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Surviving in a Warming and Fragmented World: Long-Term Population Dynamics of the Lizard *Gonatodes humeralis*

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ABSTRACT

Climate change presents significant challenges to species survival; however, the long-term effects on tropical lizard populations remain poorly understood. Previous studies have predicted contrasting outcomes, with some forecasting a high risk of extinction due to rising temperatures, while others suggest greater resilience in tropical habitats. To address this gap, we analysed the population dynamics of *G. humeralis* at two time points, spaced 20 years apart, in Central-Eastern Amazonia, focusing on how temperature increases and habitat quality affect population growth rates. We surveyed *G. humeralis* across 24 sampling plots, each with 1000 m of trails, in 2001 and 2021, to assess the impact of high temperatures (restriction hours), forest area, isolation from continuous forest, differences in invertebrate biomass and differences in forest cover between 2021 and 2001 on *G. humeralis* population growth rates using Generalised Linear Mixed Models (GLMM). Our findings indicate that the *G. humeralis* population increased significantly, with 192 individuals recorded in 2001 and 452 in 2021, demonstrating resilience to increases in temperature during that period. While growth rates were slightly impacted by higher temperatures, the overall population did not decline, contradicting previous extinction predictions due to climate change. Moreover, the analysed environmental variables did not significantly affect the species' population growth rates. Our data clearly indicate that *G. humeralis* is resilient to long-term habitat fragmentation and that the predictions of previous models are not supported by our findings, suggesting that the extinction of the species before 2070 may be less likely than previously proposed.

RESUMO

As mudanças climáticas representam desafios significativos para a sobrevivência das espécies; no entanto, os efeitos de longo prazo sobre as populações de lagartos tropicais ainda são pouco compreendidos. Estudos anteriores previram resultados contrastantes, com alguns apontando alto risco de extinção devido ao aumento das temperaturas, enquanto outros sugerem maior resiliência em habitats tropicais. Para preencher essa lacuna, analisamos a dinâmica populacional de *Gonatodes humeralis* em dois momentos, com intervalo de 20, anos na Amazônia Centro-Oriental, com foco em como o aumento da temperatura e a qualidade do habitat afetam as taxas de crescimento populacional. Realizamos amostragens de *G. humeralis* em 24 parcelas, cada uma com 1000 m de trilhas, nos anos de 2001 e 2021, para avaliar o impacto das altas temperaturas (horas de restrição), área florestal, isolamento em relação à floresta contínua, diferenças na biomassa de invertebrados e diferença na cobertura florestal entre 2021 e 2001 sobre as taxas de crescimento populacional de *G. humeralis*, utilizando Modelos Lineares Mistos Generalizados (GLMM). Nossos resultados indicam que a população de *G. humeralis* aumentou significativamente, com 192 indivíduos registrados em 2001 e 452 em 2021, demonstrando resiliência ao aumento das temperaturas nesse período. Embora as taxas de crescimento tenham sido levemente impactadas por temperaturas mais altas, a população como um todo não apresentou declínio, contradizendo previsões anteriores de extinção devido às mudanças climáticas. Além disso, as variáveis ambientais analisadas não afetaram significativamente as taxas de crescimento populacional da espécie. Nossos dados mostram claramente que *G. humeralis* é resiliente à fragmentação de habitat em longo prazo e que as previsões de modelos anteriores não são corroboradas por nossos resultados, indicando que a extinção da espécie antes de 2070 pode não ser tão provável quanto anteriormente sugerido.

1 | Introduction

Accelerated global warming, driven by human activities, severely impacts ectothermic organisms, particularly lizards, which are highly vulnerable to extinction (Huey et al. 2009). These animals depend on external environmental conditions to regulate their body temperature, making them especially susceptible to climate change, particularly in tropical regions (Huey et al. 2009; Sinervo et al. 2010). Despite the increasing amount of research on the impact of rising temperatures, much of the existing literature relies on predictive modelling without integrating long-term field data to understand actual population trends. Understanding these effects is crucial for predicting species resilience and biodiversity declines in a warming world (Huey et al. 2009; Doucette et al. 2023). To capture these dynamics accurately, physiological models linked to population models are essential (Diele-Viegas et al. 2019). However, estimating population trajectories proves more complex than measuring short-term physiological responses, as long-term data on population trends are not available for most species. Using integrated physiological and population models, Diele-Viegas et al. (2019) predicted that some Amazonian lizard species are likely to go extinct or be subjected to large reductions in population size. However, those projections differ from some earlier predictions about species vulnerable to climate change (Sinervo et al. 2010).

Besides temperature, other environmental variables also structure lizard populations. Habitat characteristics and resource availability, for example, can act as ecological filters that directly affect species viability by shaping population growth or decline (Santos et al. 2008; Silva et al. 2022; Souza-Oliveira et al. 2024). Factors such as vegetation structure (Souza et al. 2020; Souza-Oliveira et al. 2024; Ganança et al. 2025) and food supply play a critical role, affecting survival, reproduction and population density (Zeng et al. 2014). Moreover, forest fragmentation, often driven by human activities such as deforestation and land use change, creates isolated patches of habitat. These forest fragments are dynamic systems that can change in size over time and such variation in forest cover may influence the populations that inhabit them, particularly species with limited dispersal capacity or strict habitat requirements. Consequently, changes in these parameters can lead to shifts in population dynamics, including variation in birth rates, mortality and dispersal, ultimately affecting the stability and persistence of lizard populations over time.

Another key factor influencing lizard population dynamics is reproductive seasonality. Most tropical lizards reproduce seasonally (Fitch 1982), leading to fluctuations in the proportions of age/size classes throughout the year (Magnusson 1987; Miranda and Andrade 2003). This seasonal variation can pose challenges for demographic analysis, particularly for life-table models, which may yield unstable results if reproductive seasonality is not adequately accounted. N, the population models used by Diele-Viegas et al. (2019) were based on life-table analyses but did not incorporate how reproductive seasonality affects the relative proportions of different age/size classes in the population. Population projections ignoring reproductive seasonality and temperature variation may misestimate extinction risks, especially for tropical species. To address this, we developed a long-term demographic approach incorporating these factors.

The lizard *Gonatodes humeralis* (Sphaerodactylidae) is an excellent model for ecological studies due to its wide distribution in the Amazon (Oliveira et al. 2021; Diele-Viegas et al. 2019), where it is one of the most abundant and easily detectable lizards (Avila-Pires 1995). Its range extends from the coast of Venezuela, through the Guianas and Trinidad and Tobago, to the Brazilian Cerrado (Avila-Pires 1995; Miranda et al. 2010). Its body temperature is generally 1°C–2°C higher than air and substrate (Diele-Viegas et al. 2019). Additionally, as a forest non-heliothermic species (thermoconformer), it is less likely to produce generations that gradually adapt to rising global temperatures (Huey et al. 2009). Furthermore, its reliance on forest habitats makes it particularly vulnerable to the combined impacts of deforestation and climate change, which tend to reinforce each other, exacerbating environmental degradation (Huey et al. 2009).

Sinervo et al. (2010) projected that lizard populations in the Sphaerodactylidae family face a negligible risk of extinction due to climate change in both the medium (2050) and long-term (2080). This low vulnerability is primarily attributed to the fact that their physiological activity is only restricted during periods of the day when air temperatures exceed 33°C (restriction hours). However, extended exposure to such temperatures, particularly during reproductive periods, could lead to declines in Sphaerodactylidae populations. Under these conditions, the lizards seek thermal refuges to protect themselves from the heat. This behaviour reduces the time they spend foraging and can impair essential metabolic functions, such as reproduction. These effects could reduce population growth rates and increase the risk of extinction (Doucette et al. 2023; Sinervo et al. 2010). Conversely, studies on the genus *Gonatodes* (Altamirano-Benavides et al. 2019; Diele-Viegas et al. 2019) indicated a high risk of extinction by 2050 and 2070 due to increases in temperature. Diele-Viegas et al. (2019) predicted that *G. humeralis* could face local extinction in most areas throughout its range by 2070 due to increasing temperatures, if they resulted in mean daily temperatures exceeding 29.49°C.

The population of *G. humeralis* was also studied by Carvalho et al. (2008) in the Área de Proteção Ambiental de Alter do Chão, located in the central-eastern Amazon, which is characterised by continuous and fragmented semideciduous forests bordered by a savanna landscape. The authors observed that, under forest fragmentation, the species tended to decline in isolated forest fragments compared to continuous forest, highlighting its vulnerability to habitat disruption. In our study, we revisited the sampling sites of Carvalho et al. (2008) and repeated the same sampling protocol to investigate the population trajectories of *Gonatodes humeralis* (Sphaerodactylidae) over a 20-year period. In 2021, when we conducted our lizard survey, mean world temperatures increased by about 0.4°C since 2001 (NOAA 2024), when Carvalho et al. (2008) conducted the first survey. Also, mean average temperatures (26.3°C) of the Alter do Chão are similar to those in regions studied by Diele-Viegas et al. (2019), which had mean temperatures of 26.5°C and 26.2°C. Within the region, survey plots varied in vegetation density (do Amaral et al. 2017), size of surrounding forest patches (Cintra et al. 2013), fire intensity (Magnusson et al. 2021), all of which influence mean temperatures. This environmental variation allowed us to assess whether population growth rates over the 20-year period were related to temperature, as well as other factors such as food availability and distance to continuous forest.

The objectives of our study are: to determine the influence of temperature (thermal restriction hours) and other environmental variables (fragment size, isolation from continuous forest, tree density and food availability) on *G. humeralis* population growth rates over 20 years; to assess whether the abundances of *G. humeralis* changed significantly over 20 years; to compare the relative impact of the environmental factors on the species' abundance in 2001 and 2021; and to assess whether *G. humeralis* populations in our study area are at risk of extinction by 2070 due to rising temperatures, as suggested by Diele-Viegas et al. (2019). We hypothesised that population growth rates of *G. humeralis* populations would decline with increasing thermal restriction hours, defined as periods with temperatures equal to or exceeding 33°C (Sinervo et al. 2010). We further predicted that habitat quality and food availability would modulate these growth rates. Finally, we expected that interactions between temperature and other environmental variables would drive significant changes in lizard relative abundances over a 20-year period, with habitat variables influencing lizard abundances differently in 2001 compared to 2021. Understanding how tropical lizard populations respond to long-term environmental changes is essential to predict their resilience to ongoing climate change and to guide future conservation strategies.

2 | Methods

2.1 | Study Area

The study area, on the south bank of the Tapajós River, comprises continuous and fragmented semideciduous forests, surrounded by a savanna matrix, within an Environmental Protection Area (APA) near the village of Alter do Chão, Santarém municipality, Pará, Brazil (centroid coordinates: 02°31′S, 55°00′W). The landscape was likely covered by continuous forest until 2000 years ago (Sanaiotti et al. 2002). The origins of the forest patches are unclear, but records by Bates (1863) indicate their presence for at least 150 years. The transition to savanna may have resulted from fires set for Paleo-Indian agriculture, as the region has been populated by humans for millennia (Maezumi et al. 2018).

The mean temperature in the region remains relatively stable at around 26°C throughout the year (INMET 2020), but average temperatures increased by 1.1°C, from 24.9°C in the period 1961–1990 to 26.0°C in 1991–2020 (INMET 2020). Precipitation shows significant seasonality, with a distinct dry season from July to December. The mean annual rainfall from 1991 to 2020 was 1878 mm (INMET 2020).

2.2 | Sampling Design

Surveys for *G. humeralis* were carried out in forest patches with plots traversed by 1000 m of trails. Most plots had four trails of 250 m separated by 50 m, but one plot had fewer trails of different lengths to accommodate fragment shape differences.

We sampled a total of 24 plots, including five continuous forest sites and 19 forest fragments (Figure 1), with fragment sizes ranging from 3.6 to 360 ha, between August and December of 2021. We counted lizards along the 1000 m of trails in each plot and data from all four transects were combined for analysis. The trails began at the edge and extended towards the center of the fragments, ensuring a balanced sampling between the edge and the interior, regardless of fragment size. In the 360-ha fragment, we sampled two different locations and pooled the data from the two sets of transects to calculate the mean values for that fragment.

Surveys in 2021 followed the same methods and were conducted during the same time of year (August to December—dry season) as the sampling in 2001 by Carvalho et al. (2008). All surveys were undertaken between 09:00 and 16:00. Plot sampling order was not related to fragment size and sampling in continuous forest was interspersed with sampling in forest fragments. We could not sample

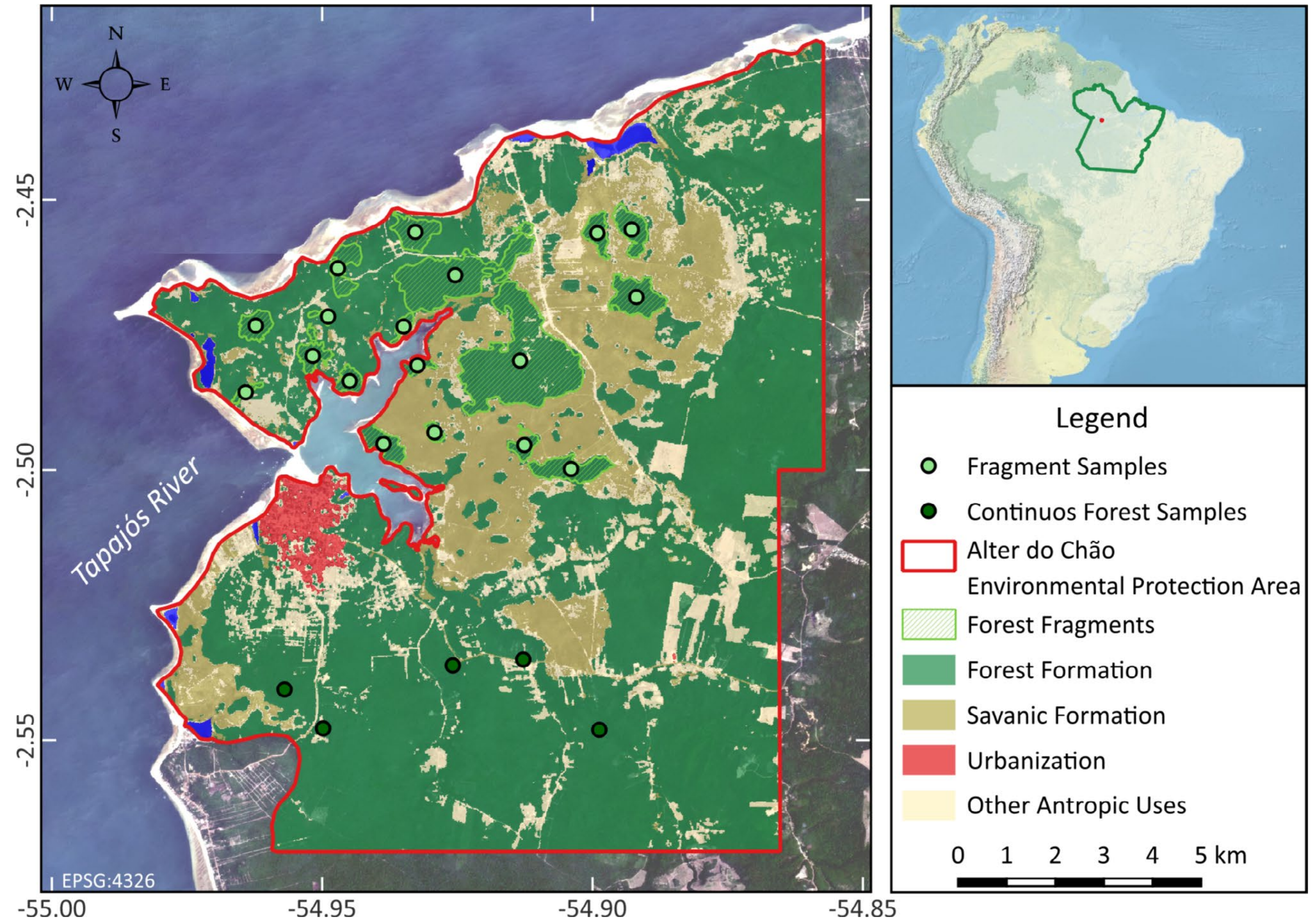

FIGURE 1 | Study area in central-eastern Amazonia, showing the location of the 24 sampling plots.

all plots sampled by Carvalho et al. (2008) because some had been degraded for real-estate speculation (Fadini et al. 2021), so we work with 24 sampling plots, from the original 29 plots.

To sample lizards in the plots, two researchers walked side by side along the trails, searching for individuals within a 6-m-wide strip (3 m on each side) and up to 3 m in height, counting each lizard. One of the observers participated in both the 2001 and 2021 surveys. Each trail was sampled once each year.

2.3 | Environmental Variables

We measured the temperature related to *G. humeralis* thermal restriction hours following Sinervo et al. (2010), as well as forest size, isolation from continuous forest, tree density and food availability with the same methods as Carvalho et al. (2008).

We used Hobo Dataloggers (AK172) to record temperatures hourly during 2017 in all plots, during December 2017, which is one of the hottest months in the study area. While October and November are also characterised by high temperatures, some dataloggers malfunctioned during those months, so we assumed December restriction hours were representative of the hot season. The dataloggers were installed on trees at approximately 40 cm above the ground, the same microhabitat where *G. humeralis* typically live, ensuring that temperature measurements accurately reflect the thermal environment experienced by the species. Although the climate data used in this analysis are from 2017, we chose to use them as representative of the thermal conditions in 2021 due to the high temporal correlation observed among recent years in the study region. Annual mean temperature data for central Amazonia tend to exhibit low interannual variation in forest areas. To test the hypothesis that thermal restriction hours, with temperatures equal to or exceeding 33°C (Sinervo et al. 2010), impact the population growth rates of *G. humeralis*, we calculated the average number of hours for each day with temperatures above 33°. Additionally, we calculated, also in December (2017), the mean temperature during the activity period of *G. humeralis* from 08:00 to 17:00 (Diele-Viegas et al. 2019), to investigate whether *G. humeralis* populations can tolerate temperatures above 29.49°C, the threshold at which Diele-Viegas et al. (2019) suggested the species may face extinction.

Data on tree density were collected in 2001 by counting trees in four diameter-at-breast height (dbh) classes: 1.6–9.9 cm, 10–19.9 cm, 20–29.9 cm and > 29.9 cm, in four 250 m × 2 m subplots (total area = 0.2 ha) in each sampling unit see (Carvalho et al. 2008). We did not resample tree densities in 2021, but our subjective observations indicate that tree densities in the fragments remained relatively stable over the 20-year period.

We assessed food availability for *G. humeralis* using invertebrate biomass (wet weight) in 2001 and 2021 following Carvalho et al. (2008). We collected invertebrates using pitfall traps made from 2-L plastic bottles positioned along the same trails where lizards were surveyed. Each trap had a 23×15cm opening cut along one side and was buried horizontally in the soil with the opening parallel to the ground surface. We filled the traps with a 1% formalin solution mixed with detergent to reduce surface tension. We placed five traps at 50-m intervals along each transect, totalling 20 traps per plot. To prevent accidental capture of lizards, traps were set after the lizard surveys. Invertebrates were left in the traps for 48h and then preserved in 70% alcohol. We measured the wet weight of the invertebrates after removing excess water with filter paper using an electronic balance accurate to 0.0001g. We identified and categorised the size and types of prey to assess food availability, following Carvalho et al. (2008) and Vitt et al. (1997). We included potential prey up to 1cm from Araneidae, Collembola, Coleoptera, Hymenoptera, Isoptera, insect larvae and Mollusca.

We used data collected in 2001 to calculate forest size (forest area) and distance to continuous forest was calculated following Carvalho et al. (2008). We digitalised the data using the CAMRIS software based on a Landsat TM5 image. We measured the minimum distance between forest fragments and continuous forest in the ARC-VIEW 3.2 program, using straight lines in the 'nearest distance' tool; corrected manually, when needed, to avoid large bodies of water. The fragments are surrounded by savanna and have changed little in size over the 20-year interval (Appendix S1). For analyses of forest area, we considered the arbitrary value of 500ha for plots in continuous forest, following Cintra et al. (2013).

Despite the limited change in fragment size between 2001 and 2021, we considered it relevant to assess whether size variation influenced lizard population dynamics. To analyse the difference in forest cover in the fragments between 2001 and 2021 (Difference forest cover 2021–2001), we used land use and land cover data from MapBiomas, Collection 7 (MapBiomas 2023). This collection was chosen after a visual assessment, which indicated greater classification accuracy for the study area compared to later collections. We processed the data using the Level 1 MapBiomas classification, followed by a reclassification into two main categories: 'Forest Cover' and 'Other'. This simplification enabled the analysis of forest cover dynamics over time. We calculated the Forest Cover Index (FCI) for each forest fragment in the years 2001 and 2021. The FCI was determined as the ratio between the forested area and the total area of the fragment. We delineated fragment boundaries based on field data collected via GPS, as described in (Carvalho et al. 2008). To assess forest cover dynamics, we calculated the percentage differences in FCI between the analysed years 2021–2001. These differences allowed us to quantify changes in forest cover over time, providing insights into deforestation and regeneration processes within the study area. MapBiomas (2023). Collection 7 of Brazilian Annual Land Use and Land Cover Mapping. Accessed on December 18, 2024, from https://mapbiomas.org. We summarised all environmental gradients measured in Table 1.

2.4 | Data Analysis

We used paired *t*-tests to determine if there were significant differences in the abundance of *G. humeralis* between 2001 and 2021.

We estimated population growth rates for *G. humeralis* over the 20-year interval (2001–2021) for each sampling unit using the formula: growth rate = 1/20 × ln(number encountered 2021/number encountered 2001). To investigate the influence of environmental variables (thermal restriction hours, forest size, isolation from continuous forest, tree density, food availability and difference in forest cover between the years 2021 and 2001) on the population growth rate of *G. humeralis*, we used GLMM with the glmmTMB package (Brooks et al. 2017) in R software (R Core Team 2020). The model was fitted using the Gaussian family, which effectively captured the variability in the rate of increase. A scatter plot of predicted values and residuals assessed model adequacy and identified potential patterns or deviations. In this model, we considered the differences in food availability between 2001 and 2021. We tested for multicollinearity among the environmental variables using Variation Inflation Factor (VIF) tests, using the car R package (Fox et al. 2012). The temperature data from the HOBO device was not recorded in one of the fragments; therefore, this sample unit was excluded from the model. We estimated pseudo R^2 for each pairwise comparison using the function r^2 from the package performance (Lüdecke et al. 2021).

TABLE 1 | Minimum (Min), maximum (Max), mean and standard deviation (SD) values of environmental variables measured in 24 plots in western Pará, central-eastern Amazonia. Restriction hours (Average number of hours at or above 33°C during the days in December), Forest size (ha), Isolation to continuous forest (m), Tree density (number of trees), Food availability 2021, Food availability 2021 (g), Food availability 2021–2001 (differences in invertebrate biomass [g] between the years) and Difference in forest cover (Forest cover index) between 2021 and 2001.

Environmental variables	Min	Max	Mean	SD
Restriction hours	0.29	2.68	1.33	0.57
Forest size	3.6	500	131.8	187.6
Isolation to continuous forest	0	9135	3483.5	3195.2
Tree density	111	1020	400.8	297.3
Food availability 2001	0.068	0.577	0.336	0.155
Food availability 2021	0.155	2.954	1.386	0.827
Food availability 2021–2001	−0.027	2.670	1.050	0.803
Difference forest cover 2021–2001	−5.3	26.9	2.42174	6.79471

To compare the impact of environmental variables on the species' relative abundances separately in 2001 and 2021, considering all the plots (fragments and continuous forest) and only fragment plots separately, we used the generalised linear mixed effects model (GLMM) with the glmmTMB package (Brooks et al. 2017). The models were fitted using the negative binomial distribution family (nbinom2), which is appropriate for count data. We also tested for multicollinearity among the environmental variables using VIF tests. We used the same variables (forest size, isolation from continuous forest, tree density and food availability) as Carvalho et al. (2008), but updated the analyses, as Carvalho et al. (2008) used hierarchical partitioning (HP) to evaluate the effect of the environmental variables on the number of *G. humeralis*. The use of generalised linear mixed models (GLMM) instead of hierarchical partitioning (HP) allows for a more robust analysis of the complex interactions between predictor variables on *G. humeralis*, as GLMM can handle non-independent data and non-normal distributions.

To determine whether the species will withstand future temperature increase and to compare with the results obtained by Diele-Viegas et al. 2019, we used temperature data from the years (1979–2000) and the future (2070) obtained from WorldClim. Following Diele-Viegas et al. 2019, we used the raster package in the R software and the MPI-ESM1-2-HR (Max Planck Institute Earth System Model) climate layer at 0.0083333 degree resolution, downscaled to 1 × 1 km grid cells (30 s spatial resolution), which is an accurate climate model for representing global temperature patterns during the control period (Anav et al. 2013).

3 | Results

We encountered 452 *Gonatodes humeralis* individuals in 2021, representing an increase of 260 individuals compared to 2001, when 192 individuals were recorded. *Gonatodes humeralis* was found in most fragments in 2001 (undetected in only two fragments) and in all fragments in 2021. In continuous forest, the species was observed in all sampled areas in both years. The maximum number of individuals encountered in a single plot in 2001 was 45, whereas in 2021, the maximum rose to 82, with a minimum of 2. There was a significant difference in the relative abundances of *G. humeralis* between 2001 and 2021 (paired t-test: $t = 3.55$, df $= 23$, $p = 0.0017$).

Four of the areas in this study recorded mean temperatures during the activity period of *G. humeralis* that exceeded 29.49°C (ranging from 29.51°C to 30.45°C). The density of *G. humeralis* increased in three areas ($r = 0.020$, 0.028 and 0.066) and decreased slightly in one ($r = -0.008$).

In the Generalised Mixed Models investigating population growth rates of *G. humeralis* between 2001 and 2021, VIF values for isolation and tree density were > 5.6, due to high collinearity. Therefore, we excluded tree density from the model (Appendix S2). The final model included thermal restriction hours, forest area, isolation from continuous forest, food availability (invertebrate biomass) and difference in forest cover between 2021 and 2001 as predictors of *G. humeralis* population growth rates. There was weak evidence ($p = 0.098$) for a negative effect of restriction hours on population growth (Figure 2), but this variable explained little of the variance in relative densities of *G. humeralis* (pseudo $r^2 = 0.09$). Similarly, forest area (pseudo $R^2 = 0.11$, $p = 0.126$), isolation from continuous forest (pseudo $R^2 = 0.19$, $p = 0.716$), food availability (invertebrate biomass) (pseudo $R^2 = 0.18$, $p = 0.596$), and difference in forest cover between the years 2021 and 2001 (pseudo $R^2 = 0.19$, $p = 0.917$) showed no significant effect on population growth in the long-term (Appendix S3). Overall, the full model accounted for only 19% of the variance in population growth rates. As an exploratory approach, we also ran the model using only the 19 plots located in forest fragments; however, none of the variables significantly influenced *G. humeralis* growth rates ($p > 0.174$ in all cases). Detailed results of the GLMM are given in Appendices S4 and S5.

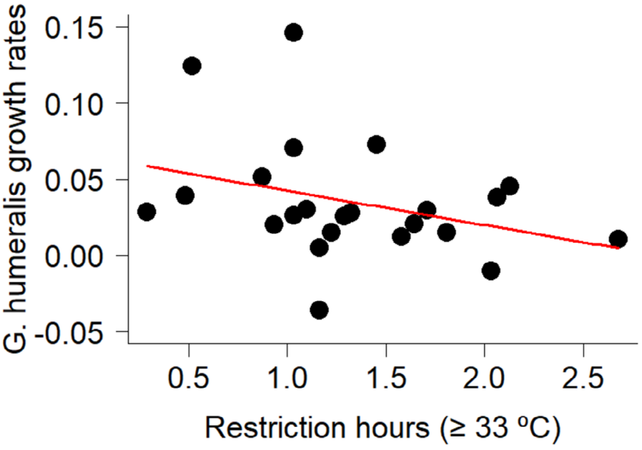

FIGURE 2 | Partial regression of growth rate of *G. humeralis* in relation to restriction hours derived from a Generalised Linear Mixed Model (GLMM).

Analyses of *G. humeralis* relative abundances for each year separately resulted in conclusions that differed from those reported by Carvalho et al. (2008). For the 2001 data, there is no influence of any variable (forest area, isolation, tree density, or food availability), both when considering all areas, fragments and continuous forest ($p > 0.200$ in all cases) (Appendix S6) and when analysing only forest fragments ($p > 0.154$ in all cases) (Appendix S7). In contrast, our model for 2021, which included all plots (both fragments and continuous forest), showed that *G. humeralis* relative abundances were positively correlated with forest area (pseudo $r^2 = 0.54$, $p = 0.012$) and negatively correlated with invertebrate biomass (pseudo $r^2 = 0.53$, $p = 0.014$) (Appendices S8 and S9); the full model explained 66% of the variance in relative abundances. When considering only forest fragments, *G. humeralis* relative abundances in 2021 were negatively influenced by food availability (pseudo $R^2 = 0.38$, $p = 0.006$) and tree density (pseudo $R^2 = 0.49$, $p = 0.022$) (Appendices S10 and S11). Overall, the full model explained 60% of the variance in relative abundances. VIF values did not indicate collinearity among the variables in either the 2001 or 2021 models (VIF < 3.2 in all cases).

4 | Discussion

Our study revealed a significant increase in *Gonatodes humeralis* populations over the 20-year period. Although we found weak evidence that thermal restriction hours (i.e., periods with temperatures exceeding 33°C) had a slight negative effect on population growth rates ($p = 0.098$), none of the other habitat quality variables: forest size, isolation from continuous forest, tree density, or food availability explained a significant portion of the variation in *G. humeralis* population growth rates. Importantly, even in areas where mean temperatures during the species' activity period exceeded 29.49°C, *G. humeralis* populations continued to grow, contradicting previous predictions (Diele-Viegas et al. 2019) that the species could not tolerate mean temperatures of 29.49°C.

Our findings contrast with the predictions of Diele-Viegas et al. (2019), who suggested that *G. humeralis* populations could face extinction due to rising temperatures by 2070. Instead, our results are consistent with Sinervo et al. (2010), who projected that species in the family Sphaerodactylidae would not experience significant declines due to climate change before 2080. While our analyses suggest that prolonged exposure to temperatures above 33°C may slightly reduce population growth rates, the overall population expansion observed in our study suggests that *G. humeralis* may be more resilient to warming than previously thought. This resilience could be attributed to physiological acclimation, behavioural plasticity, or local adaptation, as has been observed in other widely distributed lizard species (Pontes-da-Silva et al. 2018). Supporting this view, genomic data from Yves et al. (2025) reveal significant local climate adaptation across *G. humeralis* populations, highlighting that genetic variation and adaptive potential vary spatially and some populations may face higher vulnerability to future climate change. Their findings emphasise the importance of considering spatially explicit genetic contexts to fully understand species' responses to environmental changes.

Our temperature data, collected in December, one of the hottest months in the region, show that some of the sampled fragments already experience conditions similar to those predicted for 2070 by Diele-Viegas et al. (2019). In four of these fragments, mean temperatures during the species activity period exceeded 29.49°C, reaching up to 30.45°C. Despite these high temperatures, *G. humeralis* populations in three of these fragments showed positive growth rates, while abundance decreased slightly in only one fragment. Each of these fragments represents a geographically isolated habitat, suggesting that populations of *G. humeralis* in Alter do Chão are not only persisting but thriving under conditions that were previously considered potentially unsustainable (Diele-Viegas et al. 2019). Moreover, the species' ability to persist in habitats that already experience high temperatures, such as Alter do Chão, suggests that it may possess mechanisms for coping with gradual warming.

We do not know why our results differ from the predictions of Diele-Viegas et al. (2019), but one possible explanation is the methodological approach used in population projections. Models based on life tables and size-structured demographic data from short time frames may not adequately capture long-term population dynamics. Additionally, population responses to climate change may vary across different environmental contexts (Magnusson et al. 2021) and factors beyond temperature, such as predation, competition, or microhabitat availability, may play a more significant role in regulating *G. humeralis* populations in this region.

Climate projections from WorldClim indicate that the average regional temperature is expected to rise by ~2.5°C by 2070, reaching 28.8°C in our study area. Sinervo et al. (2010) warned that prolonged exposure to temperatures above 33°C could limit physiological activity and lead to population declines. Moreover, WorldClim projections suggest that mean temperatures in the study region are not expected to exceed 33°C for extended periods by 2070. Considering Sinervo et al. (2010) and the WorldClim temperature projections for the study region, our results suggest that the populations of *G. humeralis* living there are unlikely to be negatively affected by this temperature increase by 2070. Therefore, previous predictive models should be updated to better predict future outcomes.

In addition to temperature, other ecological factors have been widely recognised as important determinants of lizard abundance at local scales, such as forest structure, food availability and landscape connectivity, which are often recognised as key factors influencing lizard abundance at local scales (Santos et al. 2008; Silva et al. 2022; Souza-Oliveira et al. 2024). For example, higher tree density can change microclimatic conditions and provide more shelter and basking spots, which are important for thermoregulation and avoiding predators. In addition, greater food availability, especially arthropod biomass, is generally linked to higher lizard abundance because it directly affects individual growth, reproduction and survival (Vitt et al. 1997). Larger and less isolated forest patches also tend to support more stable and diverse animal populations, due to reduced edge effects and better habitat connectivity (Laurance et al. 2002). In general, we expected these ecological patterns to influence *G. humeralis* population dynamics in fragmented landscapes. However, in our study, even though we observed spatial variation in these factors, none of these variables explained the changes in *G. humeralis* population growth over the two decades. This suggests that drivers affecting short-term abundance patterns may not reliably predict long-term demographic trends in this species.

This temporal aspect becomes even more evident when we compare the two sampling periods in our study. The differences we observed between 2001 and 2021 indicate that *Gonatodes humeralis* has changed its responses to environmental factors over time. In 2001, we found no significant relationship between the species' abundance and variables (forest area, isolation, tree density and food availability). However, in 2021, some of the variables influenced *G. humeralis* abundance. For instance, forest area had a positive effect, while food availability (measured as invertebrate biomass) showed negative effects. Additionally, when considering only fragment plots, both food availability (invertebrate biomass) and tree density negatively influenced lizard abundance. These shifts may reflect changes in habitat quality and structure, local population dynamics, or even the species' ability to adjust its habitat use in response to environmental pressures and ongoing fragmentation over the years. The unexpected negative effect between *G. humeralis* abundance and invertebrate biomass might indicate increased competition or predation pressure in areas with richer arthropod communities. These findings highlight the importance of considering temporal variation in ecological responses, demonstrating that factors initially deemed unimportant can become critical as environmental conditions evolve.

In conclusion, the ecological conditions that affected *G. humeralis* abundance at local scales (e.g., forest structure, food availability, etc.) do not appear to drive long-term population trends. The differences observed between 2001 and 2021 highlight the importance of long-term monitoring to understand population dynamics in fragmented landscapes. Our results show that *G. humeralis* populations in the studied region are resilient to long-term habitat fragmentation and to temperatures above those projected by Diele-Viegas et al. (2019) for 2070, where local extinction had been predicted. In these areas, *G. humeralis* populations not only persist but have increased in abundance over time, highlighting the need for further studies incorporating physiological, behavioural and genetic analyses that would help clarify the species' capacity for adaptation and resilience in the face of climate change.

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Disclosure

Permission to reproduce material from other sources: We permit reproducing this material from other sources.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support this finding of the study are openly available in the DataONE repository at https://search.dataone.org/view/PPBioAmOc.722.12, reference number PPBioAmOc.722.16.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Satellite images of the study area in (A) 2001 and (B) 2021. The images illustrate that the size of habitat fragments changed very little over the two decades, showing minor observable differences, indicating stability in land cover and fragmentation patterns within the region. **Appendix S2:** Variance Inflation Factor (VIF) values for the explanatory variables included in the GLMM analysis. **Appendix S3:** Partial regression of growth rate of *G. humeralis* in relation to (A) Fragment size (ha), (B) Isolation to continuous forest (m) and (C) differences in food availability (G) between 2001 and 2021, (D) Difference forest cover 2021–2001, derived from a Generalised Linear Mixed Model (GLMM). **Appendix S4:** Results of the generalised linear model analysis (GLMM) on the growth rates of *G. humeralis*, presenting the estimates, standard error (SE), *z* values and *p* values for each variable across all plots. Significant results are in bold. **Appendix S5:** Results of the generalised linear model analysis (GLMM) on the growth rates of *G. humeralis*, presenting the estimates, standard error (SE), *z* values and *p* values for each variable in 19 fragments plots. Significant results are in bold. **Appendix S6:** Results from the GLMM model predicting *G. humeralis* abundance in 2001 across all plots. The table shows the estimates, standard errors (SE), *z* values and *p* values for the predictor variables. **Appendix S7:** Results from the GLMM model predicting *G. humeralis* abundance in 2001 in fragments plots. The table shows the estimates, standard errors (SE), *z* values and *p* values for the predictor variables. Significant results are in bold. **Appendix S8:** Partial regression of abundance of *G. humeralis* in 2021 in relation to (A) forest size (ha) and (B) Food availability (Invertebrate biomass) in derived from a Generalised Linear Mixed Model (GLMM). **Appendix S9:** Results from the GLMM model predicting *G. humeralis* abundance in 2021 across all plots. The table shows the estimates, standard errors (SE), *z* values and *p* values for the predictor variables. Significant results are in bold. **Appendix S10:** Partial regression of abundance of *G. humeralis* in 2021 in relation to (A) tree density (number of trees) and (B) food availability (Invertebrate biomass) in 19 fragments plots, derived from a Generalised Linear Mixed Model (GLMM). **Appendix S11:** Results from the GLMM model predicting *G. humeralis* abundance in 2021 in fragments plots. The table shows the estimates, standard errors (SE), *z* values and *p* values for the predictor variables. Significant results are in bold. Significant results are in bold.