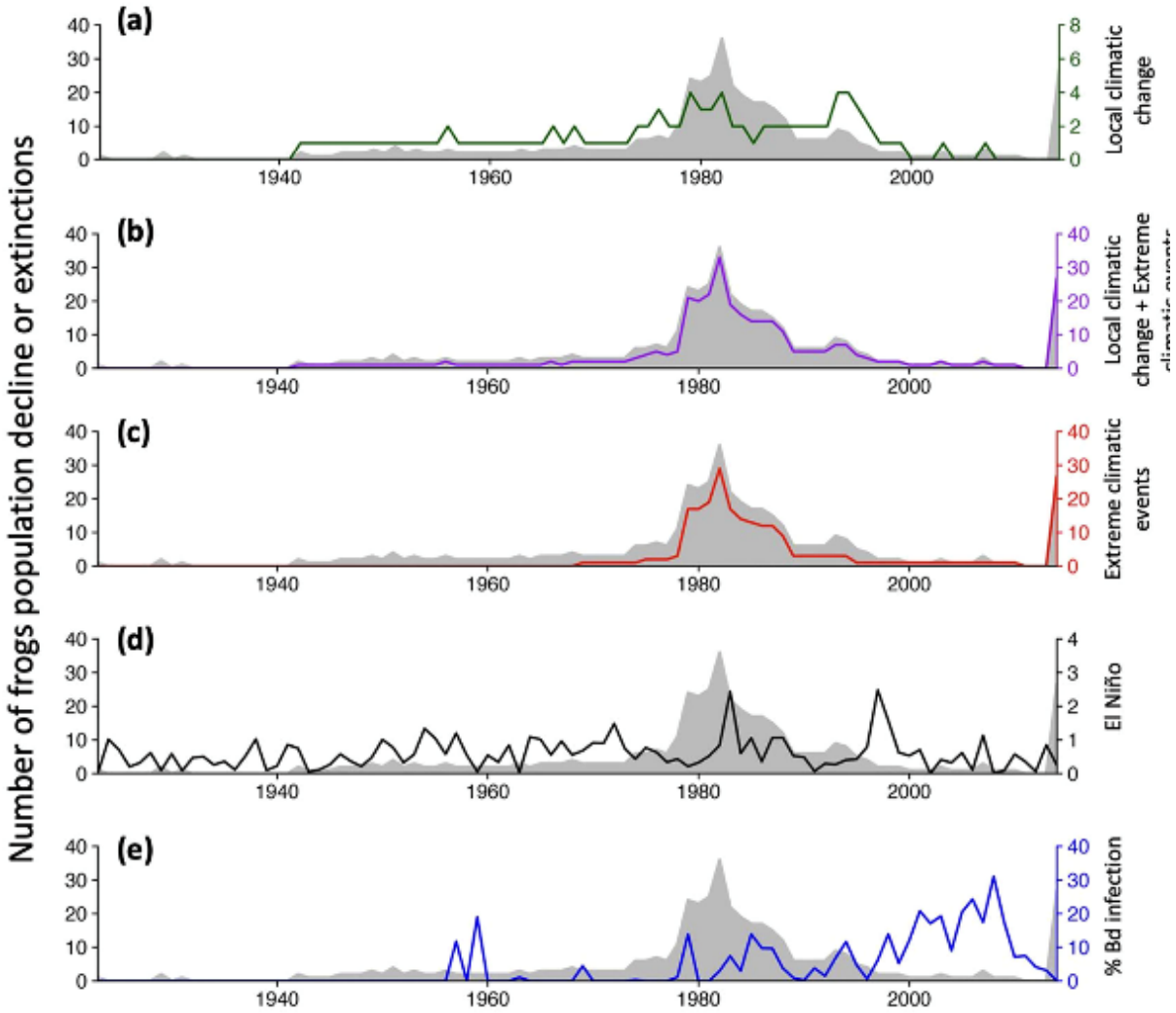


FIGURE 1 Over time the number of Brazilian frog population declines and extinctions relative to (a) local, gradual climate changes, (b) climatic events (sum of extreme weather events and local, gradual climate changes), (c) extreme weather events, (d) climate anomalies caused by El Niño, and (e) *Batrachochytrium dendrobatidis* (Bd) infections.

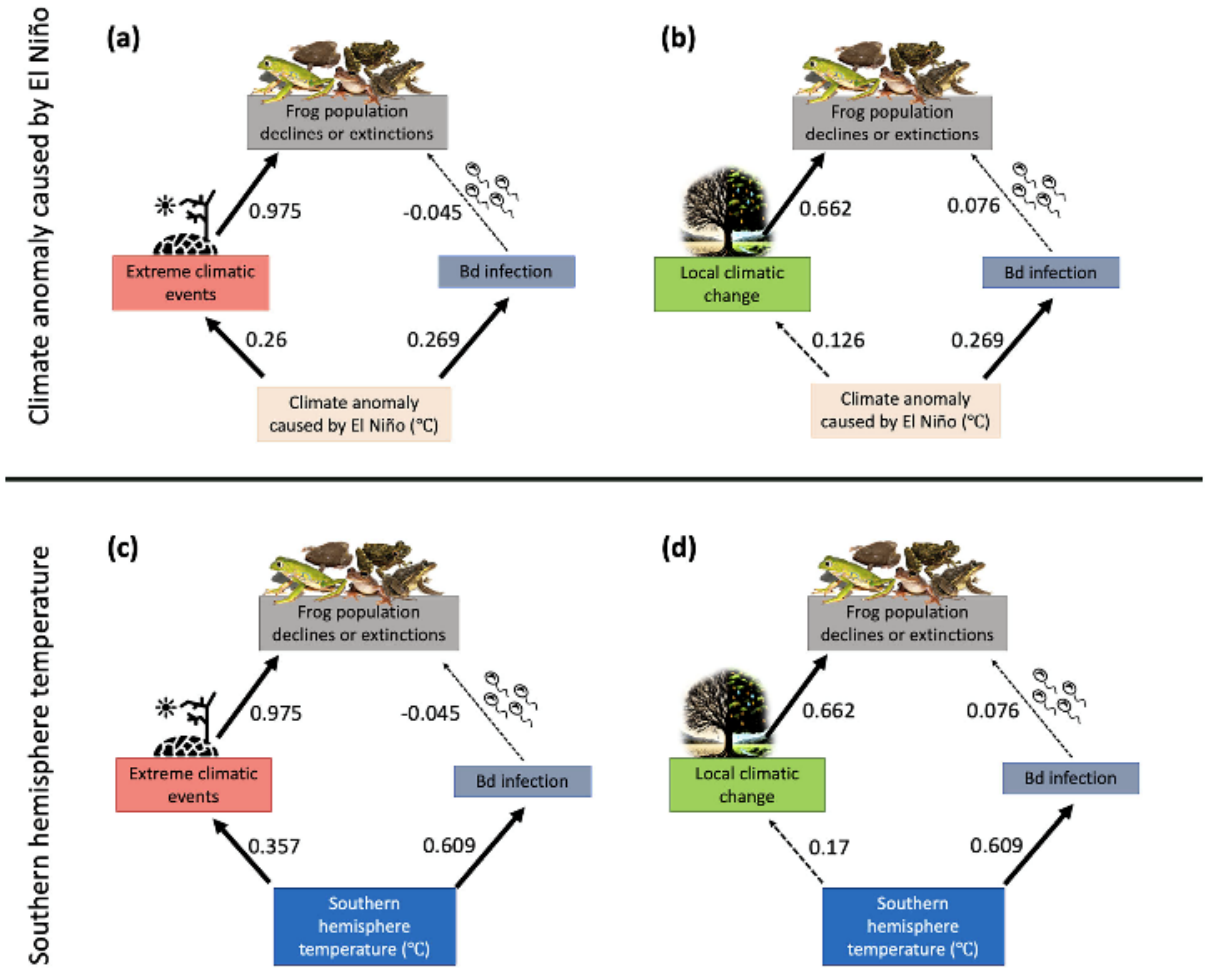


FIGURE 2 Structural equation models showing how in Brazil (a, c) El Niño-induced climatic anomalies and (b, d) rising temperatures in the Southern Hemisphere directly influence extreme weather events, and thus affect amphibian declines and *Batrachochytrium dendrobatidis* (Bd) pathogen loads, and how localized climate changes may contribute to population declines and local extinctions (solid lines, statistically significant relationships; dashed lines, nonsignificant relationships).

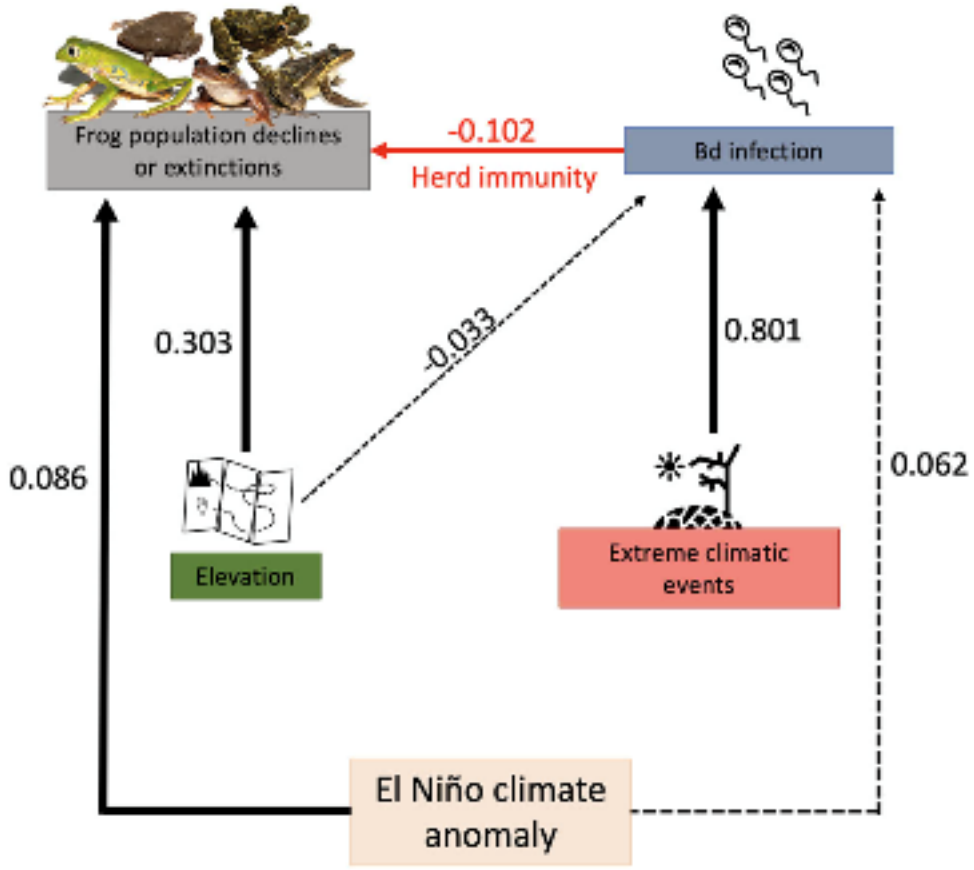


FIGURE 3 Structural equation models with elevation showing a negative relationship between *Batrachochytrium dendrobatidis* (*Bd*) infection rates and frog declines and extinctions in Brazil (solid lines, statistically significant relationships; dashed lines, nonsignificant relationships).