Effects of Amazonian flying rivers on frog biodiversity and populations in the Atlantic rainforest

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ABSTRACT

Given the speed at which humans are changing the climate, species with high degrees of endemism may not have time to avoid extinction through adaptation. We investigated through teleconnection analysis the origin of rainfall that determines the phylogenetic diversity of rainforest frogs and the effects of microclimate differences in shaping the morphological traits of isolated populations (which contribute to greater phylogenetic diversity and speciation). We also investigated through teleconnection analysis how deforestation in Amazonia can affect ecosystem services that are fundamental to maintaining the climate of the Atlantic rainforest biodiversity hotspot. Seasonal winds known as flying rivers carry water vapor from Amazonia to the Atlantic Forest, and the breaking of this ecosystem service could lead Atlantic Forest species to population decline and extinction in the short term. Our results suggest that the selection of morphological traits that shape Atlantic Forest frog diversity and their population dynamics are influenced by the Amazonian flying rivers. Our results also suggest that the increases of temperature anomalies in the Atlantic Ocean due to global warming and in the Amazon forest due to deforestation are already breaking this cycle and threaten the biodiversity of the Atlantic Forest hotspot.

INTRODUCTION

"It takes all the running you can do, to keep in the same place" said the Red Queen in Alice Through the Looking Glass (Carroll, 1960).[EM1] Lack of time for species to adapt to rapid changes in ecosystems or in climate can cause extinctions (Van Valen, 1973; Quental & Marshall, 2013). This is equivalent to a race to stay in the same place: either species adapt to the rapidly changing environment or they disappear. To adapt to global change, some species undergo phenotypic changes within a few generations (Charmantier et al., 2008; Oostra et al., 2018); however, knowledge about the ability of most taxonomic groups to adapt is still incipient. The Earth's sixth mass extinction (Barnosky et al., 2011; Dirzo et al., 2014) is attributed to anthropogenic changes in atmospheric composition and direct human impacts on terrestrial andquatic ecosystems (Lewis & Maslin, 2015). Although the climate and biodiversity crises are recognized, the connections between them and the best ways to mitigate their advance are poorly understood.

Brazil, with its tremendous biodiversity, has had environmental policies that threaten biodiversity and global climate due to increasing deforestation and greenhouse gas emissions (Ferrante & Fearnside, 2019; 2021a). These threats are mainly due to the increase in deforestation in the Amazon due to large projects, such as roads (Andrade et al., 2021; Ferrante & Fearnside, 2020a; Ferrante et al., 2021a; Ferrante et al., 2021b), and new deforestation cycles generated by the expansion of cattle ranching and agriculture (Ferrante & Fearnside, 2020b; 2022a; Ferrante et al., 2021c). This expansion at the expense the Amazon forest is a threat both locally and beyond the borders of Amazonia, whether by the emission of greenhouse gases caused by deforestation or by the alteration of flows of water vapor carried to other parts of South America by winds known as "flying rivers" or "aerial rivers" (Salati et al., 1979; Salati & Vose, 1984).

Water vapor that evaporates from the Atlantic Ocean is carried by trade winds into the Amazon basin, where rain is recycled by the forest and complex atmosphere-biosphere interactions in the boundary layer as air masses drift toward the Andes (Salati et al., 1979; Salati & Vose, 1984). When reaching the physical barrier of the Andes, the low-level zonal water vapor in the aeial lake that has been generated over the Amazon basin moves south along the eastern edge of the Andes toward the subtropics, especially during austral summer (December-March) (Salati & Vose, 1984; Arraut & Satyamurty, 2009; Arraut et al., 2012). These winds turn toward southeastern Brazil, where the water in these flying rivers irrigates another major biodiversity hotspot -- the Atlantic Forest (Salati & Vose, 1984; Arraut & Satyamurty, 2009; Arraut et al., 2012). Amazon deforestation can therefore affect the Atlantic Forest, putting this biodiversity hotspot in jeopardy (Ferrante & Fearnside, 2018; 2022b).

The unique conditions and diversity of environments in the Atlantic Forest hotspot led to the emergence of a large number of endemic species. Amphibians have the highest proportion of endemic species among the vertebrates in this biome (Haddad et al., 2013). Climatic variation produced the phylogenetic diversity and morphological variations within these clades for several species of endemic anurans in the Atlantic Forest (Carnaval et al., 2009; Paz et al., 2019; Santos et al., 2019; 2020; Thomé et al., 2020). However, recent climate change has been a factor in population declines and extinctions of anuran species (Pounds & Crump, 1994; Pounds et al., 1999; Ferrante et al., 2019), making this the most threatened group among vertebrates worldwide (IUCN, 2022).

In addition to climate change, urban and agricultural expansion have resulted in various Atlantic Forest amphibian species becoming endangered in recent decades (Ferrante et al., 2019). The Atlantic Forest hotspot has experienced and is experiencing habitat loss and fragmentation, resulting in an increase in forest isolation (Rosa et al., 2021). Frogs in the Atlantic Forest are often unable to cross landscapes fragmented by agriculture (Ferrante et al., 2017). Even populations of species with high self-dispersal potential have been isolated by fragmentation (Ferrante et al., 2020). Climate change in the Atlantic Forest has been increasing, and water scarcity is especially severe in southeastern Brazil (Getirana, 2016; Getirana et al., 2021). This cluster of threats raises the questions of how species could be affected by a breakdown of the water-vapor flows that supply rain to the Atlantic Forest and how they could adapt to these changes. Amphibians would be especially vulnerable to such a breakdown because they depend on water for reproduction. Amphibian population declines worldwide are occurring due to synergetic effects of climate and habitat change, mainly the disconnection of aquatic and terrestrial habitats (Becker et al., 2007; 2010).

Population declines and extinctions have occurred for torrent frogs in the genus *Hylodes* (Heyer, 1988; Weygoldt, 1989; Eterovick et al., 2005). This genus, endemic to the Atlantic rainforest, contains 26 species (Frost, 2022) whose reproductive and ecological behavior are associated with fast-flowing streams in the forest interior, making them highly dependent on water (Haddad et al., 2013; de Sá et al., 2015). The south and southeast regions of Brazil, where *Hylodes* species are endemic (Haddad et al., 2013; Frost, 2022), have been affected by severe climatic events (e.g., droughts), which have affected reproduction and population recruitment of several species (Pedroso et al., 2021) and the water supply to large cities (Fearnside, 2004; 2021; Getirana, 2016; Getirana et al., 2021).

Patterns of phylogenetic structure and morphological variation in Brazilian frogs are sensitive to changes in precipitation patterns; this sensitivity generates diversity (Simon et al., 2016). Due to rapid climate changes (IPCC, 2022), the time available for these species to adapt to them may be insufficient (Van Valen, 1973; Quental & Marshall, 2013). We investigated the teleconnections affecting rainfall (which determines the phylogenetic diversity of Atlantic Forest amphibians) and the effects of microclimate differences in shaping the morphological traits of isolated populations. These effects contribute to greater phylogenetic diversity and speciation. We also considered how deforestation in Amazonia can affect ecosystem services that are fundamental to the Atlantic Forest, such as the breakdown of the water-vapor transport by the Amazon flying rivers, which could lead to population declines and species extinctions in the short term.

METHODS

Phylogenetic and morphological inferences

We utilized phylogenetic inference based on maximum likelihood for *H. sazimai* and other species in the genus *Hylodes* to identify the populations and define phylogenetic isolations (Fig. 1a). To differentiate the populations of *H. sazimai*, we sequenced a fragment of the 16S rRNA gene from 14 individuals and compared the results with those from other species in the *Hylodes lateristrigatus* group analyzed by de Sá et al. (2015). We used the primers 16Sar-L and 16Sbr-H (Kessing et al., 1989) under standard polymerase chain reaction (PCR) conditions. We also used a haplotype network that encompasses different populations. Nodal support values above the nodes correspond to ML bootstrapping, and a haplotype network was reconstructed using Haploviewer software (Fig. 1a).

We used principal component analysis (PCA) for 12 morphological traits (back foot membrane, distance between nostrils, eye nostril distance, fibula length, foot length, head width, length (snout vent length [SVL]), metatarsal membranes of digit IV and V of the food, snout angle, tibia length, and tympanum diameter) to assess morphological similarity among populations (Fig. 1b). Differences in overall morphological traits among the 4 populations were compared using a permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance. We used analysis of variance (ANOVA) to compare each of the morphological traits among the 4 populations. We recorded populations of *H. sazimai* in the municipalities of Campinas (CP: 22°54'14.19"S, 46°49'26.64"W), Caldas (CA: 21º 52' 52" S, 46º 27' 11" W), Poços de Caldas (PC: 21°46'29.27"S, 46°33'24.56"W), and Areado (AR: 21°22'30.57"S, 46°11'53.37"W) (Appendix S1).

Spatial and temporal climatic analyses

For each area with a population of *H. sazimai*, we obtained values of mean temperature, rainfall, and soil moisture at 10 cm and 40 cm depth. The data used are from NASA's Global Land Data Assimilation System (GLDAS) (Rodell et al., 2004), collected monthly from 2002 to 2017 at 0.25° spatial resolution. Anomalies in terrestrial water storage (TWS), which is the integrated amount of water stored in the vertical column, including surface water (rivers, lakes, wetlands, etc.), soil, and aquifers, are derived from the Gravity Recovery and Climate Experiment (GRACE) (Tapley et al., 2004) and the GRACE Follow On (GRACE-FO) missions. We used the monthly 0.25° gridded Mascon solution RL06 processed by the University of Texas at Austin's Center for Space Research (CSR) (Save et al., 2016). The collection for each area was performed in the 0.25° resolution grid point corresponding to each occurrence of the species. Based on averages from these data, we constructed the patterns of precipitation, soil moisture, and temperature at the 4 locations to allow comparisons (Fig. 1d).

The teleconnection analyses were performed using the Climate Exploration platform (https://climexp.knmi.nl/start.cgi) (Trouet & Van Oldenborgh, 2013). We used GLDAS precipitation data (Rodell et al., 2004) for the rainy season (i.e., breeding season for anurans in the Atlantic Forest [Haddad et al., 2013]). Data are from November to February from 2002 through 2017. They were subsequently correlated in the Climate Exploration platform with sea surface temperature data from HadlSST1 SST for 2002-2017, cloud pressure data from FRESCO 6 for 2002-2012, and zonal wind data from NASA's Modern-Era Retrospective analysis for Research and Applications 2 (MERRA-2) (Reichle et al., 2017) for the same months and years (Fig. 2). For the teleconnection analyses of climatological anomalies, we used 2002-2017 monthly surface temperature anomalies from gridded data in a blend of the CRUTEM5 land surface air temperature data set and the HadSST4 sea surface temperature (SST) data set (Morice et al., 2021). All teleconnections used the automatic filter in the Climate Exploration platform with $p < 0.10$, an acceptable threshold for teleconnection analyses (Trouet & Van Oldenborgh, 2013). For the interpretation of the results, we considered only areas with $p < 0.05$ to assure a greater level of certainty. For each of the teleconnection analyses, 2 maps were generated showing the p value and the correlation coefficient. For interpretation of the results, we considered only areas with correlation coefficients >0.2, an acceptable threshold for teleconnection analyses (Siedlecki, 2010; Zhang et al., 2022).

Monitored population

Population monitoring was restricted to the Areado population. We delimited the occurrence area of the population to a 300-m stretch of a single stream. In all surveys the same 3 people searched a transect parallel to the watercourse in 3 diurnal and 3 nocturnal monthly survey sessions. During each survey, the number of vocalizing males was quantified and the location of the vocalization site was recorded. This made it possible to census active males in the population given their territoriality, high phyloptry, and low vagility.

The surveys were conducted December 2011-March 2012, November 2012-March 2013, and November 2014-March 2015. From November 2012 to March 2013 and from November 2014 to March 2015, we also monitored continuously with a SongMeter+ recorder to confirm the exact number of males in the population and to validate field observations. The male activity data were compared with the precipitation data (millimeters per day from GLDAS) to assess the relation between rainfall and oscillations in activity.

RESULTS

Shaping of morphological traits in torrent frogs populations

The torrent frog (*Hylodes sazimai*) is genetically structured into only 4 known populations (Fig. 1a). These populations are distributed in a climatic gradient with different temperature, precipitation, and humidity conditions. Only the population at the type locality (Campinas municipality, São Paulo state) was previously known, and the 3 new populations are the first records for Minas Gerais state in the municipalities of Caldas, Poços de Caldas, and Areado. We found very little genetic variation between the new populations analyzed and the population from the type locality. The sequences of the 14 individuals analyzed were grouped into 6 haplotypes (maximum p distance 0.8%, 4 bp among haplotypes), but there was no haplotype sharing among populations. The chronic fragmentation of the Atlantic Forest isolated all of the 4 known locations (Appendix S2). The 4 populations were distributed between 2 habitat types: seasonal semideciduous Atlantic rainforest fragments (Areado and Campinas) and ombrophilous high Montane Atlantic Forest fragments (Caldas and Poços de Caldas). The 4 known populations showed both phylogenetic structures (Fig. 1a).

The PCA (Fig. 1b) and PERMANOVA analyses (Table 1) showed that the morphological traits of the population in the municipality of Caldas were more similar to those of the populations in Campinas than of populations in Poços de Caldas, despite these localities being closer to each other, having similar elevations, and being isolated from the other localities by a volcanic craton. Based on axis 1 of the PCA and PERMANOVA, we observed a division into 2 groups: the first encompassing Campinas and Caldas and the second encompassing Poços de Caldas and Areado. These groups reflected the latitudinal gradient in which each population was inserted and showed that 2 different populations occurred in the volcanic craton area. Axis 2 of the PCA reflected the latitudinal gradient, where the population in Areado was at a higher latitude, whereas Caldas and Campinas populations were at lower latitudes (see. Fig 1b).

Of the 12 morphological traits analyzed for the 4 populations, 3 showed relatively strong divergence among locations (Fig. 1c; Table 2). These traits were foot size ($p = 0.04$), back foot membrane ($p = 0.01$), and metatarsal membrane of digit V of the foot ($p = 0.01$) (Fig. 1c; Table 2). These results suggest that functional characteristics linked to displacement diverge among different populations. The metatarsal membrane of digit IV of the foot appeared to follow the same divergence trend in the 4 populations. In this case, the divergence was not statistically significant (Fig. 1c).

Climate stress, reproductive activity, and population recruitment

According to our visual and auditory observations, the number of vocalizing males of *H. sazimai* in the forest fragments decreased as proximity to the forest edge increased and in areas with little forest cover. Comparing the fluctuation of rains at 1 of these localities (Areado) with the density of vocalizing males of *H. sazimai* (Fig. 4 a, b), we observed that drier seasons had fewer vocalizing males or even the total absence of males. In some seasons with very severe drought, as in 2014, there was complete absence of male activity, which represents less reproduction for the species and, consequently, lower recruitment of individuals. This explained the lower density of vocalizing males following rainy seasons, even with increased rainfall (Fig. 4b).

In 2014, when there was extensive water scarcity (as compared with years with normal precipitation, such as 2012 and 2013), data on terrestrial water-storage anomalies for the whole of Brazil showed the formation of a cell of climate instability and severe drought in southeastern Brazil, where the 4 populations of *H. sazimai* were located (Fig. 4c, d, e). The climatological data series indicated this climate instability cell located over southeastern Brazil (Fig. 4c, d, e) was a significant contributor to the very low rainfall at the locations of the torrent frog populations we studied. In turn, the lower rainfall caused population fluctuations, influencing the recruitment of individuals needed to maintain the population (Fig. 4b). Areado's population of torrent frogs was embedded in a small area that encompassed only 2 forest fragments in the entire region, connected by a small stream <1.5 m wide and 50 cm deep at the deepest points. Considering theterritorial behavior and diurnal vocalization habits of males sitting on rocks in the stream and due to their exclusive occurrence in forested stretches, it was easy to carry out the census of reproductive adult males in this population. On-site observations in 2014 showed complete absence of water in the stream in which the torrent frogs occurred, which was the period when activity of the species was absent (Fig. 4b).

Teleconnections and climate at the studied localities

An analysis of teleconnections based on 17 years of monthly precipitation data (2000-2017) at each of the studied localities (GLDAS data, monthly precipitation in mm) during the rainy season (November, December, January, and February) showed a correlation of precipitation with higher sea surface temperature of the Central Atlantic Ocean, which originates from the African coast and reaches the coast of northern Brazil in November and December (Fig. 2). This caused an increase in rainfall and high vapor-pressure cells in the central Amazon during the same period (Fig. 2). In turn, the winds passing through these high vapor-pressure cells over the Amazon forest (Fig. 3) carried the moisture generated from these Amazonian areas to the locations of the 4 populations of *H. sazimai* in the Atlantic Forest.

The high vapor-pressure cells were distributed from the northernmost to the southernmost extremes of Amazonia and were concentrated in 3 distinct blocks by region: northern Amazonia (NA), encompassing part of the Jaua-Sarisariñama National and Parima Tapirapecó National Parks in Venezuela and the border between Venezuela and the Brazilian state of Roraima, covering the Yanomami indigenous land and a still-preserved part of terra firme (unflooded upland) Amazon rainforest extending from the Brazilian state of Roraima through Guyana, Suriname, and the state of Amapá; center-western Amazonia (CWA); and southern Amazon under pressure (SAUP), an area that encompasses the state of Acre, the southern portion of the state of Amazonas, and the states of Rondônia and Mato Grosso in the arc of deforestation (Fig. 2).

Climate anomalies breaking the cycle of Amazonian flying rivers

Our teleconnections analysis showed statistically significant correlations between precipitation at *H. sazimai* sites and water temperature anomalies in the Atlantic Ocean and between precipitation and thermal alterations in the Amazon region believed to have resulted from deforestation (Fig. 5). Statistically significant intracontinental thermal anomalies occurred in the entire arc of deforestation in southern and eastern Amazonia (Fig. 5a-f), influencing rainfall disturbances at the locations of each of the *H. sazimai* populations except for the type locality of the species in Campinas (Fig. 5g, h). Campinas was more affected by the Amazonian flying rivers than the other 3 locations. The intracontinental climatic anomalies that correlated with precipitation at 3 of the 4 locations were in areas in Amazonia with relatively higdeforestation. Our data also showed a pattern of synchrony between the climatic instability cell formed in southeastern Brazil over the 4 locations where *H. sazimai* occurred (Fig. 4e) with the effects of these climatic anomalies on precipitation at each location. The more central the location of site in the climate instability cell the greater the magnitude and the statistical significance of the climatic anomalies in the water cycle that favored rainfall at the site (Fig. 5). This reflects the correlation of climatic anomalies in the water cycle with the formation of the climate instability cell in southeastern Brazil.

DISCUSSION

Morphological traits shaped by local climate

The morphological traits we evaluated are essential for the movement of torrent frogs in the cascading streams in which they live, where the size of these functional traits can represent greater efficiency in climbing a stream where the water flow has increased due to greater precipitation. The greatest local variation of the morphological traits for movement in the aquatic environment was observed in Poços de Caldas, which is the location with the highest average rainfall in the rainy season, the greatest humidity throughout the year, and the mildest temperatures (Fig. 1c , d). This greater spectrum of local variation in the functional traits of the Poços de Caldas population denotes a neutral trait selection in locations with minimal climatic stress compared with locations with drought conditions (Fig. 1c , d). In locations with frequent lack of water, natural selection appeared to act more forcefully to reduce characters that imply water loss, including those characters that provide greater efficiency of movement in the aquatic environment. Climate components (such as precipitation and temperature) at the locations of the 4 populations of <="" span="" style="font-family: "Times New Roman"; font-style: italic;">*sazimai* would exert selective pressure on the functional characters of the morphology of individuals in each population. The 4 populations were well defined morphologically by their functional traits, which may allow classification by subspecies (Fig. 1b). The lack of haplotype sharing among *Hylodes sazimai* populations suggested that the 4 populations might be currently isolated, at least from a mitochondrial point of view.

The climate cycle shaping this biodiversity

Our results suggest that selective pressures on the functional characters of populations in the areas with higher temperatures and lower precipitation and humidity are selecting individuals with more economical characters, thereby preventing the loss of water from the bodies of these individuals. This makes individuals more adapted to drier and warmer environments, as seen from the reduction in the back foot membrane in the population in Campinas compared with the other populations (Fig. 1c, d). Individuals in the Areado locality, the second driest and hottest, also showed a reduction in the size of the feet and the metatarsal membrane of digit V of the foot. Populations with larger swimming membranes (Caldas and Poços de Caldas) were located in wetter locations with lower temperatures, which may be related to reducing these membranes at the other locations (Campinas and Areado). This would occur due to selective pressures for characters to provide energy savings in the drier environment because these animals would face less water flow in the streams where they occur. This is in addition to the reduction of membranes being potentially advantageous by providing less water loss from the animal’s body while they move through the terrestrial environment. This water savings would occur due to the reduction of thin permeable surfaces on the animals’ bodies in places with lower humidity and higher temperatures, which varied by up to 2.5º C on average (Fig. 1d).

Our results showed that some morphological traits have diverged among populations of torrent frogs in the Atlantic Forest, probably due to selective pressures from the local climate. These morphological trait changes were correlated with climatic factors where each population occurs, with the divergence or similarity between different populations of *H. sazimai* being reflections of the divergence or similarity of climatic variables between these locations (Figs. 1c, d).

The climate at these locations was correlated with a series of much broader meteorological events in other parts of the globe. The high degree of deforestation and disturbance in at least part of the TACA (Transamazon collapse area) may have already passed a tipping point for the maintenance of atmospheric ecosystem services. A portion of the TACA that is roughly bounded by the Transamazon Highway (BR-230) to the south and by the Amazon River to the north and stretches from Manaus (Amazonas state) to Belém (Pará state) has high vapor-pressure cells that were negatively correlated with precipitation at the locations of the 4 populations of *H. sazimai*. A concern for future deforestation is the CWA (center-western Amazonia) area, a large block of untouched forest whose only access via land is the BR-319 Highway that connects this block of forest to the arc of deforestation (the heavily deforested strip along the southern and eastern edges of the Amazon forest),

Although the Amazonian flying rivers were correlated with surface water temperatures in the Atlantic Ocean, our data also showed that water temperatures in the Pacific Ocean (i.e., El Niño and La Niña) also affected precipitation in the area of occurrence of *H. sazimai*. Precipitation in the localities with the highest elevations (Caldas and Poços de Caldas) were more strongly influenced by temperatures in the Pacific Ocean compared with the other localities (Campinas and Areado) (Fig. 2).

Frogs and the Red Queen effect

Although our results indicated that *H. sazimai* populations have undergone morphological adaptations to the climatic stresses to which they have been exposed, it is crucial to investigate whether the pace of climate change in these locations is not faster than the rate at which these populations can evolve adaptations. Our results suggested an ongoing population decline due to annual climatic fluctuations over the area of occurrence of *H. sazimai*, despite morphological adaptations to water stress. This could lead to extinction of this population, or even of the species, within a short period.

Climate change affects reproduction, recruitment, and food availability for amphibians (Donnelly & Crump, 1998; Duarte et al., 2012). Some cases of sudden extinction of anurans in Central America are related to increases in mean temperature, reduction of precipitation, and strengthening of El Niños (Pounds & Crump, 1994; Pounds et al., 1999). The phenotypic changes in anurans, such as size decrease and allometry, reflect continuous environmental stresses on individuals and their ability to persist despite environmental change (Delgado-Acevedo & Restrepo, 2008), as indicated by our results for the *H. sazimai* population in locations with greater hydric stress and higher temperatures.

Our results showed that, *H. sazimai* populations in drier areas (such as populations in Areado and Campinas) presented adaptations of functional traits to the climate. Our results indicated that the magnitude and speed of climate change had surpassed the adaptive capacity of the species, causing population declines of mature individuals and preventing the recruitment of new individuals into the population. These results illustrate the Red Queen effect (i.e., species have to keep changing to avoid extinction) (Van Valen, 1973; Quental & Marshall, 2013), so named for what the Red Queen in *Alice Through the Looking Glass* (Carroll, 1960) said: “It takes all the running you can do, to keep in the same place."

The population in Areado was only observed in 2 forest remnants of semideciduous Atlantic Forest located on the Taquaruçu ranch. The *H. sazimai* population of Areado is reported in Ferrante et al. (2017)

as *Hylodes* aff. *sazimai,* and at the time of that publication, when genetic analysis was lacking, we believed it was a new species given the small morphological size and bioacoustic variations. Caldas and Poços de Caldas are in the Serra da Mantiqueira area, which is an ancient crater of an inactive volcano and is an area of endemism for anurans (Cruz & Feio, 2007).

H. sazimai populations have morphological adaptations that suggest advantages under the climatic conditions at the locations where the populations were found. However, these adaptive changes have not been fast enough to keep up in this evolutionary race against climate change. This is worrying, given that the region in which the climate instability cell formed (Fig. 3e), which includes locations of the *H. sazimai* populations, is one of the areas with the greatest amphibian biodiversity in the world (Haddad et al., 2013; Rossa-Feres et al., 2017). Most species in this area are endemic and have restricted geographic distributions (Haddad et al., 2013; Rossa-Feres et al., 2017). This climatic instability cell also explains morphological variations among other populations of anurans endemic to the Atlantic Forest, such as *Adenomera thomei*. The population of this species in the municipality of Areado has smaller individuals and more acute vocalizations due to its smaller size in relation to other places where the species occurs, which lie outside this area of climatic instability (Ferrante et al., 2014). *Scinax caldarum*, anothr endemic species in this area of climatic instability, has declined in its area of occurrence by more than 85% over the last 27 years; it no longer occurs in Areado and is reported only in Caldas and Poços de Caldas (Ferrante et al., 2019). Extirpations of anurans have occurred for all species recorded in this region due to forest fragmentation, disconnection of aquatic habitats from the terrestrial environment (Becker et al., 2007, 2010), and from the harmful effects of agriculture (Ferrante et al., 2017). These threats tend to act synergistically to extinguish isolated populations in forest fragments, which will be especially susceptible to climate change.

The absence of water bodies in the Atlantic Forest fragments is one of the greatest threats leading to the extinction of amphibians, including species that are wholly aquatic and those that are terrestrial with aquatic larvae (Becker et al., 2007; 2010; Fonseca et al., 2008). Amphibians are highly sensitive to dry forest fragments, where even the most water-independent species (species with direct development without a larval stage) are affected by internal moisture changes (Becker et al., 2007; 2010; Fonseca et al., 2008), which makes amphibians that are bioindicators extremely sensitive to microclimatic changes in forest fragments. As we found, the 2014 drought was responsible for completely drying up the watercourse in which the population of *H. sazimai* lives in Areado, which stopped the reproductive activity of this population during this period. The water scarcity that has affected southern and southeastern Brazil has transformed many forest fragments with watercourses into dry fragments, aggravating one of the biggest factors in the extinction of amphibians in the Atlantic Forest (Appendix S3).

The Water cycle and Amazon deforestation

Our results suggest that the water cycle responsible for the diversity and population dynamics of anurans in Brazil's Atlantic Forest depends on the temperature dynamics of the Atlantic Ocean that drive humidity to the Amazon basin (Drumond et al., 2014), from which the flying rivers carry water vapor to southeastern Brazil and areas farther south in South American (Van der Ent et al., 2010; Zemp et al., 2014). Maintaining the hydrological cycle in the Amazon basin depends on the water import provided by trade winds carrying water vapor generated by warm sea surface temperatures in the tropical Atlantic Ocean, where temperatures have continuously increased over the last decades (Gloor et al., 2013; 2015). It also depends on the mechanism of water recycling provided by the forest in an interaction between the atmosphere and the biosphere by evapotranspiration processes (Salati et al., 1979; Salati & Vose, 1984; Salati & Nobre, 1991) and the emission of biogenic particles (volatile organic compounds and primary biological aerosols, such as pollen, spores, bacteria, and biogenic salt particles) (Pöschl et al., 2010; Pöhlker et al., 2012). This has a strong influence on the water balance and energy fluxes in the atmospheric boundary layer that affects climate (Foley et al., 2003). As deforestation increases, especially in the southern portion of the Amazon, the increase in sensible heat loss and decrease in latent heat loss (reduced evapotranspiration) reduces precipitation (Spracklen & Garcia-Carreras, 2015). In the northern arc of deforestation, a negative correlation can already be observed with precipitation in the Atlantic Forest locations we studied (Fig. 2). Climatic anomalies extended throughout the entire arc of deforestation (Fig. 5), and this might already be a factor contributing to the increase in dry season length (mainly through delayed onset of the rainy season) in the southern Amazon basin in recent decades (Marengo et al., 2015). In the northern portion of the Amazon basin an increase in rainfall has been observed in recent decades, creating a climatic dipole across Amazonia (Barichivich et al., 2018; Espinoza et al., 2019; Gloor et al., 2013; 2015; Wang et al., 2018). The maintenance of Amazonia's hydrological cycle also involves stabilizing the temperature of the Atlantic Ocean (Fig. 2), which may be affected by climate changes that are already underway (IPCC, 2022).

Our results also showed a correlation between rainfall at the locations with *H. sazimai* and the presence of high-pressure areas with clouds over the Amazon rainforest. These clouds tend to occur as a result of evapotranspiration from the forest, which recycles rainwater coming from the Atlantic Ocean and the Amazon basin itself (Arraut et al., 2012; Van der Ent et al., 2010; Zemp et al., 2014; Staal et al., 2018). Our results also indicate a correlation between the precipitation at the locations with *H. sazimai* and the surface winds in the Amazon region (Fig. 3), these being aligned with the high-pressure areas where clouds have formed over the Amazon rainforest (Fig. 2). Surface winds in the Amazon region are related to the transport of moisture from the region tsouthern and southeastern Brazil (Marengo et al., 2002; 2004; Makarieva et al., 2013). Condensation in the high-pressure cells (Fig.

2) induces a decline in air pressure in the lower atmosphere, influencing the formation of surface winds that transport water vapor to the to these regions (Makarieva et al., 2013), as demonstrated by our results (Fig. 3). We conclude that the recycling of water by the Amazon forest and the transport of water vapor via flying rivers affect the climate in the Atlantic Forest, thereby influencing the diversity, selection of functional traits (Fig. 1), and population dynamics of Atlantic Forest frogs (Fig. 4).

Disturbance of a part of this water cycle tends to trigger a domino effect leading toward a climatic collapse, which should generate feedbacks leading to further disturbances affecting this ecosystem (Wunderling et al., 2021). Variability in the behavior of the oceans, resulting in increase in severe droughts in southeastern Brazil, has already increased and is expected to continue in light of global warming (IPCC, 2022). If a significant loss of the volume of water vapor transported from the Amazon were added to this effect, the result would be catastrophic in many ways (Getirana et al., 2021; Fearnside, 2021; Ferrante & Fearnside, 2022b). Among the victims of these major droughtswould be the endemic amphibians of Atlantic Rainforest, such as *H. sazimai,* which is restricted to this region (Fig. 2).

With the advance of global warming, there is a greater risk that various ecosystems will reach tipping points beyond which they cannot be sustained, including the Amazon forest (Wunderling et al., 2021). Amazonia is close to the limit of deforestation that can be tolerated by the region’s ecosystems (Lovejoy & Nobre, 2018), and deforestation projections indicate the collapse of Amazonian evapotranspiration (Correia et al., 2006) and consequently the collapse of water vapor transport by flying rivers (Arraut et al., 2012; Van der Ent et al., 2010; Zemp et al., 2014). Our results are consistent with the dependence of the precipitation regime in the Atlantic Forest on a cascade of effects linking the temperature of the oceans and flying rivers coming from the Amazon. Approximately one-third of the rain exported by flying rivers originates in the Amazon basin, reinforcing the importance of the biome for the South American water cycle (Staal et al., 2018). Our results also indicated the dependence of the Atlantic Forest's amphibian biodiversity on the maintenance of this ecosystem service from Amazonia (Appendix S4).

Anthropogenic climate change has hastened savannization and reduced resilience of the Amazon forest (Staal et al., 2015; Boulton et al., 2022). Deforestation is expanding from the southern portion of Amazonas to the central Amazon (Ferrante & Fearnside, 2022a), a shift that could enlarge the areas with climatic anomalies in the Amazon (Fig. 5). Deforestation for plantations for biofuels is also expanding in the central and northern portions of the Amazon in Amazonas and Roraima (Ferrante & Fearnside, 2020b; Ferrante et al., 2021c), and this trend could affect the high vapor-pressure cells in these areas (Fig. 2). The high vapor-pressure cells in the northern Amazon could also be a threatened by expansion of mining (Ferrante & Fearnside, 2020d; 2022b; 2022c). The Yanomami Indigenous Land, where some of these high vapor-pressure cells are located (Fig. 2), has been invaded by more than 20,000 miners (Ferrante & Fearnside, 2022c), significantly increasing deforestaion and environmental degradation (Ferrante & Fearnside, 2022c). These areas act as shields protecting not only traditional peoples, but also biodiversity, carbon stocks, and ecosystem services (Ferrante & Fearnside, 2020d).

This and the need to safeguard atmospheric cycles make actions to curb deforestation urgent (Ferrante et al., 2021a; Ferrante & Fearnside, 2022b). Denialism by decision makers in Brazil in the face of scientific data tends to intensify the climate crises (Ferrante & Fearnside, 2021b) and take the country's biodiversity to a critical point (Diele-Viegas et al., 2021).

This has potential consequences beyond Brazil's borders, such as increasing the risk of emergence of new global pandemics (Diele-Viegas et al., 2021; Ferrante et al., 2021c).

Conservation considerations

While it is possible that other *Hylodes sazimai* populations exist, this species is clearly restricted to forest fragments in a very small part of the Atlantic

Forest. According to the endangered species classification methodology of the International Union for Conservation of Nature, *Hylodes sazimai* already falls in the endangered category (Appendix S5), although the species is currently classified as data deficient based on an evaluation carried out in 2004 (Garcia & Pimenta, 2004).

Our results showed that morphological variations in phylogenetically structured frog populations in Brazil's Atlantic Forest are sensitive to changes in rainfall patterns and other climatic variables, with the speed of ongoing climate change having exceeded the time required for adaptation of these currently declining populations. The observed effects on *H. sazimai* serve as an umbrella indicator for the conservation of anurans and species in other taxonomic groups that are endemic to southeastern Brazil (Appendix S6). Our results are particularly important because they demonstrated the dependence of population dynamics and morphological adaptations of Atlantic Forest species on Atlantic Ocean temperatures and Amazonian flying rivers.

Brazil needs to adopt a zero-deforestation policy in the Amazon region as a measure to maintain the hydrological cycle and to slow the advance of climate change. Among other benefits, this would provide greater possibility of adaptation of the Brazilian species facing extirpation or extinction due to climate change. These measures must be implemented immediately given that the rate of ecosystem change exceeds the rate at which the species can adapt. To be expected are population declines and extinctions of species endemic to southeastern Brazil and severe economic and social impacts from the intensification of droughts in this region that, in addition to being a hotspot of biodiversity, is one of the most populous parts of Brazil.

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SUPPORTING INFORMATION

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

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Table 1. Results of comparison of morphological variation among the 4 populations of *Hylodes sazimai* by permutational multivariate analysis of variance analyses.

Interpopulation comparisons	F	R^2	p
Areado vs. Caldas	1.94	0.21	0.093
Areado vs. Campinas	2.27	0.22	0.036[a]
Areado vs. Poços de Caldas	0.77	0.04	0.577
Caldas vs. Campinas	1.67	0.24	0.123
Caldas vs. Poços de Caldas	2.72	0.17	0.027[a]
Campinas vs. Poços de Caldas	3.15	0.18	0.006[b]

[a] Statistically significant.

[b] Very significant.

Table 2. Comparison of individual morphological traits among the 4 populations of *Hylodes sazimai* by analysis of variance.

Morphological trait	*F*	*p*
Back foot membrane	4.448	0.014[a]
Distance between nostrils	1.930	0.156
Eye nostril distance	2.474	0.090
Fibula length	1.684	0.201
Foot length	3.134	0.047[a]
Head width	0.263	0.851
Length (SLV)	0.405	0.751
Metatarsal membrane of digit IV of the foot	2.799	0.065[b]
Metatarsal membrane of digit V of the foot	4.449	0.014[a]
Snout angle	1.446	0.258
Tibia length	0.122	0.946
Tympanum diameter	0.464	0.71

[a] Statistically significant.

[b] Marginally significant.

Fig. 1 (a) Phylogenetic structure of the 4 populations of *Hylodes sazimai* (numbers, bootstrap branch support percentage values) (b) structuring of *H. sazimai* populations based on 12 morphological traits, (c) morphological divergence of functional traits among the 4 populations of *H. sazimai*, and (d) climatic and soil moisture temporal variation at the 4 locations of *H. sazimai* occurrence based on monthly data from 2002 to 2017.

Fig. 2 Teleconnections between rainy season (November-February) precipitation for 2002-2017 from Global Land Data Assimilation System data for a 1-km^2 cell in the *H. sazimai* population occurrence area with the HadlSST1 sea surface temperatures for 2002-2017 and cloud pressure data from FRESCO (Fast Retrieval Scheme for Clouds) 6 for 2002-2012 (mainland): (a) Areado *p* value, (b) Areado correlation coefficient, (c) Poços de Caldas *p* value, (d) Poços de Caldas correlation coefficient, (e) Caldas *p* value, (f) Caldas correlation coefficient, (g) Campinas *p* value, and (h) Campinas correlation coefficient (A, northern Amazonia; CWA, center-western Amazonia; SAUP, southern Amazon under pressure; TACA, Transamazon collapse area).

Fig. 3 Teleconnections between rainy season (November-February) precipitation for 2002-2017 from Global Land Data Assimilation System data for a 1-km^2 cell in the *H. sazimai* population occurrence area with the surface zonal winds from MERRA-2 data: (a) Areado *p* value, (b) Areado correlation coefficient, (c) Poços de Caldas *p* value, (d) Poços de Caldas correlation coefficient, (e) Caldas *p* value, (f)

Caldas correlation coefficient, (g) Campinas *p* value, and (h) Campinas correlation coefficient.

Fig. 4 (a) Locations of the 4 populations of *H. sazimai* in southeastern Brazil (black lines, Brazilian regions; purple dot, Areado; green dot, Caldas; light blue dot, Poços de Caldas; red dot, Campinas), (b) census of adult males in the population in the municipality of Areado, Minas Gerais state, and rainfall in the same period, and GRACE-based (GRACE, Gravity Recovery and Climate Experiment) Terrestrial Water Storage Anomalies (TWSA) subtracted from the 2002–2014 average during the austral autumn in (c) 2012, (d) 2013, and (e) 2014.