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Climate change in the central Amazon and its impacts on frog populations

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Abstract. Frog population declines have already been observed in the central Amazon even for common species that are considered not to be in danger of extinction. The Amazon is close to its limit of tolerated deforestation, and parts of the forest have already been modified by climate change, which raises questions about how the fauna in these areas would adapt to climate changes by the middle and the end of this century. In this study we used population density data on seven species of Amazonian frogs and analyzed the relationship between the activity of these species and temperature, precipitation, and relative humidity. We also used the least-squares method with logarithmic models to assess whether climate change projected by the Intergovernmental Panel on Climate Change (IPCC) would be an indicator of the population dynamics of these species. Our results suggest that even common species may be may experience population declines and extinction in the next decades due to climate changes.

Key Words: Anurans; Amphibian decline; Amazon Forest; biodiversity crises; bioindicators; Climate change; deforestation; Tropical Forest; Umbrella species.

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INTRODUCTION

In Amazonia, as in other parts of the world, the fate of amphibians serves as a harbinger of loss of biodiversity and much wider environmental destruction (Zipkin et al. 2020; Strona and Bradshaw 2022). Climate change has altered the geographical distributions of multiple anuran species around the world (e.g., Vieira et al. 2018; Hu et al. 2019). Climatic disturbance events have been responsible for the sudden population decline and extinction of several anuran species in Central America (Pounds and Crump 1994; Pounds et al. 1999). Other factors acting in synergy with climatic events have caused local extinctions in the Atlantic Forest of Brazil (Heyer et al. 1988; Weygoldt 1989; Eterovich et al. 2005; Ferrante et al. 2019).

In the central Amazon some anuran species would be unable to migrate to climatically suitable locations, as in the case of the endemic central-Amazonian frog *Atelopus manauensis* (Jorge et al. 2020). This is especially so since Amazonian rivers are geographical barriers for various vertebrate groups, such as birds (Ribas et al. 2012; Ferreira et al. 2016; Braga et al. 2022) and also amphibians and squamates (Moraes et al. 2016). Barriers can also be imposed by land-use change, particularly the growing areas of deforestation that leave remaining areas of natural forest as islands surrounded by a landscape that is hostile to the forest's endemic frogs (Ferrante et al. 2017, 2019), and even to some species with significant dispersal and colonization ability (Ferrante et al. 2020).

Deforestation is expanding from Manaus into surrounding areas of the central Amazon (Ramos et al. 2018; Santos et al. 2022), and this transformation would be greatly accelerated by the planned reconstruction of Highway BR-319 connecting Manaus to Brazil's "arc of deforestation" - the highly deforested strip of land along the southern and eastern edges of Brazil's Amazon region (Ferrante et al. 2021a). Other processes creating barriers include forest degradation through fire and consequent expansion of savannas (Sales et al. 2020; Flores and Holmgren 2021). When climate change occurs in areas isolated by barriers, the species must either adapt to local environmental changes or become extinct (Quental and Marshall 2013; Ferrante et al. 2023) unless they succeed in colonizing new ecologically suitable habitats. Climate change is considered to be one of the greatest threats to amphibians (Stuart et al. 2008; Bishop et al. 2012), which is the most threatened group among vertebrates (Baillie et al. 2010; Bishop et al. 2012). Characteristics that make frogs vulnerable to climate change include the fact that their skin is permeable, and they have exposed eggs and embryos - most species have a free-swimming larval stage in the life cycle (Blaustein et al. 1994, 2001; Blaustein and Kiesecker 2002; Blaustein and Bancroft 2007; Duellman and Trueb 1996; Stebbins and Cohen 1995).

Climate change has already affected different taxonomic groups in the central Amazon, especially in valley and stream areas, as shown by more than 20 years of monitoring (Costa et al. 2020). For some locations in Brazil, anthropogenic climate change in synergy with landscape change have been shown to threaten anuran populations and cause local extinctions (Ferrante et al. 2019) even more than invasive species or lethal pathogens (Ferrante et al. 2020). This means that anthropogenic climate change should be a priority for studies of threats to Brazilian amphibians (Verdade et al. 2012). In addition, structural changes in the landscape (such as deforestation, forest fragmentation, edge effects and neighboring agricultural crops) can alter the microclimate of amphibian habitats, leading to subtle increases in temperature and losses of moisture that can affect population density, species richness and community composition (Urbina-Cardona 2006; Ferrante et al. 2017).

Amphibians are extremely vulnerable to climate change in the Amazon (Vasconcelos et al. 2018), and the distribution of anuran taxa is directly influenced by the rainy season and by proximity to humid environments, such as valleys and streams (Moraes et al. 2016), which are already altered by ongoing climate change (Costa et al. 2020). The present study aims to show how Amazonian frog species are responding to climate change. We hypothesize that ongoing climate change could even threaten the populations of common species that are now abundant and have so far not been considered to be threatened.

METHODS:

Study Site

The region denominated here as the “central Amazon” (Fig. 1) is bounded to the east by the border between the states of Amazonas and Pará (a NE-SW diagonal from approximately 57 to 60º W longitude), thus avoiding the “dry corridor” that crosses the Amazon River at Santarém, Pará. To the west, the central Amazon can be considered bounded at 66º W Longitude, thus avoiding the area with a dry season < 2 months in length in the NW corner of Brazilian Amazonia. To the north it is bounded by the equator, and to the south at approximately 6º S latitude, thus avoiding the Humaitá savanna and areas with a dry season > 3 months in length. This region encompasses a range of ecoregions (Olson et al. 2001; Fearnside 2023), with a predominance of dense ombrophilous forest and is in the morphoclimatic domain classified as “equatorial forested lowlands,” with average temperatures of 24 to 27°C (Ab'Sáber 2003). The central Amazon is vulnerable to climate change and is becoming increasingly susceptible to forest fires, especially in El Niño years (Reis et al. 2021).

Data used in the present study were obtained in the Adolpho Ducke Forest Reserve, in the municipality of Manaus in the central Amazon. The Adolpho Ducke Forest Reserve is located in *terra firme* (upland) forest. Although these forests are not seasonally flooded by large rivers (Braga 1979), they have many permanent and temporary pools that are used by amphibians for reproduction (Menin et al. 2008; Najar and Ferrante 2018). The study area has an average annual temperature of 26 °C and annual rainfall ranging from 1750 to 2500 mm (Oliveira et al. 2008) - a sampling interval that encompasses the rainfall regimes of the different ecoregions included in the central Amazon (Ab’Sáber 2003). All of the landscape studied here has the same forest type (dense ombrophilous forest) and is the best-studied area in the central Amazon. The Adolpho Ducke Forest Reserve has a large sampling effort in terms of biodiversity and physical and climatic variables and, as a permanently protected area, the sampled sites are not susceptible to impacts other than anthropogenic climatic effects (Oliveira et al. 2008; Magnusson et al. 2013).

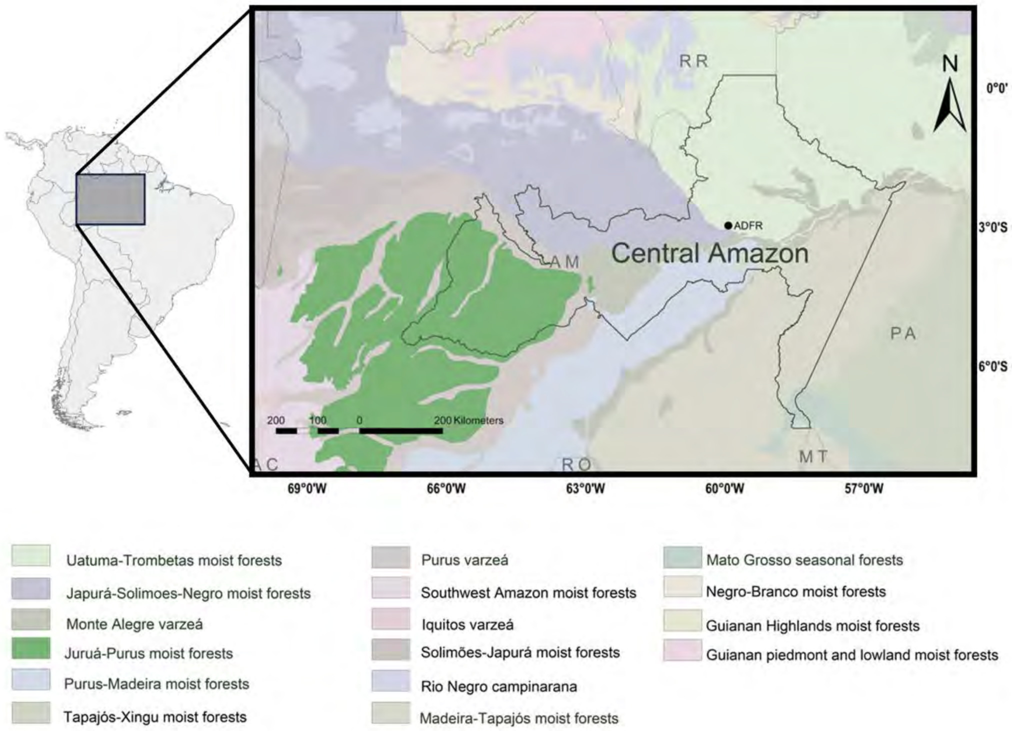

Figure 1. Map of ecoregions in the central Amazon and Adolpho Ducke Forest Reserve (ADFR).

Sampling design

Declines in anuran populations can be caused by the lengthening of the dry season and by reduced rainfall in the wet season; these changes lower the activity of individuals, and a substantial drop in a single season can affect the recruitment of new individuals in the population and decrease the population density in subsequent years (Ferrante et al. 2023). Population data for the seven species in the present study were collected in five samplings: November-December 2002; March-May 2003; November-December 2003; February to May 2004 (Data from Menin et al. 2008). The sampling periods included both the dry season, from June to November, and the rainy season, from December to May (Ribeiro 1976), thereby allowing us to associate fluctuations in the active frog populations with climatic fluctuations in the central Amazon.

This means that alterations in the dry and wet seasons caused by global climate change can shape anuran population dynamics in the long term, since there is not enough time for adaptation, as has already been observed for frogs in Brazil’s Atlantic Forest (Ferrante et al. 2023). In the present study we use data from monitoring anuran populations over a period that covers both the dry and wet seasons and that can capture population oscillations due to local climatic variations. Knowing the temporal dynamics of the species and the abundance variation in the observed samples, it is possible to assess the degree of dispersion of the probability values. The range of variation therefore allows testing a climate-change scenario and obtaining a model that allows projection of how the species will behave within the limits of this model.

Population census data were analyzed for seven anuran species (*Atelopus manauensis* (n=21), *Leptodactylus pentadactylus* (n=63), *Leptodactylus rhodomystax* (n=15), *Osteocephalus oophagus* (n=3222), *Pristimantis fenestratus* (n=6702), *Synapturanus mirandariberoi* (n=1459) and *Synapturanus salseri* (n=996)) and average climatological data (average temperature, maximum temperature, relative humidity of the air and precipitation) for the different collection periods. Linear and logarithmic regressions were used to test the relationship between the population activity of these seven species in relation to climatic oscillations.

Sampling was performed by visual and auditory means simultaneously (Crump and Scott 1994) considering only mature individuals. The measure of “population density” is the abundance of individuals per sampling period. Each sampling period lasted an average of 49 days with two observers searching the plots for 2 hours per day, each sampling period having 196 hours of observation (49 days × 2 hours per day × 2 observers). The plots were 250 × 40 m (1 ha) in area (Magnusson et al. 2005), and in the shorter sampling periods the number of plots was increased to keep the sampling effort constant. Due to gaps in the climatic data and the aggregation of the anuran population data by season in Menin et al. (2008), we used the values for temperature and relative humidity of the air provided by the National Institute of Meteorology (INMET 2023); precipitation data were collected during the anuran collection itself (See. Appendix S1).

Both analyses of continuous data and of aggregated data have been used in ecological studies, with losses and gains between these two types of analysis depending on the question to be answered (Gotelli and Ellison 2004; Magurran 2004; Magnusson and Mourão 2005). Aggregated individual abundance data are common in ecological analyses (Gotelli and Ellison 2004). Here, the aggregation of biological data by season makes it possible to visualize the population response of each species to climate change in each season. Climatic anomalies that may occur on certain days, or local stochastic effects in certain plots, do not tend to generate outliers or sampling artifacts in the data analysis. This also allows us to have greater reliability in population density projections in relation to future climate change (Mills 2013) because the data are for censuses of active individuals over a long period with an established climate pattern. Grouping the data avoids population fluctuations based on the gradual change in temperature or humidity through the course of the day.

Statistical analyses

We performed simple linear regressions, together with tests of homoscedasticity using the Bartlett test (Bartlett 1937) and Shapiro Wilk normality tests (Shapiro and Wilk 1965) (See. Appendix S2 and S3). Subsequently, data on the abundance of individuals in relation to climate variables were projected through logarithmic regressions using the least-squares method (Luenberger 1997; Tang and Wang 2001) in relation to the annual progression of climate variables predicted for this area from 2002 to 2100 by the RCP 8.5 scenario of the IPCC’s fifth assessment report (AR5) (IPCC 2014; 2022; Magrin et al. 2014). We used a natural logarithm distribution. Least squares can be derived as a method-of-moments estimator (Luenberger 1997) and are used here to estimate the moments of the frog population declines assuming the progression of climate change projected under the RCP 8.5 scenario (IPCC 2014; Magrin et al. 2014). We only tested the average and maximum effect of temperature on the species since an increase in temperature is expected by the RCP 8.5 model. Annual estimates under the RCP 8.5 scenario were taken from Science on a Sphere (2023). These models are well-suited for calculating local changes based on the least-squares method (Tang and Wang 2001). This method has advantages over other regression tests commonly used in ecology due to its capacity to generate scenarios that enlarge the range of projections (Carrascal et al. 2009). All analyses were run in Statistica 8 software (Statsoft 2007).

RESULTS:

Linear regressions (Fig. 2) showed that at least one of the climatic variables significantly influenced the activities of three of the seven species studied: *Atelopus manauensis* in relation to the average temperature of the air (n=21, p = 0.01, R^2 = 0.87); *Leptodactylus rhodomystax* in relation to the average temperature of the air (n=15, p = 0.01, R^2 = 0.91) and; *Synapturanus mirandaribeiroi* in relation to the precipitation (n=1459, p = 0.05, R^2 = 0.77).

Results for two additional species are suggestive of climate effects but were not significant at the p<0.05 level: *Leptodactylus pentadactylus* with a value of activity of this species with a suggestive relation to precipitation (n=996, p = 0.07, R^2 = 0.70). In addition, *Synapturanus mirandaribeiroi* had a suggestive relation to precipitation average temperature of the air (n=1459, p = 0.07, R^2 = 0.69), in addition to its significant relation to precipitation.

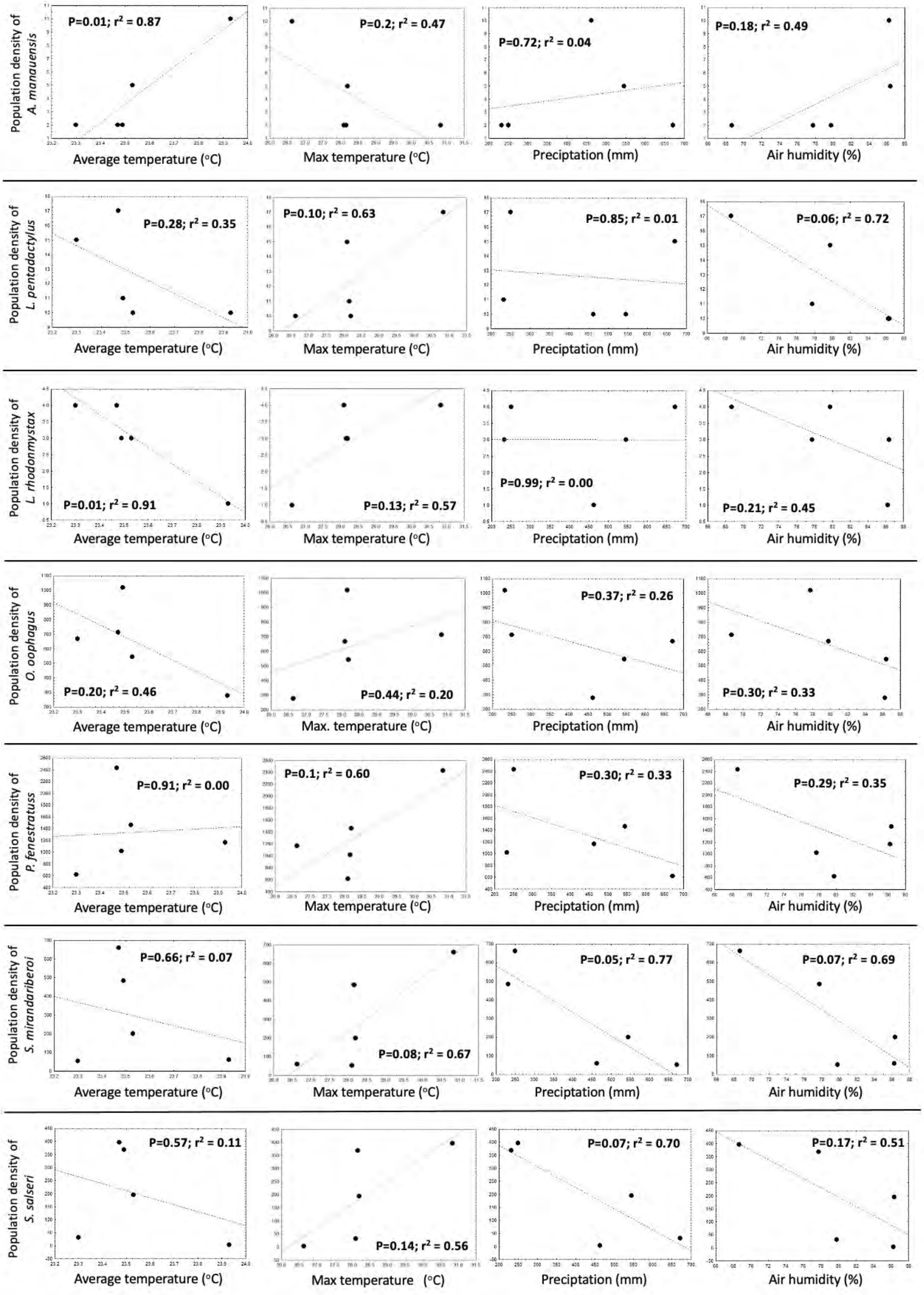

Figure 2. Relationships between the population density (calling individuals per sampling period) of the seven target species in the study and the climate variables for the collection area.

Due to lack of data on the thermal tolerance thresholds of species that responded positively to temperature increase, we did not project population trends for these species. Logarithmic regressions indicated that *L. rhodomystax* would have reduced activity under the climate projected for the middle and the end of the current century based on the relationships between population density and climatic variables (Fig. 3). An increase in the annual mean temperature in the frogs' habitat to a level above 30 °C tends to eliminate the activity of *L. rhodomystax*. Increases of 2 to 4 °C in the annual average temperature in the central Amazon would decrease the activity of this species, causing lower recruitment of individuals and population declines.

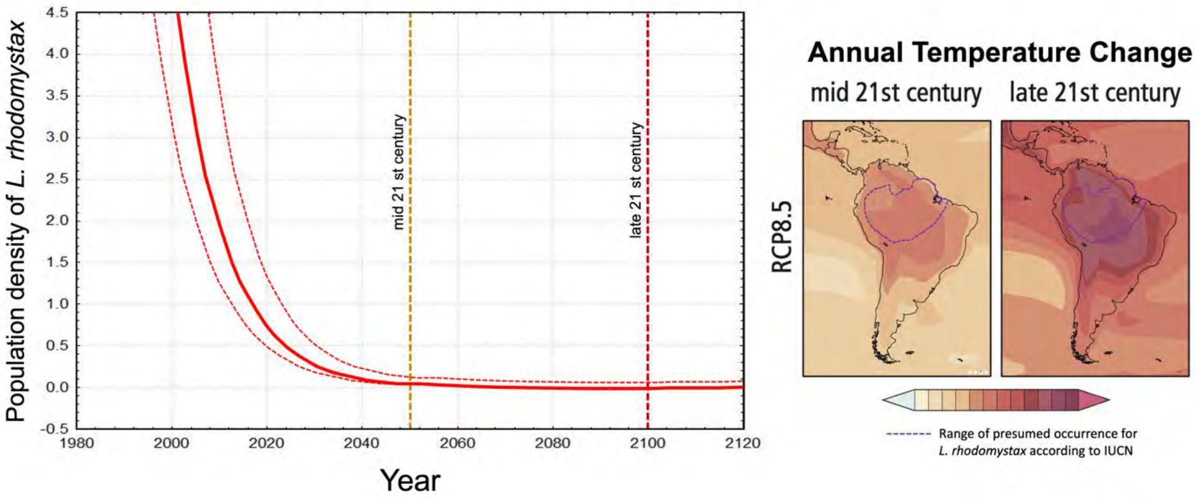

Figure 3. Effect of projected climate change on *L. rhodomystax* population densities per hectare in response to increases in the annual average temperature in the central Amazon. The maps show the projected climate in the mid-21st century (2050) and the late 21st century (2100) (Magrin et al. 2014).

Our results point to a decrease in the density (calling individuals per hectare) of *L. rhodomystax* due to increased average annual temperature, with the possibility of extinction of the species in the next 20 years. These results indicate that the density of active individuals would decrease substantially in the next decades. Monthly fluctuations in humidity and temperature naturally occur in the central Amazon, causing the density of active individuals indicated here to vary over the course of the year. The reductions indicated here are per hectare at the location of the plots, and declines in other populations are likely because of reductions in the distribution areas of these species.

DISCUSSION:

Anurans in the central Amazon had a strong response to climate and can be considered as bioindicators of climate change. Our results indicate that species with different ecological habits and adaptations may respond differently to certain climatic variables (see methods), and their activity may be negatively affected by both the average and the maximum temperatures, since changes in climate range affect tolerance limits of frogs, as is the case for the observed climatic oscillations in the central Amazon at present. The different thermal sensitivities of anuran species point to the need to classify species according to their ecological habits in studies at the landscape level, as in the studies by Urbina-Cardona et al. (2006) and Ferrante et al. (2017).

We note that the RCP 8.5 scenario from the IPCC's fifth assessment report (AR5) (IPCC 2014) has been criticized as being overly pessimistic in its emissions assumptions for the remainder of this century, especially with regard to use of coal (e.g., Ritchie and Dowlatabadi 2017). However, the RCP 8.5 scenario's best estimate for global mean temperature increase by 2100 (4.8 ºC relative to the 1850–1900 mean) is only slightly higher than the SSP5-8.5 estimate in the AR6 (4.4 ºC) (IPCC 2022). While restraining global emissions to levels below those used in these scenarios is hoped to occur, analyses assuming unrestrained emissions have value in illustrating the consequences of continued insufficient action in mitigating global warming. While assumptions regarding the use of coal create upward bias, these scenarios also contain biases in the downward direction by not including a variety of "indirect" emissions sources (e.g., Barros and Fearnside 2019). In addition, with the increase in the use of fossil fuels (Ferrante and Fearnside 2023) and the success of "ruralist" politicians in Brazil in dismantling many of the protections of the Amazon forest (Ferrante and Fearnside 2019; Ferrante 2023), which doubled carbon emissions in the Amazon (Gatti et al. 2023), make the most pessimistic scenarios today, such as RCP 8.5, conservative for the climate change expected in the region.

Ongoing climate change has already led to an increase in annual mean temperature in the Amazon rainforest (Marengo et al. 2021), with forecasts of a continued increase reaching up to 8 °C in some areas of the Amazon by the end of the century (IPCC 2014, 2022). In addition to the expected changes in average temperature precipitation and wind patterns, extreme weather events are expected to increase greatly both in terms of frequency and intensity (IPCC 2014, 2022). According to our data, these climate changes may negatively affect the population dynamics of frogs in the central Amazon.

Data on population declines and local extinctions of frogs caused by climate change in the Amazon region are still scarce (Stuart et al. 2008), although some population declines have already been observed due to other threats, such as the use of herbicides (Ferrante and Fearnside 2020a). The data presented here shed light on how Amazonian frog populations may react in the face of climate change by the end of this century.

Physiological studies have shown that some Brazilian amphibians lack adaptive plasticity even to seemingly small increases in temperature, negatively affecting their physiological performance in the larval stage (Longhini et al. 2021). This reinforces the hypothesis of declines and extinctions in the face of climate change. The decline of amphibian populations is also related to climate change due to ultraviolet radiation (Blaustein and Kiesecker 2002; Blaustein et al. 1994, 2001). This could prove to be catastrophic for local anuran populations because higher incidence of ultraviolet radiation is expected for the central Amazon (IPCC 2022). Amphibian eggs are sensitive to increases in ultraviolet radiation, consequently causing high mortality of embryos (Blaustein et al. 1994). This would have a profound impact, especially on diurnal species such as *A. manauensis* (Menin et al. 2008). The climatic optimum for this species is currently in a range of warm average temperatures (Fig. 2), but the behavior of the species may change given the high temperatures predicted in climate-change scenarios for the central Amazon.

Extreme weather events have already caused the extinction of several amphibian species in Central and South America (Pounds and Crump 1994; Pounds et al. 1999; Stuart et al. 2008). The frequency of extreme drought events (due to strong El Niño episodes) has increased in the Amazon Basin since the 1970s, departing from the long-term pattern that had predominated since 1901 (Paredes-Trejo et al. 2021). "Unprecedented" droughts are projected to occur in Amazonia in the coming decades (Kay et al. 2022). Climate change that is already underway across South America, including tropical forests such as the Amazon and Atlantic Forests (Stuart et al. 2008), motivated the inclusion of climate change in the Brazilian Amphibian Conservation Action Plan (Verdade et al. 2012).

Future scenarios proposed through modeling portend a worldwide loss of amphibian species through climate change, with some groups being more threatened than others (Loyola et al. 2013). Our results suggest that even common species, such as *L. rhodomystax*, can be expected to undergo reductions in their population densities as a result of the increase of temperature (by 2100 under the RCP 4.5 scenario, which, unlike the RCP 8.5 scenario, assumes substantial reductions in global greenhouse-gas emissions). We should therefore expect decreases in the activity levels of these anurans in the central Amazon. This would result in lower recruitment of individuals and population declines of these species.

The impact of increases in the annual mean values of climatic variables are much more serious than only anuran population declines, as climate change affects much more than the activity of frogs (Costa et al. 2020). There are also threats to the central Amazon from burning (Fearnside 2021), land grabbing (Ferrante et al. 2021b), illegal logging (Andrade et al. 2021), illegal mining (Ferrante and Fearnside 2022a), and the expansion of agriculture and cattle ranching (Ferrante and Fearnside 2018, 2020a, 2020b, 2022b; Ferrante et al. 2021c). These multiple threats have substantial impacts on forest structure and consequently affect the microclimate, which in turn affects both the richness and the abundance of amphibians (Urbina-Cardona et al. 2006; Ferrante et al. 2017). Shifts in the amplitude of variation in climatic variables may force species generally to the limits of their physiological tolerance and restrict their geographical distributions (Mills 2013). Loss of certain species in an ecosystem can collapse trophic chains and unbalance the dynamics of populations of other species, causing extinctions at the local and regional levels or for the species as a whole (Zipkin et al. 2020; Strona and Bradshaw 2022). Endemic species, such as *A. manauensis*, are likely to be the most affected due to their restricted geographical distributions (Jorge et al. 2020). The species in the present study can be considered to constitute an umbrella species group whose conservation would confer protection to a large number of naturally co-occurring species. The loss of amphibian species around the world has triggered a cascade effect, which has affected other taxonomic groups, mainly predators, as is already seen in Neotropical snakes (Zipkin et al. 2020). Our results warn of a potential widespread loss of biodiversity in the central Amazon by 2050 and even greater impacts by 2100, as anurans are bioindicators for declines in other taxonomic groups (Zipkin et al. 2020). It is crucial that Brazil adopt measures to mitigate climate change and to protect biodiversity.

The threat to Amazon biodiversity (by climate change documented here) is embedded in a context of widespread destruction of the region’s native ecosystems by deforestation, logging, forest fires, mining, dams, and other economic ventures (e.g., Fearnside 2021). These processes accelerated under the 2019-2022 Jair Bolsonaro presidential administration in Brazil, with the dismantling of the country’s environmental agencies, including hundreds of changes in internal operating rules in ways that impede enforcement of environmental regulations, multiple legislative changes loosening environmental restrictions, and a constant discourse denying scientific results on climate, deforestation, and fire and suggesting that environmental crimes would be ignored or pardoned (Ferrante and Fearnside 2019; Diele-Viegas et al. 2021; da Silva and Fearnside 2022). Many of these setbacks will have lasting effects irrespective of current and future efforts to reverse them. Building roads, for example, allows migrations and unleashes processes that are largely outside of government control, a fact that is particularly relevant to the central Amazon given the advance of a project to reconstruct Highway BR-319 connecting this relatively intact area to Brazil's "arc of deforestation" (Andrade et al. 2021; Ferrante et al. 2021a,b; Fearnside 2022). President Luiz Inácio Lula da Silva, who took office in January 2023, has promised to reduce deforestation, but restoring the control capacities of environmental agencies will not be enough because avoiding large-scale habitat loss in the central Amazon will also require blocking major projects such as the reconstruction of Highway BR-319 and opening oil and gas fields in the proposed Solimões Sedimentary Basin project (e.g., Bustamante et al. 2023; Ferrante and Fearnside 2023; Vilani et al. 2023).

In addition to contributing to the climate change that would affect frogs and other groups, the deforestation provoked by BR-319 and its associated side roads would have severe impacts on biodiversity through habitat loss (Magnusson 2020; Ferrante et al. 2021a). Highway BR-319 would bring to the central Amazon the land-use change processes already present in Brazil's "arc of deforestation." This would be catastrophic for Amazonian amphibians. In addition to habitat loss and a contribution to the climate change that threatens these species, the highway is likely to act as a disperser of new pathogens that are lethal to amphibians, such as the fungus *Batrachochytrium dendrobatidis* (Bd) (Becker et al. 2016). Bd has already been recorded in the "arc of deforestation" (Becker et al. 2016), and Highway BR-319 would offer a direct route for the fungus to spread to the central Amazon. The massive population declines of amphibians for the central Amazon that the present study suggests because of projected climate change are therefore conservative due to the other simultaneous threats resulting from the BR-319 project. The BR-319 project's direct and indirect threats to frogs add to the many reasons indicating that the project should not be undertaken (Fearnside 2022).

Control of Brazil's National Congress by the "ruralist" voting block has been increased by the 2022 elections (ClimaInfo 2022), suggesting likely passage in the coming months and years of a series of proposed laws further weakening environmental control, facilitating Amazonian land grabbing, and opening indigenous lands to agribusiness, mining and other activities by nonindigenous people (Ferrante and Fearnside 2021, 2022c; Ruaro et al. 2021, 2022). The combination of impacts from climate change and from habitat destruction by direct human action implies massive losses of Amazonian biodiversity (e.g., Joly et al. 2019). However, both Brazil's policies affecting deforestation and global accords on measures to contain climate change are subject to human decisions, and efforts must not be spared to avoid the bleak future that current trends imply.

CONCLUSION:

The population density of anurans in the central Amazon is strongly influenced by temperature, precipitation, and relative humidity. By the end of the 21st century, projected climate change would even affect the population dynamics of common species that today are considered to be out of danger, causing population declines and possibly local extinctions in many species through extreme climatic events. Habitat loss from deforestation and other direct anthropogenic impacts further increase the risks to frogs and other groups in the central Amazon.

DECLARATIONS

All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that, with minor exceptions, no changes can be made to authorship once the paper is submitted.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

L.F. designed the research; D.R. conducted fieldwork and examined material; L.F. conducted statistical analyses; L.F., D.R. and P.M.F. wrote the manuscript; L.F., D.R. and P.M.F. revised the manuscript.

DATA AVAILABILITY STATEMENT

All data are available upon request to the corresponding author.

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Supplementary Material

Climate change in the Central Amazon and its impacts on frog populations

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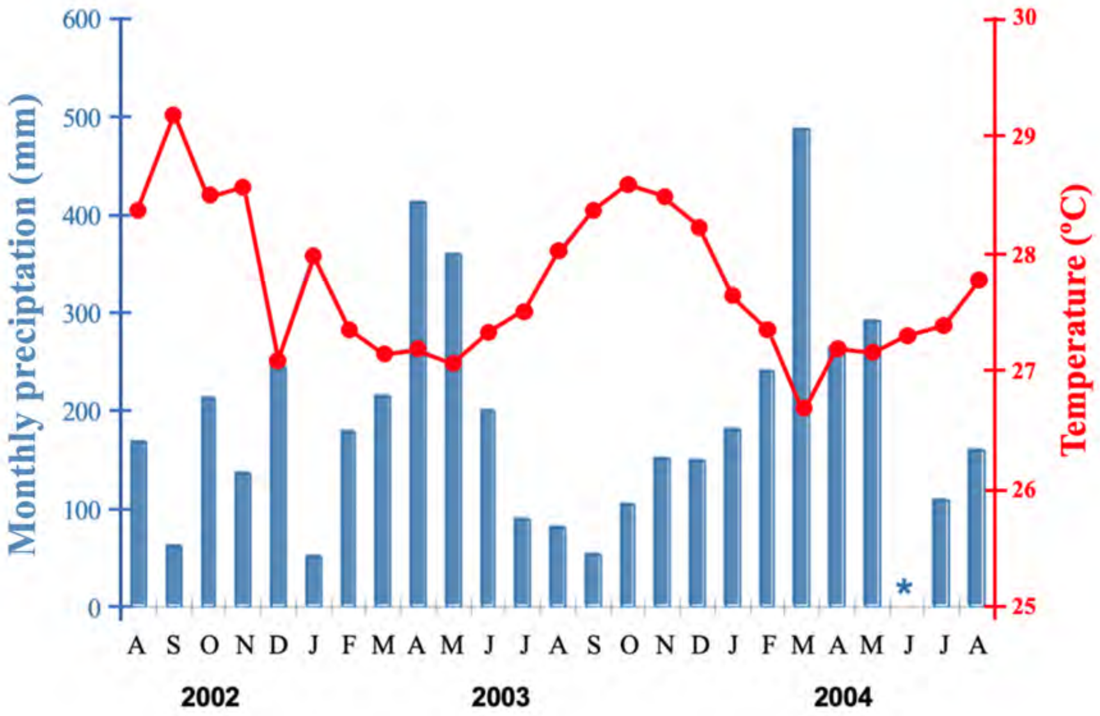
Appendix S1 Climate data



Appendix S2. Normality tests (Shapiro-Wilk test):

Shapiro-Wilk results:

A. spumarinus
W: 0.7478694
p-value: 0.02843795
A. spumarinus has explosive reproduction, which tends to interfere with the density of individuals and which explains the absence of normality for this species.

L. pentadactylus
W: 0.8332792
p-value: 0.1471844
There is no evidence to reject the null hypothesis of normality.

O. oophagus
W: 0.981019
p-value: 0.9399969
There is no evidence to reject the null hypothesis of normality.

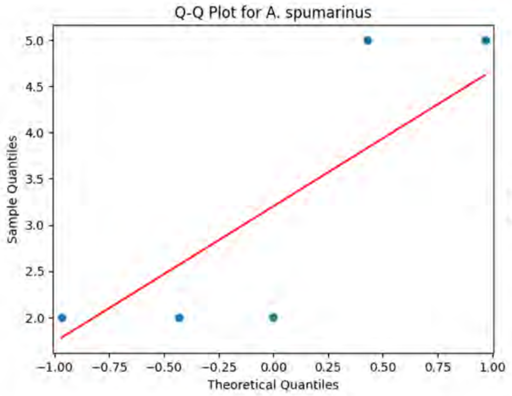
L. rhondonmystax
W: 0.8327445
p-value: 0.1458437
There is no evidence to reject the null hypothesis of normality.

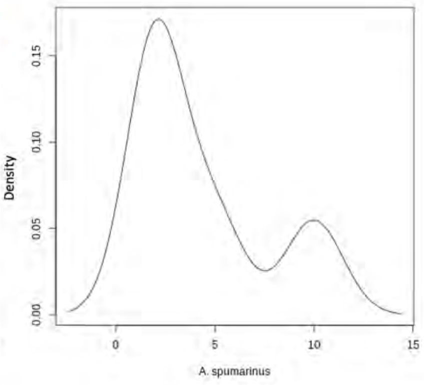
P. fenestratus
W: 0.925325
p-value: 0.5648562
There is no evidence to reject the null hypothesis of normality.

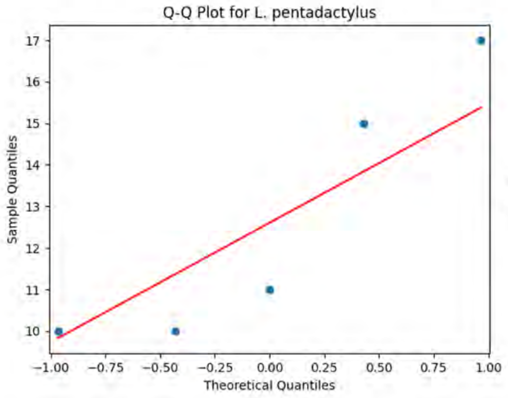
S. mirandariberoi
W: 0.8767309
p-value: 0.2947585
There is no evidence to reject the null hypothesis of normality.

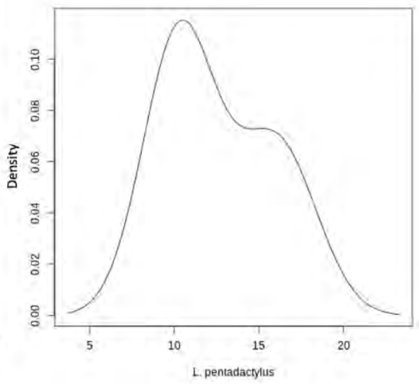
S. salseri
W: 0.874595
p-value: 0.2855315
There is no evidence to reject the null hypothesis of normality.

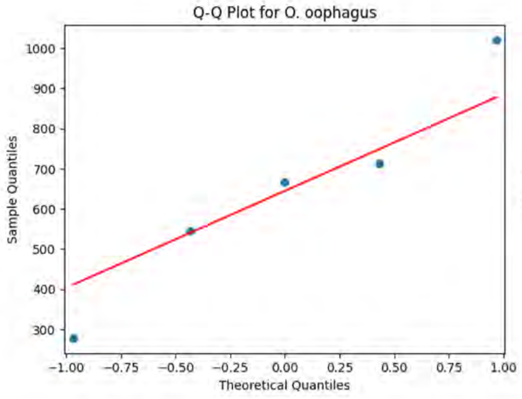
Shapiro-Wilk graphs:

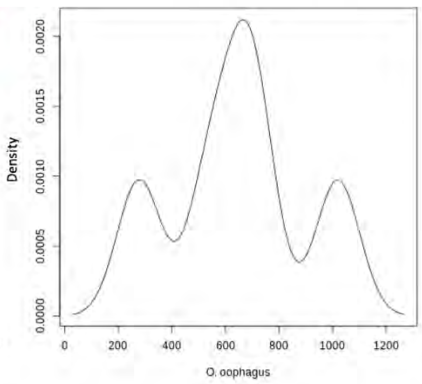

Q-Q Plot for A. spumarinus

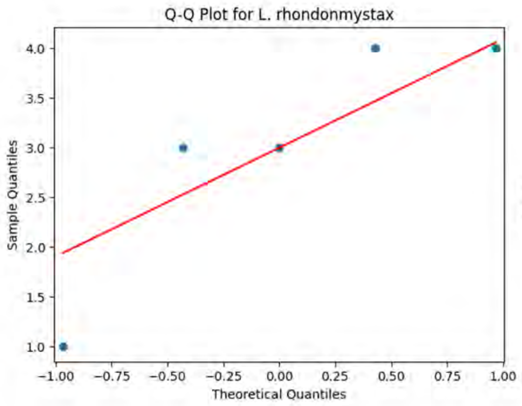


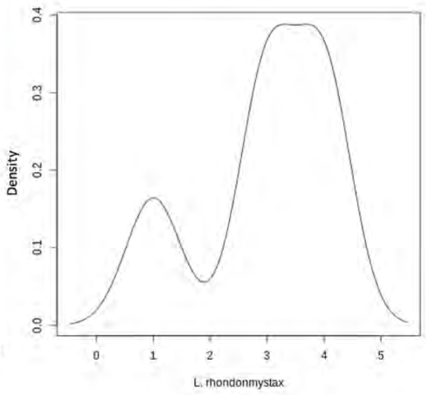

Q-Q Plot for L. pentadactylus

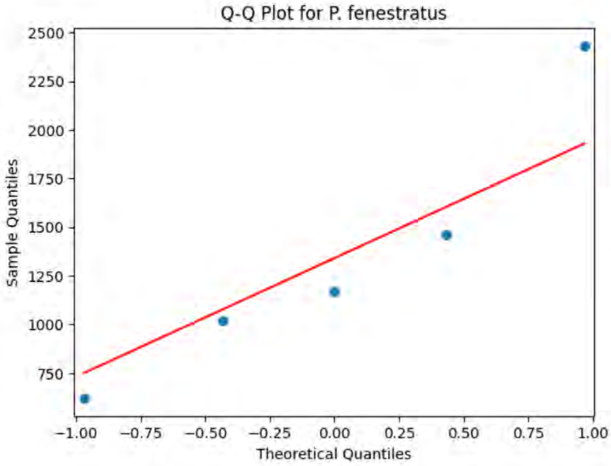


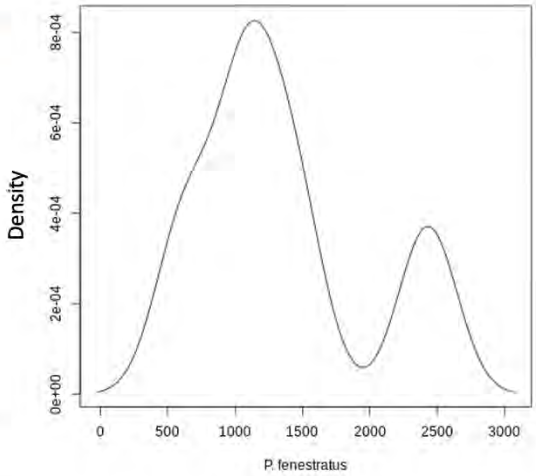

Q-Q Plot for O. oophagus

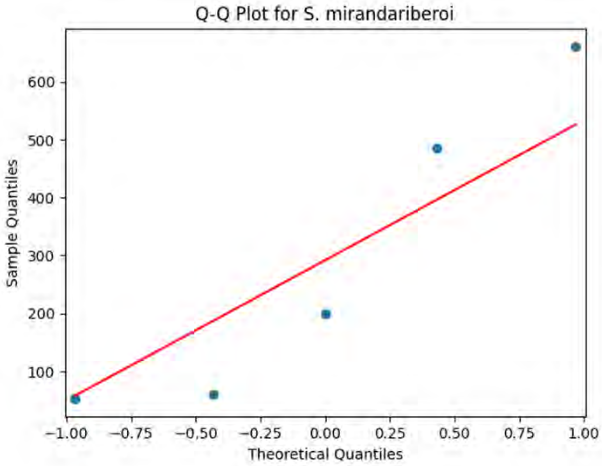


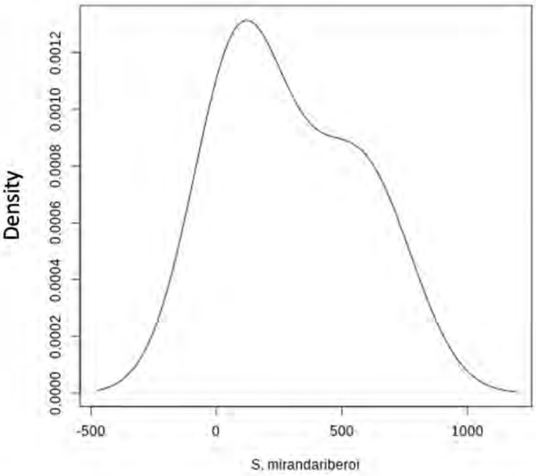

Q-Q Plot for L. rhondonmystax

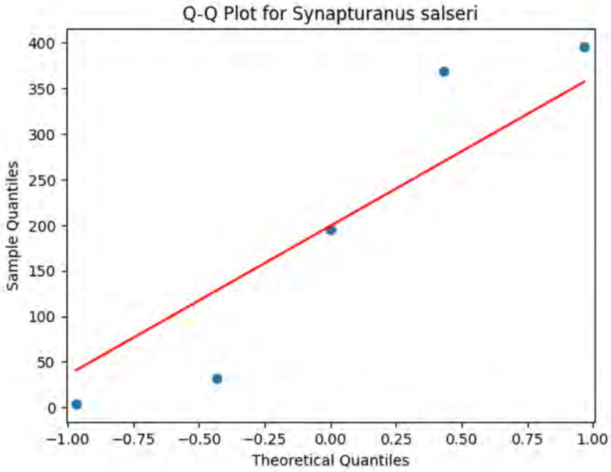


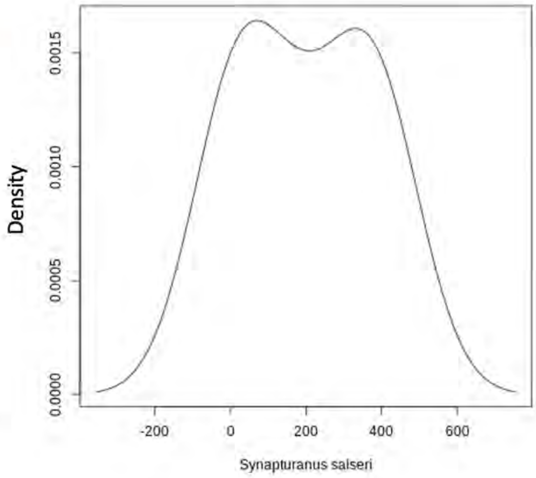

Q-Q Plot for P. fenestratus
Sample Quantiles
2500
2250
2000
1750
1500
1250
1000
750
−1.00
−0.75
−0.50
−0.25
0.00
0.25
0.50
0.75
1.00
Theoretical Quantiles


Density
0e+00
2e-04
4e-04
6e-04
8e-04
0
500
1000
1500
2000
2500
3000
P. fenestratus


Q-Q Plot for S. mirandariberoi
Sample Quantiles
600
500
400
300
200
100
−1.00
−0.75
−0.50
−0.25
0.00
0.25
0.50
0.75
1.00
Theoretical Quantiles


Density
0.0000
0.0002
0.0004
0.0006
0.0008
0.0010
0.0012
-500
0
500
1000
S. mirandariberoi


Q-Q Plot for Synapturanus salseri
Sample Quantiles
400
350
300
250
200
150
100
50
0
−1.00
−0.75
−0.50
−0.25
0.00
0.25
0.50
0.75
1.00
Theoretical Quantiles


Density
0.0000
0.0005
0.0010
0.0015
-200
0
200
400
600
Synapturanus salseri

Appendix S3. Homoscedasticity test:

Largest set of species with homogeneity of variances: *L. pentadactylus* (n=63), *L. rhodomystax* (n=15), *O. oophagus* (n=3222), *P. fenestratus* (n=6702), *S. mirandariberoi* (n=1459) and *S. salseri* (n=996).

p >0.05 (There is no evidence to reject homoscedasticity)

L. pentadactylus: Average: 12.60, Variance: 8.24.
L. rhodomystax: Average: 3.00, Variance: 1.20.
O. oophagus: Average: 644.40, Variance: 58124.24.
P. fenestratus: Average: 1340.40, Variance: 371489.04.
S. mirandariberoi: Average: 291.80, Variance: 58563.76.
S. salseri: Average: 199.20, Variance: 26727.76.

* *A. manauensis* does not show homoscedasticity in relation to the other species; these results may have been influenced by the explosive reproduction habit of this species.