UNIVERSIDADE DE BRASÍLIA

INSTITUTO DE CIÊNCIAS BIOLÓGICAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Ritmo de vida rápido em um clima em transformação: Desafios para a persistência de um lagarto vivíparo

Maria Luiza Gonçalves Santos

Brasília - DF

Fevereiro de 2025

UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Ritmo de vida rápido em um clima em transformação: Desafios para a persistência de um lagarto vivíparo

Maria Luiza Gonçalves Santos

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de Brasília como parte dos requisitos para a obtenção do título de Mestre em Ecologia.

Orientador: Dr. Guarino Rinaldi Colli

Brasília - DF
Fevereiro de 2025

Agradecimentos

Fazer ciência não deve ser um trabalho solitário. Para que a ciência de base seja produzida, é necessário um batalhão, e é graças a esse esforço coletivo que podemos avançar, ainda que em pequenos passos, rumo a um mundo mais sustentável e igualitário. Por isso, agradeço inicialmente a todas as pessoas que valorizam a ciência e incentivam aqueles que a produzem. Sou grata à Universidade de Brasília e às instituições financiadoras (CAPES, CNPq, FAPDF e USAID) que possibilitam a realização deste e de dezenas de outros estudos, e cujo suporte tem sido fundamental para o incentivo de pesquisadores. Agradeço também aos pesquisadores, alunos e bolsistas do Laboratório de Herpetologia, por serem tão dedicados à conservação do bioma mais lindo do mundo – modéstia à parte. E agradeço profundamente às minhas professoras e professores, assim como a todos os colegas que, com carinho e paciência, foram coletividade ao me orientar nesse longo e desafiador processo de aprender a ser cientista.

Por fim, um agradecimento especial àqueles que são minha base:

à minha mãe, meu pai, minha irmã, meu irmão e meus e cunhados, por me proporcionarem tamanha inspiração e por me darem carinho, amor, acolhimento, e todo suporte necessário para seguir este caminho;

às minhas avós e avôs, que deram origem ao que há de mais belo na minha vida;

ao meu parceiro, por me entender tão bem, por ser afeto, risada e aconchego, e por me incentivar a ser a profissional que quero ser;

às amizades, que acompanharam minhas várias versões de ser, e seguiram me amando, me apoiando e me mostrando que o mundo é repleto de lutas, mas também de sonhos e coisas belas;

e às crianças da minha vida, que acreditam.

Sumário

Resumo em português

Diante da atual crise da biodiversidade, é fundamental compreender o impacto das mudanças ambientais globais sobre as populações naturais. A análise de parâmetros demográficos obtidos por meio de estudos de longo prazo é a abordagem mais eficaz para identificar padrões que descrevem a dinâmica populacional. Esses padrões podem então ser associados aos fatores ambientais que influenciam tais dinâmicas, permitindo uma compreensão precisa dos efeitos das mudanças ambientais. Este estudo tem como objetivo modelar a dinâmica demográfica de *Notomabuya frenata*, um lagarto neotropical vivíparo, para investigar seu risco de extinção em resposta às mudanças ambientais. Utilizando dados de marcação e recaptura coletados ao longo de mais de 15 anos, construímos Modelos de Projeção Integral (IPMs) para projetar trajetórias populacionais no tempo e no espaço, com base na relação entre taxas vitais e tamanho corporal. Nossos resultados indicam que *N. frenata* apresenta uma história de vida de ritmo acelerado, priorizando a sobrevivência de juvenis e o sucesso reprodutivo precoce, sendo que a reprodução impõe custos mais elevados à sobrevivência das fêmeas devido à viviparidade. Além disso, nossos achados revelam que as mudanças climáticas afetam de forma desigual os processos demográficos ao longo da distribuição da espécie. Demonstramos que temperaturas extremas têm impactado negativamente a sobrevivência e estimamos que reduções na precipitação e aumentos da temperatura global já comprometem o crescimento populacional dessa espécie, especialmente nas bordas de sua distribuição.

Palavras-chave: História de vida; Demografia; Modelo de Projeção Integral; Mudanças climáticas; Ectotérmicos.

Introdução geral

A evolução é o processo que molda a diversidade da vida na Terra, determinando a adaptação das espécies ao ambiente em que habitam. Esse processo atua sobre as estratégias que as espécies exploram para crescer, sobreviver e se reproduzir, definidas como história de vida [1]. As variações nas histórias de vida refletem diferenças na alocação de energia entre crescimento, sobrevivência e reprodução [2]. A demografia, enquanto ferramenta analítica, permite compreender como essas alocações de energia moldam as populações e, mais importante, como elas respondem às condições do ambiente, uma vez que populações sofrem mudanças em seu tamanho e estrutura ao longo do tempo e do espaço [3, 4]. A característica dinâmica da demografia se dá pois os indivíduos respondem a fatores bióticos e abióticos que afetam seu crescimento, sobrevivência, fecundidade e capacidade de dispersão, determinando um balanço entre a entrada e a saída de indivíduos [5]. Tal balanço define o tamanho e a viabilidade das populações ao longo do tempo [6].

Aumentos na temperatura média global; mudanças nos regimes de chuva e de queimadas; alterações na distribuição de ecossistemas e espécies; perda, fragmentação e isolamento de habitats são todos fatores que colocam em risco a biodiversidade global ao fazer com que a saída de indivíduos da população supere a entrada, reduzindo-as a um nível em que sua manutenção é insustentável [7–10]. Portanto, para entender como as populações respondem às mudanças ambientais, precisamos compreender como os agentes de estresse afetam o crescimento, a sobrevivência e a reprodução dos organismos, levando em conta que diferentes estratégias de vida podem desencadear respostas diferenciais [3, 4, 7].

Espécies com ritmo de vida rápido, caracterizadas por alta fecundidade, maturação acelerada e curta expectativa de vida, priorizam a reprodução em detrimento da

sobrevivência [1, 2]. Essas espécies tendem a responder rapidamente a mudanças ambientais, ajustando taxas de natalidade ou dispersão, mas são mais vulneráveis a distúrbios drásticos e consecutivos que afetam múltiplas gerações [11, 12]. Por outro lado, espécies com ritmo de vida lento, que apresentam baixa fecundidade, crescimento mais lento e maior longevidade, geralmente investem mais recursos em sobrevivência [1, 2]. Apesar de serem menos flexíveis a mudanças abruptas, espera-se que essas espécies sejam mais resilientes a longo prazo em ambientes previsíveis, devido à sua capacidade de resistir a períodos desfavoráveis sem comprometer a viabilidade populacional [3, 11].

Dessa maneira, para prever de forma confiável a resposta de uma população às mudanças ambientais, é necessário realizar monitoramentos que incorporem análises detalhadas das taxas demográficas e da variabilidade ambiental, parâmetros que geralmente requerem dados de longo prazo para serem plenamente detectados [13–15]. Contudo, esses conjuntos de dados extensivos frequentemente não estão disponíveis, destacando a necessidade de monitoramento de longo prazo e do desenvolvimento de abordagens de modelagem capazes de integrar essas informações para prever declínios populacionais com acurácia. Nesse contexto, Modelos de Projeção Integral (IPMs) surgem como uma importante alternativa, ao integrarem variações em características demográficas como sobrevivência, crescimento e reprodução para descrever a condição e a estrutura das populações ao longo do tempo e do espaço [16]. IPMs explicitam a dinâmica populacional em curso ao serem capazes de estimar parâmetros demográficos em função de preditores ambientais que afetam o desempenho individual [17]. Diferentemente dos métodos tradicionais, eles capturam nuances individuais dentro das populações, ao incorporar variáveis contínuas que indicam o estado dos indivíduos [18, 19]. Isso permite uma

interpretação mais acurada de como pressões ambientais contemporâneas afetam as populações.

Esse tipo de abordagem é essencial para organismos ectotérmicos, como lagartos. O metabolismo desses animais é diretamente influenciado pela temperatura ambiental, o que afeta o tempo de forrageamento, e consequentemente, crescimento, sobrevivência e reprodução dos organismos [20–22]. Lagartos vivíparos são especialmente afetados por aumentos na temperatura, uma vez que as condições térmicas às quais as fêmeas estão sujeitas durante a gestação podem comprometer diretamente o desenvolvimento embrionário, impondo restrições ao sucesso e à eficiência reprodutiva [23, 24]. Além disso, lagartos, de maneira geral, possuem ritmo de vida mais acelerado caracterizado por baixa sobrevivência, baixa fecundidade e maturidade precoce [25]. Isso pode torná-los ainda mais vulneráveis a eventos ambientais e demográficos extremos consecutivos, já que as populações resistem menos em curta escala de tempo a esses distúrbios, e não teriam tempo hábil suficiente para se recuperar caso os distúrbios sejam consecutivos [11, 12]. No entanto, a falta de dados de longo prazo e os vieses de coleta dificultam a compreensão dos processos que determinam o destino dessas espécies.

O sincídeo vivíparo *Notomabuya frenata* (Cope, 1862) está sujeito a significativas perdas de áreas de adequabilidade ambiental em função das mudanças climáticas e mudanças do uso da terra, o que sugere que a espécie estará sob alto grau de ameaça em um futuro próximo [26, 27]. Tendo isso em vista, busquei compreender melhor a história de vida dessa espécie ao aprofundar os conhecimentos acerca de sua demografia, para que pudesse acessar uma estimativa da condição de suas populações sob diferentes cenários futuros de emissões de CO_2. Para isso, utilizei dados de longo prazo, que permitiram uma compreensão empírica de processos demográficos em curso.

A amostragem de lagartos foi realizada como parte de um projeto de monitoramento de longo prazo de uma comunidade de lagartos em uma área de cerrado *sensu stricto* localizada na Reserva Ecológica do Roncador (RECOR), dentro da Área de Proteção Ambiental das Bacias Gama e Cabeça de Veado. O monitoramento ocorre mensalmente desde 2005 e se estende até os dias atuais (2025). Contudo, para o presente estudo, considerei os censos realizados entre dezembro de 2005 e janeiro de 2021. A cada censo, foram levantadas informações de sexo e tamanho dos indivíduos, além da marcação para identificação em posterior recaptura. Além disso, utilizei informações de ocorrência, tamanho da prole e tamanho de maturidade, todas armazenadas pela Coleção Herpetológica da Universidade de Brasília. Com base nas informações coletadas, desenvolvi modelos de crescimento, sobrevivência e fecundidade, que foram utilizados para construir IPMs. Estes, consistem em Kernels que representam as transições na condição corporal e as contribuições reprodutivas per capita da população entre os tempos *t* e *t + 1* considerando diferentes condições ambientais. A partir dos Kernels, foi possível estimar a taxa de crescimento populacional (λ) e projetar essas estimativas para toda a distribuição potencial da espécie, bem como para diferentes cenários futuros de emissões de CO_2.

Identifiquei diferenças entre machos e fêmeas de *Notomabuya frenata* na alocação de energia entre crescimento, sobrevivência e fecundidade, refletindo os custos distintos da viviparidade para os dois sexos. Essas diferenças podem ter importantes implicações ecológicas e na manutenção da espécie em ambientes em transformação, uma vez que as fêmeas alocam grande quantidade de energia para a manutenção da gestação, reduzindo a energia disponível para sua sobrevivência. De maneira geral, a sobrevivência dos adultos dessa espécie é baixa, resultando em um deslocamento demográfico em direção aos juvenis, que apresentam crescimento acelerado e atingem a maturidade sexual antes da primeira

estação reprodutiva após o nascimento. A estação reprodutiva está fortemente associada à estação chuvosa, possivelmente pelo favorecimento da sobrevivência de filhotes durante o período com maior disponibilidade de alimentos [28, 29]. Comparada a outros vertebrados terrestres, *N. frenata* possui uma vida curta, e alta sobreposição de gerações [25]. Contudo, possui vida mais longa do que lagartos não vivíparos, possivelmente por uma pressão seletiva para sobreviver durante mais ciclos reprodutivos [30]. Todas essas características refletem aspectos associados a uma estratégia de vida oportunista e ritmo de vida acelerado, tornando essa espécie vulnerável a mudanças ambientais drásticas quando essas mudanças acontecem de maneira consecutiva, com curto intervalo entre os eventos [2–4, 25]. Portanto, em ambientes que passam por mudanças rápidas e imprevisíveis, caracterizadas por distúrbios drásticos e consecutivos, essa espécie dependerá de sua plasticidade fenotípica para lidar com tais alterações [31–34].

Constatei que a sobrevivência é em grande parte explicada por eventos estocásticos, com temperaturas extremas afetando negativamente a taxa de sobrevivência mensal. Ademais, as variações observadas no λ são majoritariamente explicadas pela sazonalidade, ressaltando o efeito da reprodução sazonal da espécie e da alta sobrevivência de filhotes associada ao período reprodutivo. Em relação à distribuição espacial das projeções do λ, observei que as populações periféricas a noroeste da distribuição da espécie possuem menor λ médio, porém maior variabilidade dessa taxa, possivelmente destacando baixa plasticidade fenotípica. Isso pode indicar que já está em curso uma contração da distribuição de *Notomabuya frenata* em direção a sudeste de sua distribuição. Tal contração deve ser ainda mais acentuada no futuro, principalmente em um cenário mais pessimista, em que se projetam aumentos na emissão de CO_2.

O uso de modelos preditivos permite projetar espaço-temporalmente respostas das populações a efeitos bióticos ou abióticos que atuam sobre elas [35]. Tratam-se de ferramentas muito importantes na Ecologia, já que possibilitam a realização de previsões e permitem que sejam reconhecidas espécies que estão em risco ou mesmo em débito de extinção [36–38]. Portanto, ao fornecer previsões espacialmente explícitas e baseadas em características biológicas, os resultados obtidos com esse trabalho contribuem para o entendimento das formas complexas pelas quais as espécies podem responder às pressões ambientais das mudanças climáticas. Ao se conhecer os grupos taxonômicos e regiões que mais estão ameaçados pelas mudanças ambientais globais, pode-se direcionar esforços de conservação de maneira mais efetiva, favorecendo, assim, a proteção dos processos que mantém a biodiversidade.

Referências

[1] Stearns SC. 1977 The evolution of life history traits: A critique of the theory and a review of the data. Annual Review of Ecology and Systematics. 8:145–71. https://doi.org/10.1146/annurev.es.08.110177.001045.

[2] Stearns SC. 1976 Life-history tactics: A review of the ideas. The Quarterly Review of Biology. 51:3–47. https://doi.org/10.1086/409052.

[3] Jeppsson T, Forslund P. 2012 Can life history predict the effect of demographic stochasticity on extinction risk? The American Naturalist. 179:706–20. https://doi.org/10.1086/665696.

[4] Sæther B-E, Coulson T, Grøtan V, Engen S, Altwegg R, Armitage KB, Barbraud C, Becker PH, Blumstein DT, et al. 2013 How life history influences population dynamics in fluctuating environments. The American Naturalist. 182:743–59. https://doi.org/10.1086/673497.

[5] Dunham AE, Grant BW, Overall KL. 1989 Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology. 62:335–55. https://doi.org/10.1086/physzool.62.2.30156174.

[6] Begon M, Mortimer M, Thompson DJ. 1996 Population Ecology: A Unified Study of Animals and Plants. 3rd ed. Oxford, UK: Blackwell Scientific Publications.

[7] Selwood KE, McGeoch MA, Mac Nally R. 2015 The effects of climate change and land-use change on demographic rates and population viability. Biological Reviews. 90:837–53. https://doi.org/10.1111/brv.12136.

[8] Stephens PA, Sutherland WJ. 1999 Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution. 14:401–5. https://doi.org/10.1016/S0169-5347(99)01684-5.

[9] Brook B, Sodhi N, Bradshaw C. 2008 Synergies among extinction drivers under global change. Trends in Ecology & Evolution. 23:453–60. https://doi.org/10.1016/j.tree.2008.03.011.

[10] Channell R, Lomolino MV. 2000 Trajectories to extinction: Spatial dynamics of the contraction of geographical ranges. Journal of Biogeography. 27:169–79. https://doi.org/10.1046/j.1365-2699.2000.00382.x.

[11] Koons DN, Grand JB, Arnold JM. 2006 Population momentum across vertebrate life histories. Ecological Modelling. 197:418–30. https://doi.org/10.1016/j.ecolmodel.2006.03.034.

[12] Allen WL, Street SE, Capellini I. 2017 Fast life history traits promote invasion success in amphibians and reptiles. Ecology Letters. 20:222–30. https://doi.org/10.1111/ele.12728.

[13] Gamelon M, Grøtan V, Nilsson ALK, Engen S, Hurrell JW, Jerstad K, Phillips AS, Røstad OW, Slagsvold T, et al. 2017 Interactions between demography and environmental effects are important determinants of population dynamics. Science Advances. 3:e1602298. https://doi.org/10.1126/sciadv.1602298.

[14] Clutton-Brock T, Sheldon BC. 2010 Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution. 25:562–73. https://doi.org/10.1016/j.tree.2010.08.002.

[15] Lindenmayer DB, Likens GE, Andersen A, Bowman D, Bull CM, Burns E, Dickman CR, Hoffmann AA, Keith DA, et al. 2012 Value of long-term ecological studies. Austral Ecology. 37:745–57. https://doi.org/10.1111/j.1442-9993.2011.02351.x.

[16] Merow C, Dahlgren JP, Metcalf CJE, Childs DZ, Evans MEK, Jongejans E, Record S, Rees M, Salguero-Gómez R, et al. 2014 Advancing population ecology with integral

projection models: A practical guide. Methods in Ecology and Evolution. 5:99–110. https://doi.org/10.1111/2041-210X.12146.

[17] Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA. 2014 On using integral projection models to generate demographically driven predictions of species' distributions: Development and validation using sparse data. Ecography. 37:1167–83. https://doi.org/10.1111/ecog.00839.

[18] Ellner SP, Rees M. 2006 Integral projection models for species with complex demography. The American Naturalist. 167:410–28. https://doi.org/10.1086/499438.

[19] Rees M, Childs DZ, Ellner SP. 2014 Building integral projection models: A user's guide. Journal of Animal Ecology. 83:528–45. https://doi.org/10.1111/1365-2656.12178.

[20] Doucette LI, Duncan RP, Osborne WS, Evans M, Georges A, Gruber B, Sarre SD. 2023 Climate warming drives a temperate-zone lizard to its upper thermal limits, restricting activity, and increasing energetic costs. Scientific Reports. 13:9603. https://doi.org/10.1038/s41598-023-35087-7.

[21] Gibbon JW, Scott DE, Ryan TJ, Buhlmann KA, Tuberville TD, Metts BS, Greene JL, Mills T, Leiden Y, et al. 2000 The global decline of reptiles, déjà vu amphibians. BioScience. 50:653. https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2.

[22] Paaijmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, Murdock CC, Thomas MB. 2013 Temperature variation makes ectotherms more sensitive to climate change. Global Change Biology. 19:2373–80. https://doi.org/10.1111/gcb.12240.

[23] Lourdais O, Shine R, Bonnet X, Guillon M, Naulleau G. 2004 Climate affects embryonic development in a viviparous snake, *Vipera aspis*. Oikos. 104:551–60. https://doi.org/10.1111/j.0030-1299.2004.12961.x.

[24] Jara M, García-Roa R, Escobar LE, Torres-Carvajal O, Pincheira-Donoso D. 2019 Alternative reproductive adaptations predict asymmetric responses to climate change in lizards. Scientific Reports. 9:5093. https://doi.org/10.1038/s41598-019-41670-8.

[25] Mesquita DO, Faria RG, Colli GR, Vitt LJ, Pianka ER. 2016 Lizard life-history strategies. Austral Ecology. 41:1–5. https://doi.org/10.1111/aec.12276.

[26] Machado LPC, Caetano GH de O, Cavalcante VHL, Miles DB, Colli GR. 2023 Climate change shrinks environmental suitability for a viviparous Neotropical skink. Conservation Science and Practice. 5:e12895. https://doi.org/10.1111/csp2.12895.

[27] Cope ED. 1862 Contributions to Neotropical saurology. Proceedings of the Academy of Natural Sciences of Philadelphia. 14:176–88.

[28] Ortiz MA, Boretto JM, Ibargüengoytía NR. 2019 Reproductive biology of a viviparous lizard (*Mabuya dorsivittata*) from the subtropical Wet Chaco of Argentina: geographical variations in response to local environmental pressures. Anais Da Academia Brasileira de Ciências. 91:e20170817. https://doi.org/10.1590/0001-3765201920170817.

[29] Vrcibradic D, Rocha CFD. 1998 Reproductive cycle and life-history traits of the viviparous skink *Mabuya frenata* in Southeastern Brazil. Copeia. 1998:612. https://doi.org/10.2307/1447791.

[30] Recknagel H, Elmer KR. 2019 Differential reproductive investment in co-occurring oviparous and viviparous common lizards (*Zootoca vivipara*) and implications for life-history trade-offs with viviparity. Oecologia. 190:85–98. https://doi.org/10.1007/s00442-019-04398-w.

[31] Canale CI, Henry PY. 2010 Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Climate Research. 43:135–47. https://doi.org/0.3354/cr00897.

[32] Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biology. 8:e1000357. https://doi.org/10.1371/journal.pbio.1000357.

[33] Seebacher F, White CR, Franklin CE. 2015 Physiological plasticity increases resilience of ectothermic animals to climate change. Nature Climate Change. 5:61–6. https://doi.org/10.1038/nclimate2457.

[34] Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000 Climate extremes: Observations, modeling, and impacts. Science. 289:2068–74. https://doi.org/10.1126/science.289.5487.2068.

[35] Serra-Diaz JM, Franklin J. 2019 What's hot in conservation biogeography in a changing climate? Going beyond species range dynamics. Diversity and Distributions. 25:492–8. https://doi.org/10.1111/ddi.12917.

[36] Hylander K, Ehrlén J. 2013 The mechanisms causing extinction debts. Trends in Ecology & Evolution. 28:341–6. https://doi.org/10.1016/j.tree.2013.01.010.

[37] Travers H, Selinske M, Nuno A, Serban A, Mancini F, Barychka T, Bush E, Rasolofoson RA, Watson JEM, et al. 2019 A manifesto for predictive conservation. Biological Conservation. 237:12–8. https://doi.org/10.1016/j.biocon.2019.05.059.

[38] Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, et al. 2004 Extinction risk from climate change. Nature. 427:145–8. https://doi.org/10.1038/nature02121.

Fast life history meets climate change: Demographic challenges for a viviparous lizard

Submitted to Proceedings of the Royal Society B

Maria Luiza Gonçalves Santos[1], Heitor Campos de Souza[2], Laís Pio Caetano Machado[1] and Guarino Rinaldi Colli[1,2]

[1]Programa de Pós-graduação em Ecologia, Universidade de Brasília

[2]Departamento de Zoologia, Universidade de Brasília

Abstract

Considering the current biodiversity crisis, it is crucial to understand the impact of global environmental changes on natural populations. Analyzing demographic parameters obtained through long-term studies is the most effective approach to uncover patterns that describe population dynamics. These patterns can then be linked to the environmental factors driving such dynamics, providing an accurate understanding of the effects of environmental changes. This study aims to model the demographic dynamics of *Notomabuya frenata*, a Neotropical viviparous lizard, to investigate its extinction risk in response to environmental changes. Using mark-recapture data collected over more than 15 years, we built Integral Projection Models (IPMs) to project population trajectories over time and space based on the relationship between vital rates and body size. Our findings show that *N. frenata* exhibits a fast-paced life history, prioritizing juvenile survival and early reproductive success, with reproduction imposing greater costs on female survival due to viviparity. Furthermore, our results reveal that climate change unevenly impacts demographic processes across the

species' range. We demonstrate that extreme temperatures have been negatively affecting survival and estimate that reduced rainfall and rising temperatures are already compromising population growth, particularly at the edges of its distribution.

Keywords: Life-history; Demography; Integral Projection Model; Climate change; Ectotherms.

1. Introduction

Demography provides the foundation for the life history theory, which seeks to understand the effects of ecosystem pressures on the evolution of the reproductive and survival strategies of a species [1]. Knowing a species' life history allows us to identify the trade-offs that shape the allocation of energy between survival, growth, and reproduction all of which are critical for population resilience in response to environmental changes [2, 3]. The rapid modification of climate and habitats driven by humans has become the primary threat to biodiversity [4–6]. Human impact may lead to about one million species extinction in the coming decades [7]. These high extinction rates are alarming because biodiversity loss reduces communities' resilience to environmental changes, destabilizing ecosystems through adverse impacts on their processes [8, 9].

Factors such as climate, habitat availability, and stochastic events influence patterns of population dynamics by affecting an organism's survival and fecundity [10–12]. Populations of species with fast life cycles tend to respond promptly to environmental changes, while slow-cycle species accumulate effects over time [2, 3, 13]. These differences can be critical for predicting how life history influences population dynamics in changing environments [3]. Therefore, understanding extinction processes requires not only analyzing

the factors affecting population dynamics but also examining the dynamics themselves, as well as species life histories. To reliably predict a population's response to environmental changes, it is necessary to have long-term monitoring that incorporates detailed analyses of demographic rates and environmental variability [11, 14]. However, these extensive datasets are scarce [15], highlighting the need for long-term monitoring and the development of modeling approaches that can incorporate such information to forecast population declines accurately.

In this context, Integral Projection Models (IPMs) provide a powerful tool for demographic analysis. These models can integrate variations in key demographic characteristics (*e.g.*, survival, growth, and reproduction) to describe the condition and structure of populations over time and space [16–18]. Unlike traditional methods (matrix population models), IPMs incorporate a continuous representation of traits such as size and age, allowing for capturing individual variations within populations [19, 20]. Additionally, IPMs can integrate environmental covariates that influence these traits, providing insight into how environmental changes impact populations [17, 18, 20]. This approach allows for a demographic-level interpretation of how contemporary environmental pressures may affect species.

Ectothermic organisms, such as reptiles, are particularly vulnerable to climate change, as the thermal conditions they are subjected to directly affect their activity time, impacting their feeding, growth, and reproduction rates [21–24]. Viviparous reptiles may be even more affected by increased temperatures, as viviparity is considered an adaptation to cold climates for these organisms [25]. Thermal conditions experienced by females during gestation can directly compromise embryonic development, imposing constraints on reproductive success and output [26, 27]. Nevertheless, more than 14.5% of reptile species

still lack sufficient data to determine their threat status [28]. Moreover, limitations related to long-term data collection and geographical and taxonomic biases hinder the adequate understanding of ecological and demographic processes necessary to propose conservation actions and avoid local extinctions [29–31].

Among the lesser-studied groups, *Notomabuya frenata* (Cope, 1862) [32] stands out as a Neotropical viviparous lizard species whose populations are facing increasing pressures due to climate change [33, 34]. Lizards often have an opportunistic life strategy and a fast life history (*e.g.*, low juvenile and adult survival, low fecundity, and early maturity), making them susceptible to drastic population declines in response to demographic or environmental events, as entire generations can be compromised by unpredictable climate fluctuations [35, 36]. Therefore, here we investigate the demographic patterns of *N. frenata* in response to environmental changes by understanding its life history and estimating the impacts of different future CO_2 emission scenarios. To this end, we used estimates of vital rates and population structure to create a model of extinction risk across the species' potential geographic range. We predicted that increased CO_2 emissions would lead to reduced population growth of *N. frenata*, as the species' viviparous and ectothermic nature, combined with its fast life history, increases its vulnerability to climate change.

2. Methods

(a) Species

Notomabuya frenata is a diurnal Scincidae that measures 56.7 ± 2.0 mm snout-vent length (SVL) and forages primarily in low vegetation and shrubs, feeding on small arthropods [33, 34, 37, 38]. It ranges in the Cerrado and Chaco biomes, characterized by well-defined dry and wet seasons and low annual temperature variation, and the Atlantic Forest, where

precipitation is more evenly distributed throughout the year and temperature is relatively stable [39, 40]. The species has a life cycle exceeding one year, with overlapping generations [37]. It is viviparous, with a nine to twelve-month gestation period, and produces litters of up to eight offspring between September and November, the beginning of the rainy season [38].

(b) Sampling

We sampled lizards between December 2005 and January 2021, with a gap from April to July 2020 due to the COVID-19 pandemic. The study area comprises cerrado *sensu stricto* vegetation in the Reserva Ecológica do Roncador, within the Área de Proteção Ambiental das Bacias Gama e Cabeça de Veado, Distrito Federal, Brazil [41, 42]. A 50-ha plot was defined at the study site and subdivided into five subplots submitted to different fire regimes [43]. We installed ten pitfall traps within each subplot approximately 15 m apart. Each trap consists of four 30 L buckets connected by guide fences arranged in a “Y” shape. We checked traps monthly over six consecutive days. During trap checks and lizard captures, we recorded demographic data such as sex and body size. We took morphometric measurements, including SVL and tail length, with a ruler accurate to 1 mm, and recorded body mass with a spring scale accurate to 0.25 g. We permanently marked each captured lizard by toe-clipping and released it approximately 3 m from the capture point. All procedures were approved by the Animal Use Ethics Committee of the University of Brasília (process 33786/2016).

To assess fecundity parameters, we obtained data from 30 gravid females (SVL and number of embryos) and 83 males (SVL and testes volume) of *N. frenata* collected during the filling of the Serra da Mesa reservoir in Minaçu, Goiás, Brazil, and deposited at the Herpetological Collection from University of Brasília. We considered the SVL of the smallest

female in the sample as the size for reproductive maturity in females and the SVL of the smallest male with enlarged testes and convoluted epididymis as the size for reproductive maturity in males.

We obtained 251 occurrence records from the literature and herpetological collections to determine the species' geographic distribution (figure S1).

(c) Environmental Predictors

We sourced the environmental variables from the WorldClim database, covering the period from January 2005 to December 2020 and projections for 2021 to 2100 under two distinct socioeconomic scenarios (SSP2-4.5 and SSP5-8.5), each reflecting different CO_2 emission trajectories [44, 45]. We obtained monthly averages for maximum temperature, minimum temperature, and precipitation at a 10-minute resolution for the species' distribution with a two-degree buffer. To prevent multicollinearity issues among predictors, we calculated each variable's variance inflation factor (VIF) and excluded those with VIF values > 5 [46]. This selection process resulted in retaining two variables: maximum temperature and precipitation.

(d) Data analysis

We conducted all data analyses on R (version 4.3.3) [47]. Using body mass, sex, and tail length, we imputed SVL values when they were missing or considered outliers using the *missForest* package [48]. For the subsequent analyses, we did not consider subplot differences because we aimed to extrapolate spatially the demographic performance of *Notomabuya frenata* for its distribution range. Our subplots provide considerable

microhabitat variation to extrapolate the demographic models for other localities throughout the species range [49].

(i) Growth

After conducting normality and homoscedasticity tests on the sample, we used a Wilcoxon test to determine whether the SVL of males and females differed significantly. To describe the growth of individuals for each sex over time, we applied the Von Bertalanffy growth curve adjusted by Fabens for mark-recapture data [50]. To capture individual variation in growth rate, we fitted the model to a Non-Linear Mixed Effects Model (NLME), allowing the growth coefficient (*k*) to vary among individuals. To estimate the age of individuals at the first capture, we applied a reformulation of the Von Bertalanffy equation, isolating age:

$$a = t0 + \left(\frac{1}{k}\right) * ln\left(\frac{L\infty}{(L\infty - L)}\right) \qquad \text{(equation 1)}$$

In this equation, *a* and *L* are the age and SVL of the individual, respectively, t_0 is an estimated theoretical age when the individual's SVL is zero, *k* is the body growth coefficient, and $L\infty$ indicates the asymptotic SVL [51]. With these estimates, we built a predictive growth curve, which indicates the expected SVL of individuals in the population as a function of age.

(ii) Survival

To estimate age-specific mortality rate and survival probability for each sex, we used a Gompertz mortality model implemented in the *Bayesian Survival Trajectory Analysis* (*BaSTA*) package [52]. We built a capture history matrix to reconstruct individual mortality and survival trajectories for each sex. Additionally, we calculated the monthly survival

probability for the population using a Cormack-Jolly-Seber (CJS) capture-recapture model with the *marked* package [53, 54]. We selected the precipitation and maximum temperature estimates from Worldclim only for the pixel of our study area (15° 56' 31" S 47° 52' 47" O). We adjusted monthly survival in an additive model, relating it to precipitation and maximum temperature variation, and performed model selection based on the Akaike Information Criterion (AIC) [55]. Finally, we used a time series decomposition analysis of the observed monthly survival mean from 2005 to 2020 to identify which component better explains the variation in survival over time.

(iii) Reproduction

We considered litter size as an indicator of reproduction. We used Bayesian models fitted with the *brms* package to relate litter size (number of offspring) to the body length of reproductive females [56]. We selected the most suitable model based on the leave-one-out cross-validation (LOO) criterion.

(iv) Population growth

We used estimates of vital rates (growth, survival, and reproduction) to construct a female-based Integral Projection Model (IPM) [20] that describes the number of individuals of size *y* at time *t + 1* as follows:

$$n(y, t+1) = \int_L^U [P(x,y) + F(x,y)]n(x,t)dx$$

$$= \int_1^U K(x,y)n(x,t)dx$$

Here, *L* and *U* represent the lower and upper body size limits, respectively; *F(x, y)* is the sub-kernel describing fecundity; and *P(x, y)* is the sub-kernel representing growth conditioned on

survival, defined as $P(x, y) = S(x) + G(x, y)$, where $S(x)$ is the probability of survival for an individual of size x under given environmental conditions, and $G(x, y)$ is the probability of an individual of size x growing to size y. The kernel $K(x, y) = P(x, y) + F(x, y)$ represents the transitions of body condition and the per capita reproductive contributions, from size x to size y, between t and $t+1$.

As we estimated survival considering the environmental conditions, we built a kernel for each month from 2005 to 2100 across the species' geographic distribution. To assess population status under different environmental scenarios, we estimated the population growth rate (λ) as the dominant eigenvalue of each kernel K and obtained the mean and standard deviation of λ for five different periods (2005-2020, 2021-2040, 2041-2060, 2061-2080 and 2081-2100) [57]. Additionally, we used a time series decomposition analysis of the observed monthly mean λ from 2005 to 2020 to identify which component better explains the variation in population growth over time.

3. Results

(a) Life-history

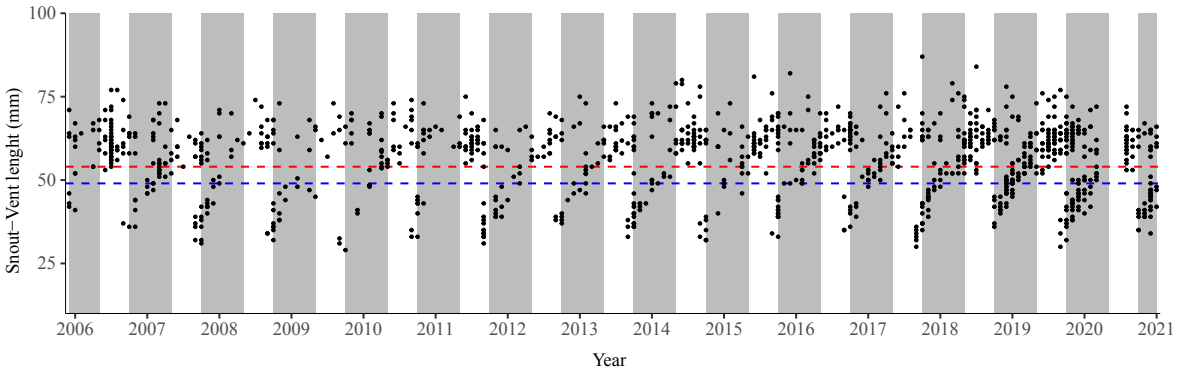

figure 1: Snout-vent length (SVL) of *Notomabuya frenata* individuals captured in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Red and blue dashed-lines represent the SVL at sexual maturity for females (54 mm) and males (49 mm), respectively. Gray bars indicate the rainy season, spanning from October to May. The y-axis markers indicate January of each year.

Over 15 years and two months of monitoring, we captured and marked 1023 individuals of *Notomabuya frenata*, of which 10 were excluded from the analyses due to data inconsistencies. A total of 838 individuals were captured only once, while 170 were captured at least twice. Adults were detected year-round, whereas juveniles were primarily observed between September and March, a period associated with the rainy season in the Cerrado (figure 1). The body sizes of adult males and females did not differ significantly (*W = 1936.5, P = 0.622*), although males reached a smaller asymptotic SVL than females ($L\infty_M$ = 70.61 ± 1.22 mm; $L\infty_F$ = 79.35 ± 2.97 mm) and grew slower (K_M = *0.070 ± 0.01;* K_F = *0.072 ± 0.01*) (figure 2).

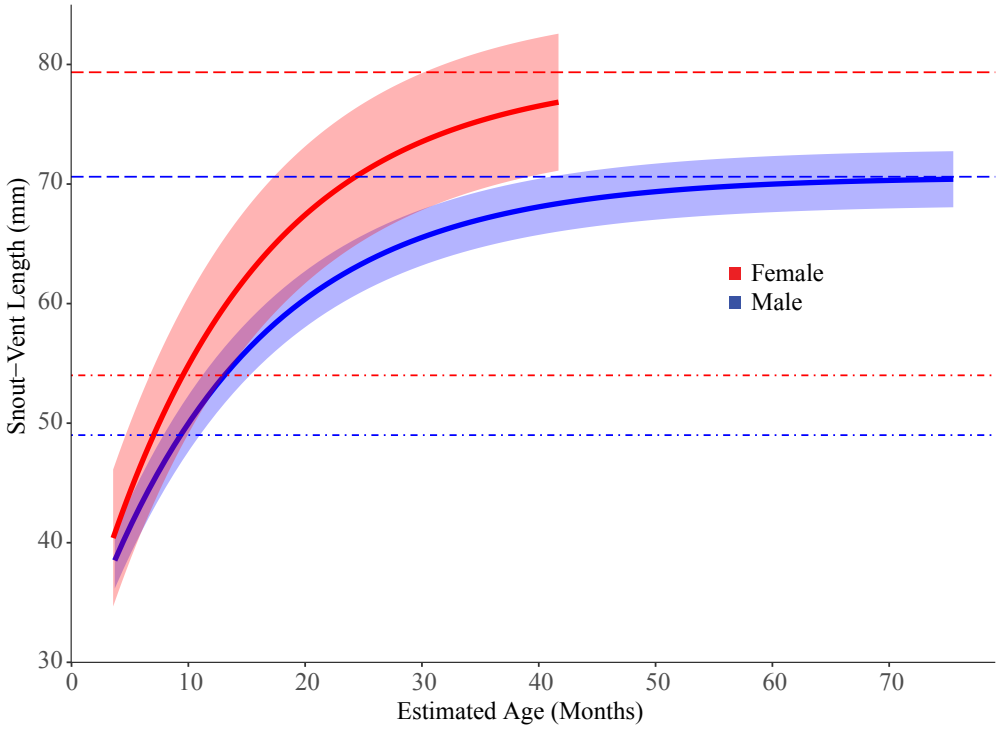

figure 2: Estimated growth curve of males (blue) and females (red) of *Notomabuya frenata* captured in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Red and blue dot-dashed lines represent the SVL at sexual maturity for females (54 mm) and males (49 mm), respectively. Red and blue dashed lines indicate the asymptotic SVL for females (79 mm) and males (71 mm), respectively.

The age-survival model converged for all parameters, and the effect of age on mortality was different between the sexes (table S1). The model indicated that males exhibit

higher initial mortality than females but a slower increase in mortality with age, suggesting that males may have a higher life expectancy than females (figure 3). The selected CJS capture-recapture model (table S2) identified an adverse effect of maximum temperature on monthly survival rates (figure 4), whereas the effect of precipitation was minimal (table S3). Regarding the temporal variation in monthly survival over the study period, the trend is more relevant than seasonality (Seasonality *= 0.04; Trend = 0.14*). However, we found no clear positive or negative trends over the period (figure S2), with the residual (random) component being much more influential (*Residual = 0.82*).

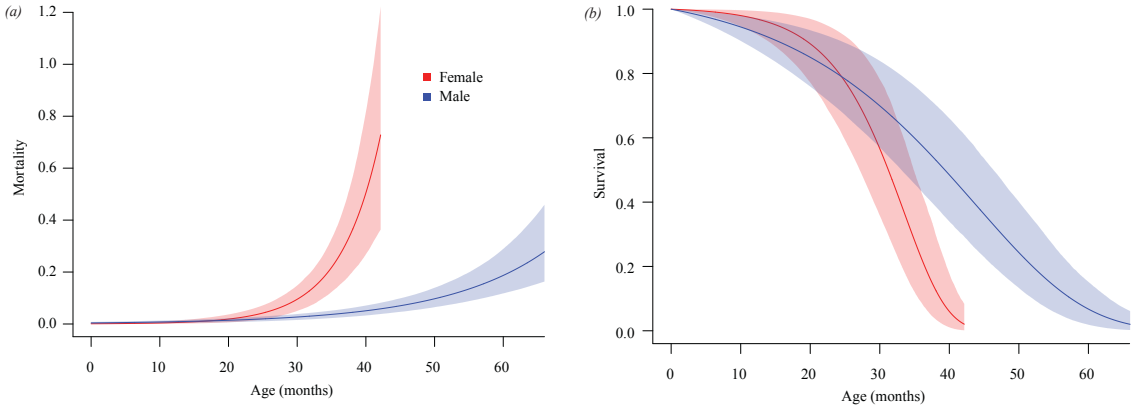

figure 3: Estimated age-specific mortality rate (a) and survival probability (b) of males (blue) and females (red) of *Notomabuya frenata* captured in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021.

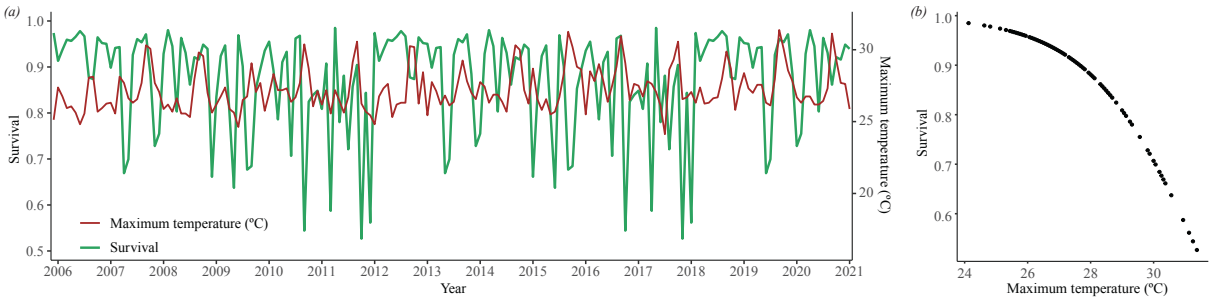

figure 4: (a) Estimated monthly survival probability of *Notomabuya frenata* and maximum air temperature in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. (b) Relationship between estimated monthly survival probability and maximum air temperature.

The smallest reproductive female had a 54 mm snout-vent length. Using equation 1, we estimated that females reach sexual maturity at six months. Males, in turn, reach sexual maturity at 49 mm, corresponding to seven months of age. Consequently, the generation

time for this species is approximately two years, considering a gestation period of 9 to 12 months [38]. The fecundity model showed no significant relationship between female SVL and litter size, although a positive trend was observed (table S4 and figure S3).

(b) Population growth

The seasonal component accounted for 99% of the temporal variation in the population growth over the study period, with the highest λ values associated with the rainy season, while the trend and random components explained less than 1% of the observed variation (figure S4 and figure S5). The geometric mean of λ between December 2005 and January 2021 for the monitored population was 1.01, indicating that it remained stable throughout the monitoring period. Spatial projections showed that populations of *Notomabuya frenata* should experience greater growth to the south and southeast of the distribution, regions where the maximum temperatures are lower (figure 5a and figure S6). We observed changes in future projections compared to the present, with a more pronounced decline related to the high CO_2 emission scenario (SSP5-8.5) (figure 8), in which λ values tend to decline more sharply to the northwest of the species' distribution (figure 6 and figure 7). The standard deviation of λ was small and increased towards the periphery of the species distribution (figure 5, figure 6 and figure 7).

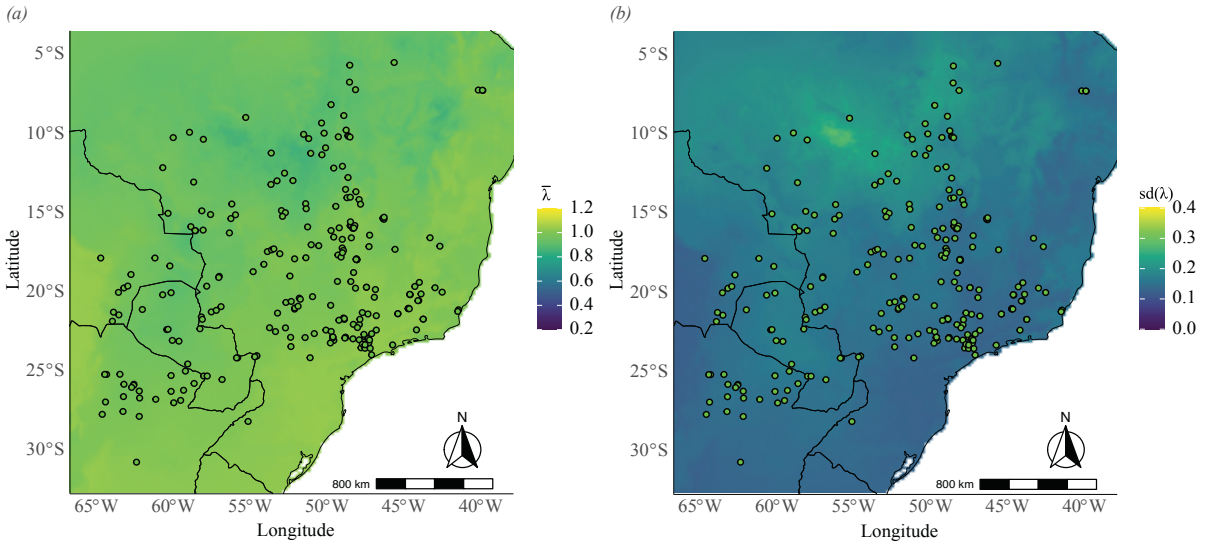

figure 5: Projected mean (a) and standard deviation (b) of population growth rate (*λ*) of *Notomabuya frenata* for the period 2005-2020. Green dots indicate occurrence points of *N. frenata*.

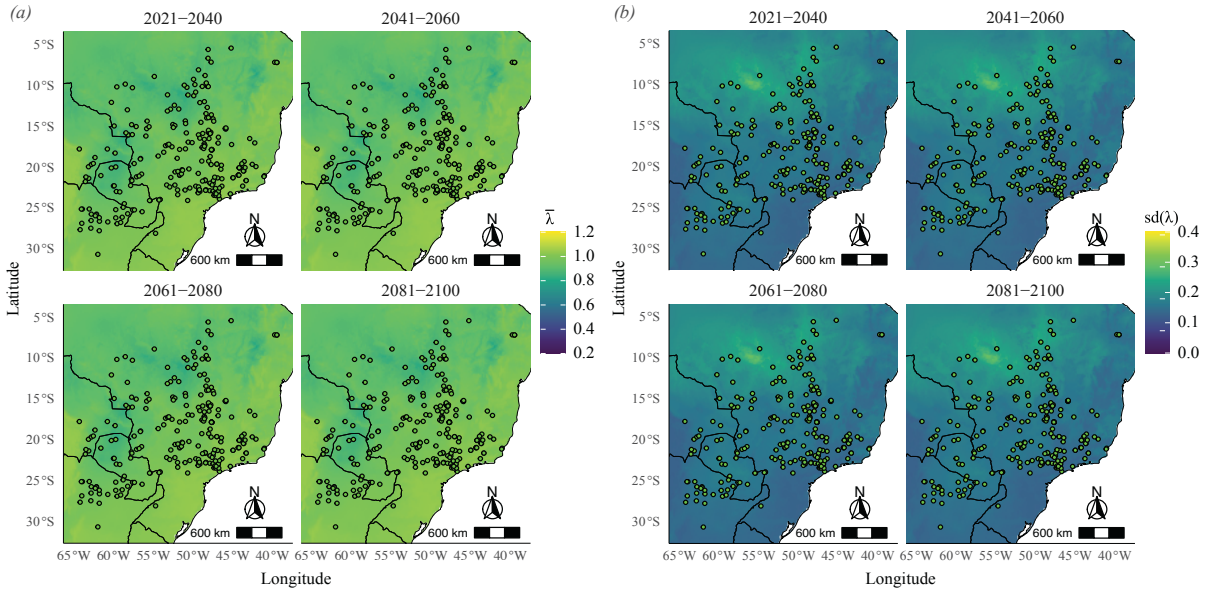

figure 6: Projected mean (a) and standard deviation (b) of population growth rate (*λ*) of *Notomabuya frenata* for the period 2021–2100 under an optimistic CO_2 emission scenario (SSP2-4.5). Green dots indicate occurrence points of *N. frenata*.

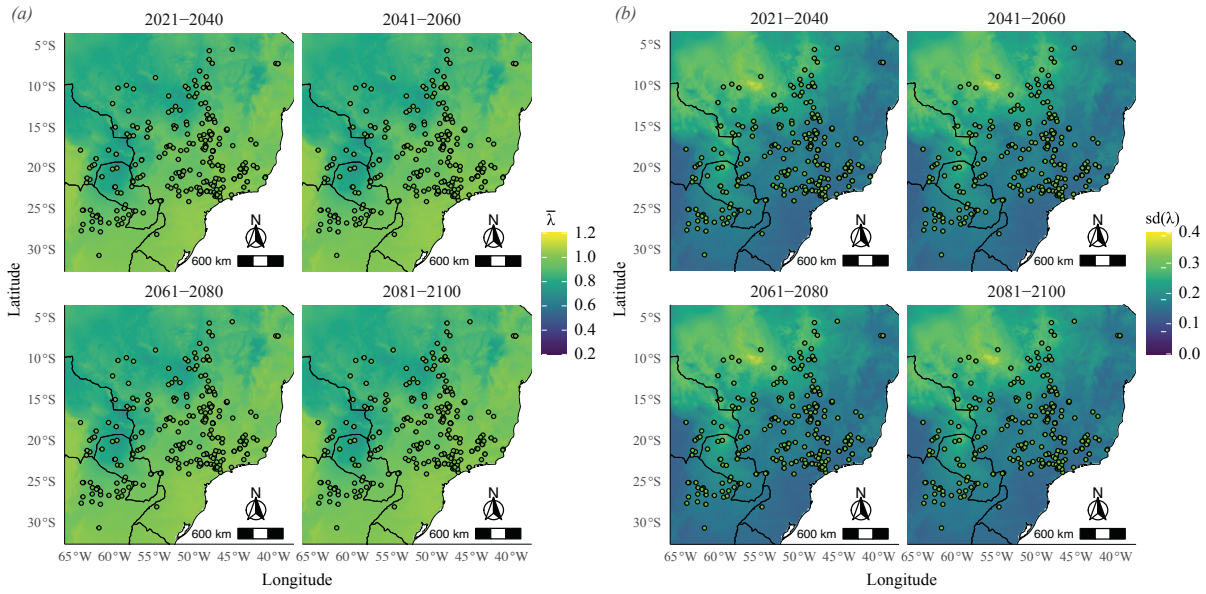

figure 7: Projected mean (a) and standard deviation (b) of population growth rate (*λ*) of *Notomabuya frenata* for the period 2021–2100 under a pessimistic CO_2 emission scenario (SSP5-8.5). Green dots indicate occurrence points of *N. frenata*.

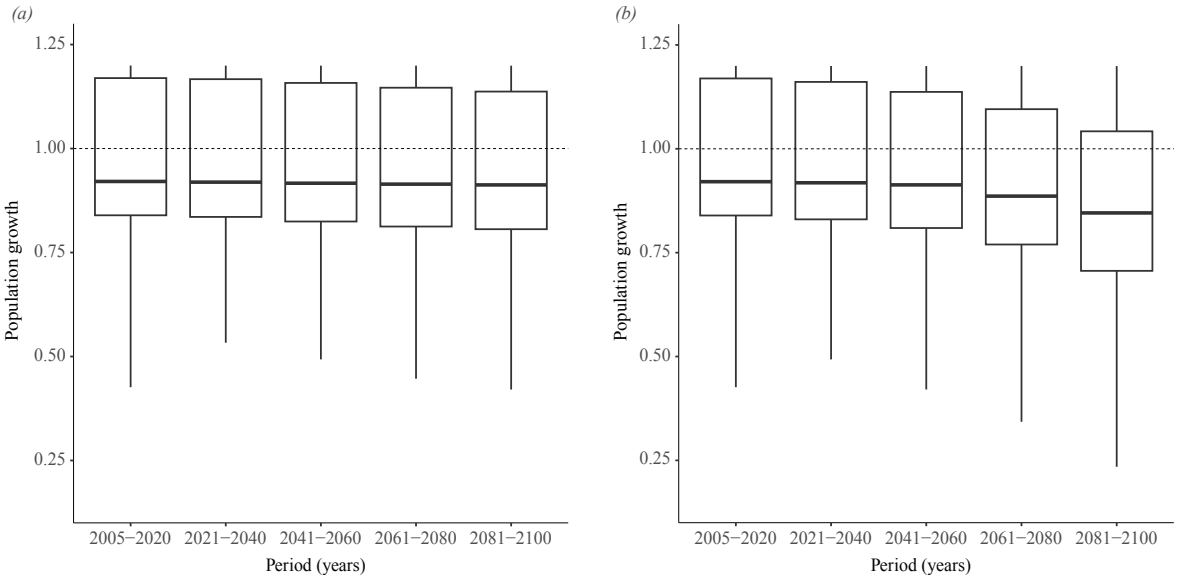

figure 8: Boxplots describing the distribution of the projected mean population growth rate (*λ*) of *Notomabuya frenata* for five different periods (2005-2020, 2021-2040, 2041-2060, 2061-2080 and 2081-2100) under an optimistic CO_2 emission scenario (SSP2-4.5) (a) and a pessimistic CO_2 emission scenario (SSP5-8.5) (b).

4. Discussion

The divergence in size and mortality between sexes is a key life-history trait in *Notomabuya frenata*, as it is strongly linked to viviparity [37, 38, 58]. Females face higher growth and mortality rates compared to males. While faster growth enables them to reach

larger sizes, allowing them to carry more embryos, the added body mass and physiological changes during pregnancy might increase predation risk due to impaired mobility [59–61]. These traits can be associated with an energy trade-off favoring reproduction (reaching sexual maturity earlier) over longevity in females. In what concerns males, in addition to attaining sexual maturity at a smaller SVL than females, they achieve maturity later in life, reflecting much lower energy allocation to growth. This pattern suggests that males may prioritize energy investment in survival, enabling them to mate with multiple females and potentially compensating for the prolonged gestation period of each female [62]. Thus, while females allocate substantial energy to a single litter over an extended period, males invest in maximizing their reproductive lifespan. This pattern highlights how reproduction imposes more significant survival costs on females than males of this viviparous species [37, 38, 63].

Nevertheless, *Notomabuya frenata* maintains high juvenile and low adult survival across both sexes, resulting in a population structure skewed toward younger individuals. Such demographic skew may reflect a life-history strategy prioritizing juvenile survival and early reproductive success [64, 65]. Low adult survival may not constrain population growth in this context, as the strategy relies on maintaining a juvenile pool to offset adult mortality and achieving early sexual maturity to enhance lifetime reproductive success [62, 66, 67]. Additionally, compared to other vertebrates, this species exhibits a high population turnover and a short lifespan, as individuals rarely live beyond five years [35, 64]. Despite this, populations show generation overlap, given that the generation time is approximately two years. Other oviparous lizard species from the Cerrado savannas rarely survive more than one reproductive cycle [12, 43]. In contrast, viviparous species, such as *N. frenata*, have high selective pressures to survive more reproductive cycles to enhance reproductive output [68, 69].

Considering their early maturity, small litter sizes, and low survivorship relative to other vertebrates, these lizards are positioned near the “fast” end of the “slow-fast” life-history continuum, characterizing them as an opportunistic species [35]. Fast-living species tend to be more vulnerable to rapid environmental changes and stochastic events as they experience considerable population declines in response to disturbances [2, 3]. Conversely, they possess a higher potential for rapid population growth, enabling their populations to recover from declines more effectively if favorable conditions are restored. [65]. By doing so, in fluctuating environments, where temperatures are constantly increasing and precipitation is decreasing, these species will rely on phenotypic plasticity or evolutionary adaptations [70, 71].

As documented in our censuses and previous studies on the species [33, 38], there is an overlap between the rainy season and the detection period of juveniles, the group with the highest survival rates. In markedly seasonal environments—like those inhabited by *Notomabuya frenata*—reproductive success and offspring fitness may be influenced by seasonality [58, 72]. Therefore, for young lizards that grow rapidly to achieve early sexual maturity, precipitation likely plays a critical role in survival by enhancing food availability during the peak growth period, leading to higher survival probabilities until maturation [38, 58]. Consequently, rapid changes in rainfall regimes may lead to population declines by compromising juvenile fitness and survival. These impacts are likely to be even more pronounced in a population demographically skewed toward juveniles, as it is expected that the juvenile pool compensates for elevated adult mortality.

Finally, we found no significant correlation between litter size and female body size. Previous studies on *Notomabuya frenata* or phylogenetically related species show that this correlation can be small and even vary among populations [37, 38, 72]. Variation in litter size

may be better explained by female age and, consequently, by differences in energy allocation between reproduction and growth throughout their lifespan, rather than by female body length [38].

In what concerns to the time series decomposition of monthly λ from 2005 to 2020, the seasonal component was the most significant, accounting for 99% of the variation in population growth over time. The highest λ values occurred during the rainy season, emphasizing the cyclic reproductive period. Moreover, this finding highlights how the population growth of *Notomabuya frenata* relies on maintaining a juvenile pool rather than investing in a prolonged reproductive lifespan, a characteristic commonly associated with species exhibiting accelerated life-history strategies [1].

Regarding temporal variation in monthly survival, extreme peaks in maximum temperature negatively affect survival on *Notomabuya frenata* (figure 3). Temperature increases could narrow the species' thermal safety margin, strongly impacting its physiological performance and time for activity, and potentially impairing survival and reproduction [73, 74]. Given that population growth is largely dependent on survival, global temperature increases, especially the occurrence of extreme temperature events, may jeopardize the persistence of *N. frenata*.

By integrating biological and climatic characteristics, IPMs allow predictions of how organisms may or may not adapt to variable conditions within their distribution ranges [17, 20]. In the northwest, the projected mean λ is lower but exhibits greater fluctuation (higher standard deviation) in response to environmental variability. A high standard deviation at the periphery suggests low phenotypic plasticity in the species. However, the species seems to persist in these areas, which would imply that peripheral populations may respond differently to environmental conditions than central populations. Alternatively, our results

indicate an ongoing shift toward the southeast in suitable areas, as has already been projected for other species inhabiting the Cerrado [75–77]. If the species' adaptive response capacity is outpaced by the rate of climate change, the species' distribution in the northwest may contract and will continue to decrease in the coming decades [78].

The spatially explicit approach we applied enables an understanding of the demographic consequences of climate-induced environmental variability across different locations, recognizing that the impacts of climate change are unevenly distributed. Despite its importance for accurately assessing species extinction risks in the face of accelerated environmental changes, such approaches integrating long-term census data remain scarce. Our work indicates that this fast-paced life-history species is already experiencing impacts from the increase in global mean temperature and the reduction in rainy periods, which compromise individuals' reproduction and survival, ultimately reducing population growth, particularly at the periphery of its distribution.

Finally, the observed differences in energy allocation to growth and survival between sexes suggest that environmental conditions may exert distinct effects on males and females of *Notomabuya frenata*. Additionally, as a viviparous ectothermic organism, temperature affects growth and the production of viable offspring. Since we considered temperature as a predictor only for survival, it is possible that population growth is being overestimated. Further analyses are therefore necessary to understand better the impacts of climate change on viviparous ectothermic populations.

References

[1] Stearns SC. 1976 Life-history tactics: A review of the ideas. The Quarterly Review of Biology. 51:3–47. https://doi.org/10.1086/409052.

[2] Jeppsson T, Forslund P. 2012 Can life history predict the effect of demographic stochasticity on extinction risk? The American Naturalist. 179:706–20. https://doi.org/10.1086/665696.

[3] Sæther B-E, Coulson T, Grøtan V, Engen S, Altwegg R, Armitage KB, Barbraud C, Becker PH, Blumstein DT, et al. 2013 How life history influences population dynamics in fluctuating environments. The American Naturalist. 182:743–59. https://doi.org/10.1086/673497.

[4] Cowie RH, Bouchet P, Fontaine B. 2022 The sixth mass extinction: Fact, fiction or speculation? Biological Reviews. 97:640–63. https://doi.org/10.1111/brv.12816.

[5] Finn C, Grattarola F, Pincheira-Donoso D. 2023 More losers than winners: Investigating Anthropocene defaunation through the diversity of population trends. Biological Reviews. 98:1732–48. https://doi.org/10.1111/brv.12974.

[6] Selwood KE, McGeoch MA, Mac Nally R. 2015 The effects of climate change and land-use change on demographic rates and population viability. Biological Reviews. 90:837–53. https://doi.org/10.1111/brv.12136.

[7] IPBES. 2019 Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo. . https://doi.org/10.5281/zenodo.3553579.

[8] Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Guangchun L, Wilmshurst JM. 2017 Biodiversity losses and conservation responses in the Anthropocene. Science. 356:270–5. https://doi.org/10.1126/science.aam9317.

[9] Strona G, Bradshaw CJA. 2022 Coextinctions dominate future vertebrate losses from climate and land use change. Science Advances. 8:eabn4345. https://doi.org/10.1126/sciadv.abn4345.

[10] Barras AG, Blache S, Schaub M, Arlettaz R. 2021 Variation in demography and life-history strategies across the range of a declining mountain bird species. Frontiers in Ecology and Evolution. 9:780706. https://doi.org/10.3389/fevo.2021.780706.

[11] Gamelon M, Grøtan V, Nilsson ALK, Engen S, Hurrell JW, Jerstad K, Phillips AS, Røstad OW, Slagsvold T, et al. 2017 Interactions between demography and environmental effects are important determinants of population dynamics. Science Advances. 3:e1602298. https://doi.org/10.1126/sciadv.1602298.

[12] de Sousa HC, Malvasio A, Colli GR, Salguero-Gómez R. 2024 Severe fire regimes decrease resilience of ectothermic populations. Journal of Animal Ecology. 93:1656–69. https://doi.org/10.1111/1365-2656.14188.

[13] Koons DN, Grand JB, Arnold JM. 2006 Population momentum across vertebrate life histories. Ecological Modelling. 197:418–30. https://doi.org/10.1016/j.ecolmodel.2006.03.034.

[14] Clutton-Brock T, Sheldon BC. 2010 Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution. 25:562–73. https://doi.org/10.1016/j.tree.2010.08.002.

[15] Proença V, Martin LJ, Pereira HM, Fernandez M, McRae L, Belnap J, Böhm M, Brummitt N, García-Moreno J, et al. 2017 Global biodiversity monitoring: From data sources to Essential Biodiversity Variables. Biological Conservation. 213:256–63. https://doi.org/10.1016/j.biocon.2016.07.014.

[16] Ellner SP, Rees M. 2006 Integral projection models for species with complex demography. The American Naturalist. 167:410–28. https://doi.org/10.1086/499438.

[17] Merow C, Dahlgren JP, Metcalf CJE, Childs DZ, Evans MEK, Jongejans E, Record S, Rees M, Salguero-Gómez R, et al. 2014 Advancing population ecology with integral projection models: A practical guide. Methods in Ecology and Evolution. 5:99–110. https://doi.org/10.1111/2041-210X.12146.

[18] Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA. 2014 On using integral projection models to generate demographically driven predictions of species' distributions: Development and validation using sparse data. Ecography. 37:1167–83. https://doi.org/10.1111/ecog.00839.

[19] Easterling MR, Ellner SP, Dixon PM. 2000 Size-specific sensitivity: Applying a new structured population model. Ecology. 81:694–708. https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2.

[20] Rees M, Childs DZ, Ellner SP. 2014 Building integral projection models: A user's guide. Journal of Animal Ecology. 83:528–45. https://doi.org/10.1111/1365-2656.12178.

[21] Doucette LI, Duncan RP, Osborne WS, Evans M, Georges A, Gruber B, Sarre SD. 2023 Climate warming drives a temperate-zone lizard to its upper thermal limits, restricting activity, and increasing energetic costs. Scientific Reports. 13:9603. https://doi.org/10.1038/s41598-023-35087-7.

[22] Gibbon JW, Scott DE, Ryan TJ, Buhlmann KA, Tuberville TD, Metts BS, Greene JL, Mills T, Leiden Y, et al. 2000 The global decline of reptiles, déjà vu amphibians. BioScience. 50:653. https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2.

[23] Paaijmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, Murdock CC, Thomas MB. 2013 Temperature variation makes ectotherms more sensitive to climate change. Global Change Biology. 19:2373–80. https://doi.org/10.1111/gcb.12240.

[24] Shine R. 2005 Life-history evolution in reptiles. Annual Review of Ecology, Evolution, and Systematics. 36:23–46. https://doi.org/10.1146/annurev.ecolsys.36.102003.152631.

[25] Shine R. 2014 Evolution of an evolutionary hypothesis: A history of changing ideas about the adaptive significance of viviparity in reptiles. Journal of Herpetology. 48:147–61. https://doi.org/10.1670/13-075.

[26] Lourdais O, Shine R, Bonnet X, Guillon M, Naulleau G. 2004 Climate affects embryonic development in a viviparous snake, *Vipera aspis*. Oikos. 104:551–60. https://doi.org/10.1111/j.0030-1299.2004.12961.x.

[27] Jara M, García-Roa R, Escobar LE, Torres-Carvajal O, Pincheira-Donoso D. 2019 Alternative reproductive adaptations predict asymmetric responses to climate change in lizards. Scientific Reports. 9:5093. https://doi.org/10.1038/s41598-019-41670-8.

[28] IUCN. 2024 The IUCN Red List of Threatened Species. IUCN Red List of Threatened Species. . https://www.iucnredlist.org/en (accessed October 25, 2024).

[29] Roll U, Feldman A, Novosolov M, Allison A, Bauer AM, Bernard R, Böhm M, Castro-Herrera F, Chirio L, et al. 2017 The global distribution of tetrapods reveals a need for targeted reptile conservation. Nature Ecology & Evolution. 1:1677–82. https://doi.org/10.1038/s41559-017-0332-2.

[30] Winter M, Fiedler W, Hochachka WM, Koehncke A, Meiri S, De la Riva I. 2016 Patterns and biases in climate change research on amphibians and reptiles: A systematic review. Royal Society Open Science. 3:160158. https://doi.org/10.1098/rsos.160158.

[31] Caetano GHDO, Chapple DG, Grenyer R, Raz T, Rosenblatt J, Tingley R, Böhm M, Meiri S, Roll U. 2022 Automated assessment reveals that the extinction risk of reptiles is widely underestimated across space and phylogeny. PLOS Biology. 20:e3001544. https://doi.org/10.1371/journal.pbio.3001544.

[32] Cope ED. 1862 Contributions to Neotropical saurology. Proceedings of the Academy of Natural Sciences of Philadelphia. 14:176–88.

[33] Machado LPC, Caetano GH de O, Cavalcante VHL, Miles DB, Colli GR. 2023 Climate change shrinks environmental suitability for a viviparous Neotropical skink. Conservation Science and Practice. 5:e12895. https://doi.org/10.1111/csp2.12895.

[34] Ribeiro-Júnior M, Amaral S. 2016 Diversity, distribution, and conservation of lizards (Reptilia: Squamata) in the Brazilian Amazonia. Neotropical Biodiversity. 2:195–421. https://doi.org/10.1080/23766808.2016.1236769.

[35] Mesquita DO, Faria RG, Colli GR, Vitt LJ, Pianka ER. 2016 Lizard life-history strategies. Austral Ecology. 41:1–5. https://doi.org/10.1111/aec.12276.

[36] Traill LW, Brook BW, Frankham RR, Bradshaw CJA. 2010 Pragmatic population viability targets in a rapidly changing world. Biological Conservation. 143:28–34. https://doi.org/10.1016/j.biocon.2009.09.001.

[37] Vitt LJ. 1991 An introduction to the ecology of Cerrado lizards. Journal of Herpetology. 25:79. https://doi.org/10.2307/1564798.

[38] Vrcibradic D, Rocha CFD. 1998 Reproductive cycle and life-history traits of the viviparous skink *Mabuya frenata* in Southeastern Brazil. Copeia. 1998:612. https://doi.org/10.2307/1447791.

[39] Vrcibradic D, Almeida-Gomes M, Borges Junior V, Kiefer M, Van Sluys M, Rocha C. 2006 Reptilia, Scincidae, *Mabuya frenata* distribution extension. Check List. 2:57. https://doi.org/10.15560/2.2.57.

[40] Nimer E. 1989 Climatologia do Brasil. 2nd ed. Rio de Janeiro: IBGE, Departamento de Recursos Naturais e Estudos Ambientais.

[41] Ribeiro JF, Walter BMT. 2008 As principais fitofisionomias do bioma cerrado. Cerrado: Ecologia e Flora. vol. 2. Brasília, DF: Embrapa Cerrados.

[42] Andrade LA, Felfili JM, Violatti L. 2002 Fitossociologia de uma área de cerrado denso na RECOR-IBGE, Brasília-DF. Acta Botânica Brasílica. 16:225–40. https://doi.org/10.1590/S0102-33062002000200009.

[43] de Sousa HC, Soares AHSB, Costa BM, Pantoja DL, Caetano GH, Queiroz TA de, Colli GR. 2015 Fire regimes and the demography of the lizard *Micrablepharus atticolus* (Squamata, Gymnophthalmidae) in a biodiversity hotspot. South American Journal of Herpetology. 10:143–56. https://doi.org/10.2994/SAJH-D-15-00011.1.

[44] Calvin K, Dasgupta D, Krinner G, Mukherji A, Thorne PW, Trisos C, Romero J, Aldunce P, Barrett K, et al. 2023 IPCC, 2023: Climate change 2023: Synthesis report. Intergovernmental Panel on Climate Change. . https://doi.org/10.59327/IPCC/AR6-9789291691647.

[45] Riahi K, Van Vuuren DP, Kriegler E, Edmonds J, O'Neill BC, Fujimori S, Bauer N, Calvin K, Dellink R, et al. 2017 The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Global Environmental Change. 42:153–68. https://doi.org/10.1016/j.gloenvcha.2016.05.009.

[46] Shrestha N. 2020 Detecting multicollinearity in regression analysis. American Journal of Applied Mathematics and Statistics. 8:39–42. https://doi.org/10.12691/ajams-8-2-1.

[47] R Core Team. 2024 R: A language and environment for statistical computing.

[48] Stekhoven DJ, Buehlmann P. 2012 MissForest - non-parametric missing value imputation for mixed-type data. Bioinformatics. 28:112–8. https://doi.org/10.1093/bioinformatics/btr597.

[49] Costa BM, Pantoja DL, Sousa HC, de Queiroz TA, Colli GR. 2020 Long-term, fire-induced changes in habitat structure and microclimate affect Cerrado lizard communities. Biodiversity and Conservation. 29:1659–81. https://doi.org/10.1007/s10531-019-01892-8.

[50] Fabens A. 1965 Properties and fitting of the Von Bertalanffy growth curve. Growth. 29:265–89.

[51] Campbell NA, Phillips BF. 1972 The Von Bertalanffy growth curve and its application to capture recapture data in fisheries biology. ICES Journal of Marine Science. 34:295–9. https://doi.org/10.1093/icesjms/34.2.295.

[52] Colchero F, Jones OR, Rebke M. 2012 BaSTA: An R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. Methods in Ecology and Evolution. 3:466–70. https://doi.org/10.1111/j.2041-210X.2012.00186.x.

[53] Cormack RM. 1964 Estimates of survival from the sighting of marked animals. Biometrika. 51:429–38. https://doi.org/10.2307/2334149.

[54] Laake JL, Johnson DS, Conn PB. 2013 marked: An R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture-recapture data. Methods in Ecology and Evolution. 4:885–90. https://doi.org/10.1111/2041-210X.12065.

[55] Akaike H. 1998 Information theory and an extension of the maximum likelihood principle. In: Parzen E, Tanabe K, Kitagawa G, editors. Selected Papers of Hirotugu

Akaike. , New York, NY: Springer New York, p. 199–213. https://doi.org/10.1007/978-1-4612-1694-0_15.

[56] Buerkner P-C. 2017 brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software. 80:1–28. https://doi.org/10.18637/jss.v080.i01.

[57] Caswell H. 2000 Matrix Population Models. vol. 1. 2nd ed. Sunderland, MA: Sinauer.

[58] Ortiz MA, Boretto JM, Ibargüengoytía NR. 2019 Reproductive biology of a viviparous lizard (*Mabuya dorsivittata*) from the subtropical Wet Chaco of Argentina: geographical variations in response to local environmental pressures. Anais Da Academia Brasileira de Ciências. 91:e20170817. https://doi.org/10.1590/0001-3765201920170817.

[59] Bauwens D, Thoen C. 1981 Escape tactics and vulnerability to predation associated with reproduction in the lizard Lacerta Vivipara. Journal of Animal Ecology. 50:733–43. https://doi.org/10.2307/4133.

[60] Olsson M, Shine R, Bak-Olsson E. 2000 Locomotor impairment of gravid lizards: Is the burden physical or physiological? Journal of Evolutionary Biology. 13:263–8. https://doi.org/10.1046/j.1420-9101.2000.00162.x.

[61] Vitt LJ, Congdon JD. 1978 Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. The American Naturalist. 112:595–608. https://doi.org/10.1086/283300.

[62] Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual conflict and the evolution of ageing and life span. Functional Ecology. 22:443–53. https://doi.org/10.1111/j.1365-2435.2008.01417.x.

[63] Sluys MV. 1998 Growth and body condition of the saxicolous lizard *Tropidurus itambere* in southeastern Brazil. Journal of Herpetology. 32:359. https://doi.org/10.2307/1565450.

[64] Jones OR, Scheuerlein A, Salguero-Gómez R, Camarda CG, Schaible R, Casper BB, Dahlgren JP, Ehrlén J, García MB, et al. 2014 Diversity of ageing across the tree of life. Nature. 505:169–73. https://doi.org/10.1038/nature12789.

[65] Allen WL, Street SE, Capellini I. 2017 Fast life history traits promote invasion success in amphibians and reptiles. Ecology Letters. 20:222–30. https://doi.org/10.1111/ele.12728.

[66] James A, Hann A, Holland EP. 2023 Brood size in an uncertain world. Royal Society Open Science. 10:221362. https://doi.org/10.1098/rsos.221362.

[67] Travers LM, Garcia-Gonzalez F, Simmons LW. 2015 Live fast die young life history in females: evolutionary trade-off between early life mating and lifespan in female *Drosophila melanogaster*. Scientific Reports. 5:15469. https://doi.org/10.1038/srep15469.

[68] Recknagel H, Elmer KR. 2019 Differential reproductive investment in co-occurring oviparous and viviparous common lizards (*Zootoca vivipara*) and implications for life-history trade-offs with viviparity. Oecologia. 190:85–98. https://doi.org/10.1007/s00442-019-04398-w.

[69] Gunderson DR. 1997 Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Canadian Journal of Fisheries and Aquatic Sciences. 54:990–8. https://doi.org/10.1139/f97-019.

[70] Seebacher F, White CR, Franklin CE. 2015 Physiological plasticity increases resilience of ectothermic animals to climate change. Nature Climate Change. 5:61–6. https://doi.org/10.1038/nclimate2457.

[71] Hofmann GS, Cardoso MF, Alves RJV, Weber EJ, Barbosa AA, de Toledo PM, Pontual FB, Salles L de O, Hasenack H, et al. 2021 The Brazilian Cerrado is becoming hotter and drier. Global Change Biology. 27:4060–73. https://doi.org/10.1111/gcb.15712.

[72] Vitt LJ, Blackburn DG. 1991 Ecology and life history of the viviparous lizard *Mabuya bistriata* (scincidae) in the Brazilian Amazon. Copeia. 1991:916. https://doi.org/10.2307/1446087.

[73] Taylor EN, Diele-Viegas LM, Gangloff EJ, Hall JM, Halpern B, Massey MD, Rödder D, Rollinson N, Spears S, et al. 2021 The thermal ecology and physiology of reptiles and amphibians: A user's guide. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology. 335:13–44. https://doi.org/10.1002/jez.2396.

[74] Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Álvarez Pérez HJ, Garland T. 2009 Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B: Biological Sciences. 276:1939–48. https://doi.org/10.1098/rspb.2008.1957.

[75] Marini MA, Barbet-Massin M, Lopes LE, Jiguet F. 2009 Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. Biological Conservation. 142:3039–50. https://doi.org/10.1016/j.biocon.2009.08.002.

[76] Oliveira JS, Santana DJ, Pantoja DL, Ceron K, Guedes TB. 2024 Climate change in open environments: Revisiting the current distribution to understand and safeguard the future of psammophilous squamates of the Diagonal of Open Formations of South America. Journal of Arid Environments. 220:105117. https://doi.org/10.1016/j.jaridenv.2023.105117.

[77] Diniz-Filho JAF, Collevatti RG, Chaves LJ, Soares TN, Nabout JC, Rangel TF, Melo DB, Lima JS, Telles MPC. 2012 Geographic shifts in climatically suitable areas and loss of

genetic variability in *Dipteryx alata* (”Baru” Tree; Fabaceae). Genetics and Molecular Research. 11:1618–26. https://doi.org/10.4238/2012.June.15.11.

[78] Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biology. 8:e1000357. https://doi.org/10.1371/journal.pbio.1000357.

Supplementary Material

Table S1: Age-specific mortality rate and survival probability analysis of *Notomabuya frenata* captured in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Values represent estimates of survival parameters and covariates of the age-survival model for males and females. SE: Standard Error; CI: Confidence Interval.

	Estimate (SE)	**95% CI (Low)**	**95% CI (High)**
Males			
Intercept	- 5.58 (0.46)	- 6.63	- 4.82
Age	0.06 (0.01)	0.05	0.08
Females			
Intercept	- 7.38 (0.87)	- 9.30	- 5.91
Age	0.17 (0.02)	0.12	0.22

Table S2: Best Cormack-Jolly-Seber models estimating the probabilities of survival (*Φ*) and recapture (*p*) of *Notomabuya frenata* in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021, constrained by climate variables. Precip: precipitation; tmax: maximum air temperature; AICc: Akaike information criterion corrected for small sample size.

Model	**AICc**	**ΔAIC**
Φ(~ tmax) p(~ precip)	1827.30	0.00
Φ(~ tmax) p(~ tmax)	1827.47	0.17
Φ(~ tmax) p(~ tmax + precip)	1827.51	0.21
Φ(~ tmax + precip) p(~ precip)	1829.02	1.72
Φ(~ tmax) p(~ 1)	1829.03	1.74
Φ(~ tmax + precip) p(~ tmax)	1829.46	2.17
Φ(~ tmax + precip) p(~ tmax + precip)	1829.50	2.20

Table S3: Monthly survival analysis of *Notomabuya frenata* in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Values represent estimates of survival parameters and covariates of the Cormack-Jolly-Seber model *Φ(~ tmax) p(~ precip)*. Coefficients (*β*) *Φ*: probability of survival, p: probability of capture. Precip: precipitation; tmax: maximum air temperature; SE: Standard Error; CI: Confidence Interval.

	Estimate (SE)	**95% CI (Low)**	**95% CI (High)**
Φ			
Intercept	17.73758 (3.79660)	10.29622	25. 17893
tmax	- 0.56193 (0.13309)	- 0.82279	- 3.01067
p			
Intercept	- 3.65153 (0.14159)	- 3.92905	3.37400
precip	- 0.00157 (0.00083)	- 0.00319	0.00005

Table S4: Size-specific litter size of *Notomabuya frenata* in Minaçu, Goiás, Brazil. Values represent estimates of fecundity parameters and covariates of the *brms* model ~ *SVL*. SVL: snout-vent length; SE: Standard Error; CI: Confidence Interval.

	Estimate (SE)	**95% CI (Low)**	**95% CI (High)**
Intercept	- 0.26 (1.08)	- 2.37	1.82
SVL	0.02 (0.02)	- 0.01	0.06

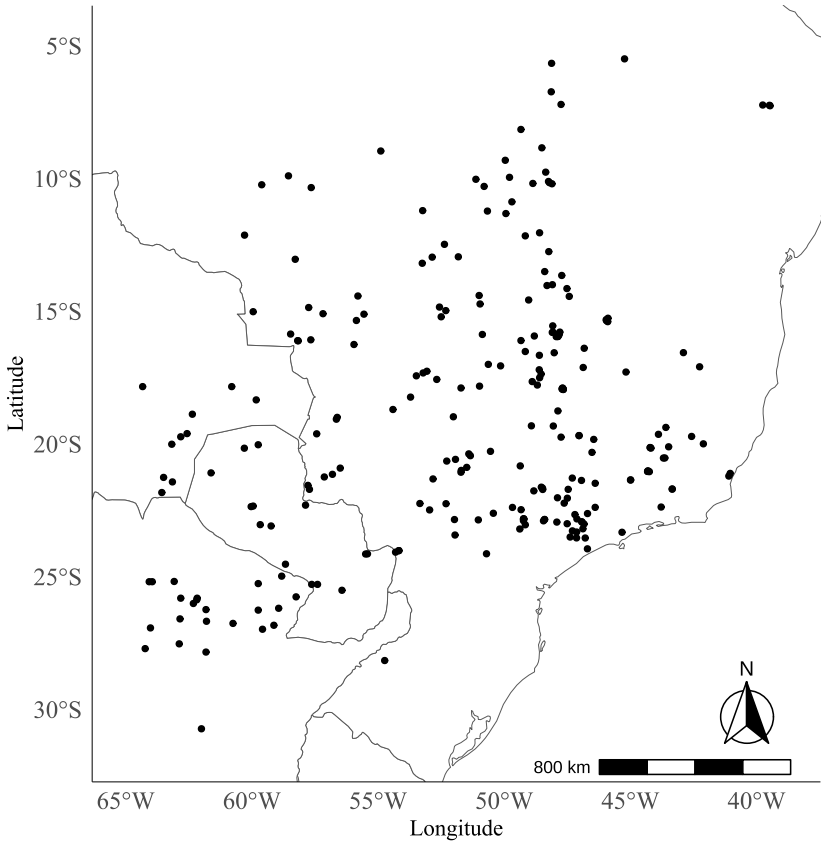

figure S1: Geographic region of the study, showing occurrence points of *Notomabuya frenata*.

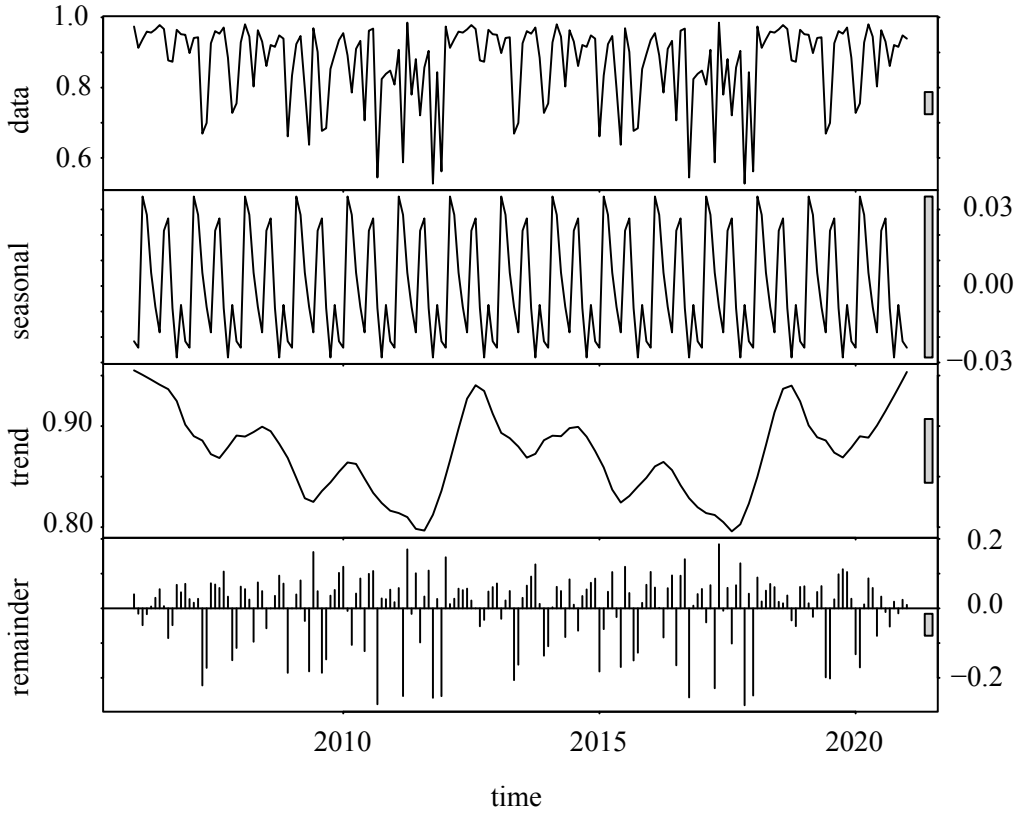

figure S2: Decomposition of the time series of estimated monthly survival of *Notomabuya frenata* in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Seasonal effect: 0.04; trend effect: 0.14; remainder effect: 0.82.

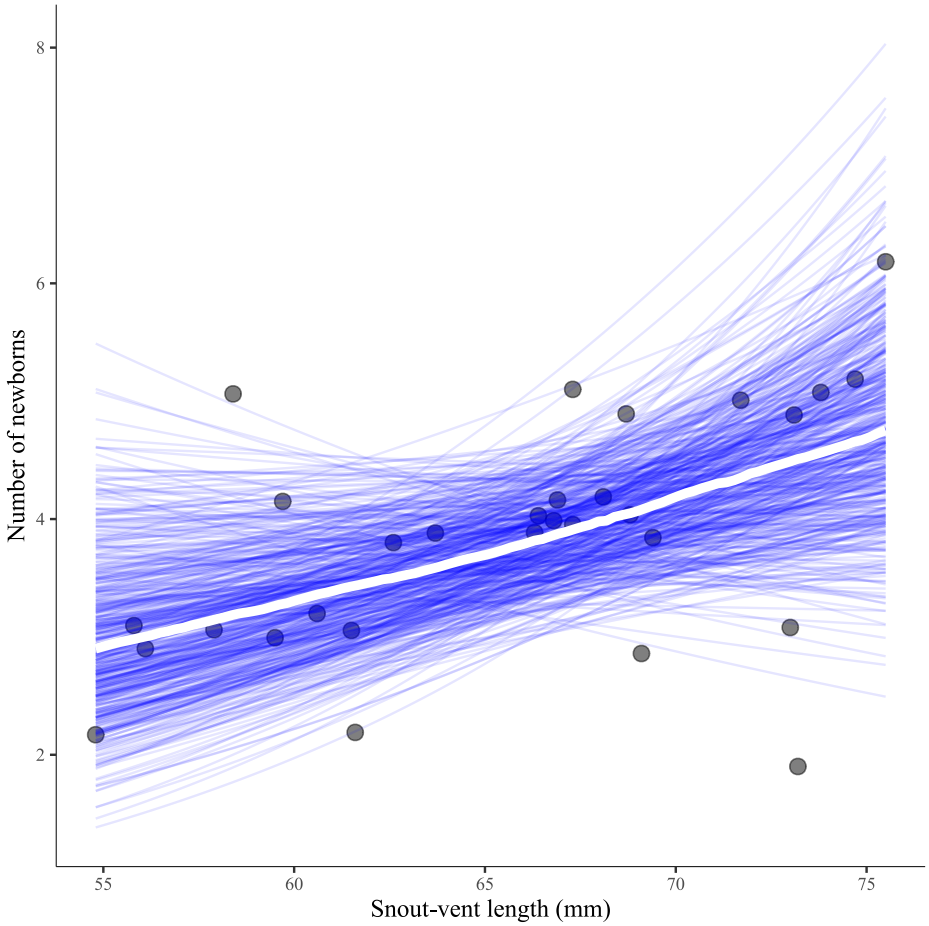

figure S3: Relationship between litter size and female snout-vent length (SVL) in adult *Notomabuya frenata* at Minaçu, Goiás, Brazil.

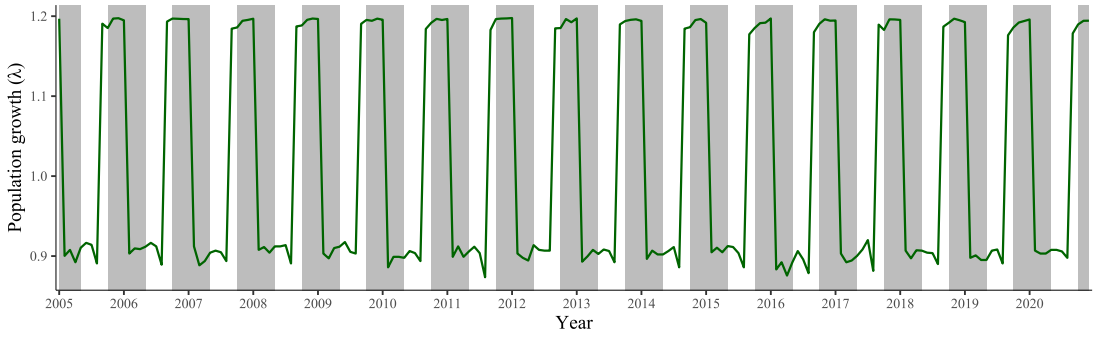

figure S4: Estimated monthly population growth (*λ*) of *Notomabuya frenata* in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Gray bars indicate the rainy season, spanning from October to May. The y-axis markers indicate January of each year.

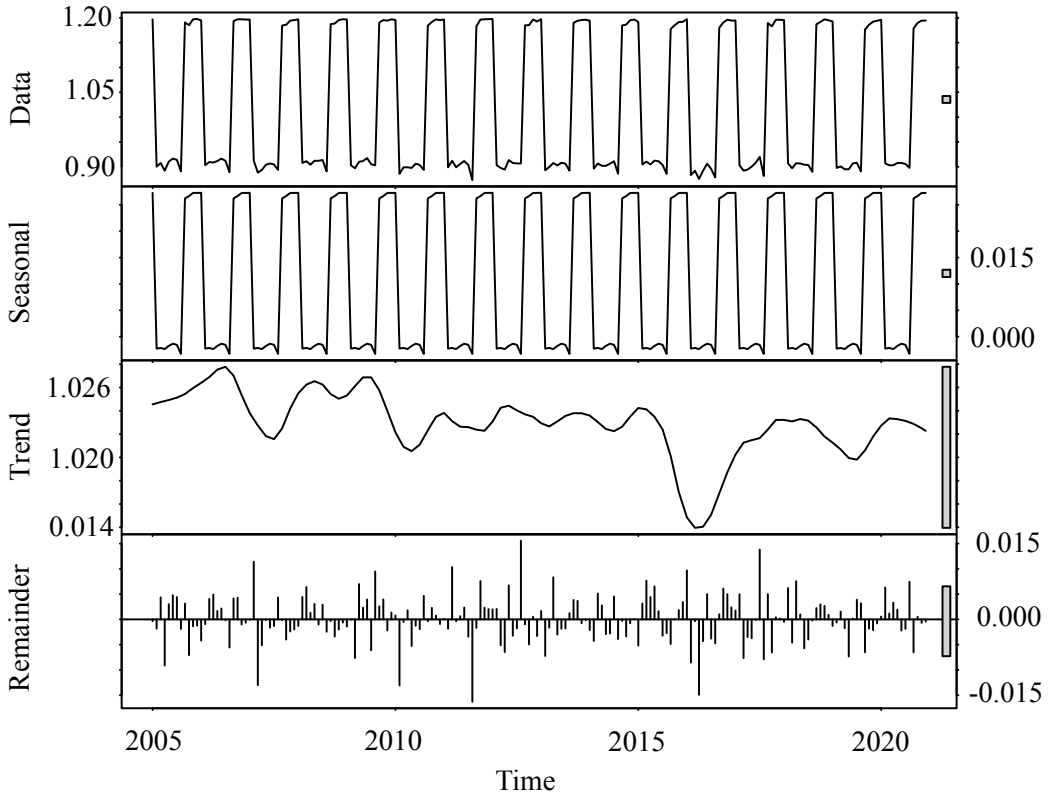

figure S5: Decomposition of the time series of estimated monthly population growth (*λ*) of *Notomabuya frenata* in Brasília, Distrito Federal, Brazil, from December 2005 to January 2021. Seasonal effect: 0.9986; trend effect: 0.0003; remainder effect: 0.0011.

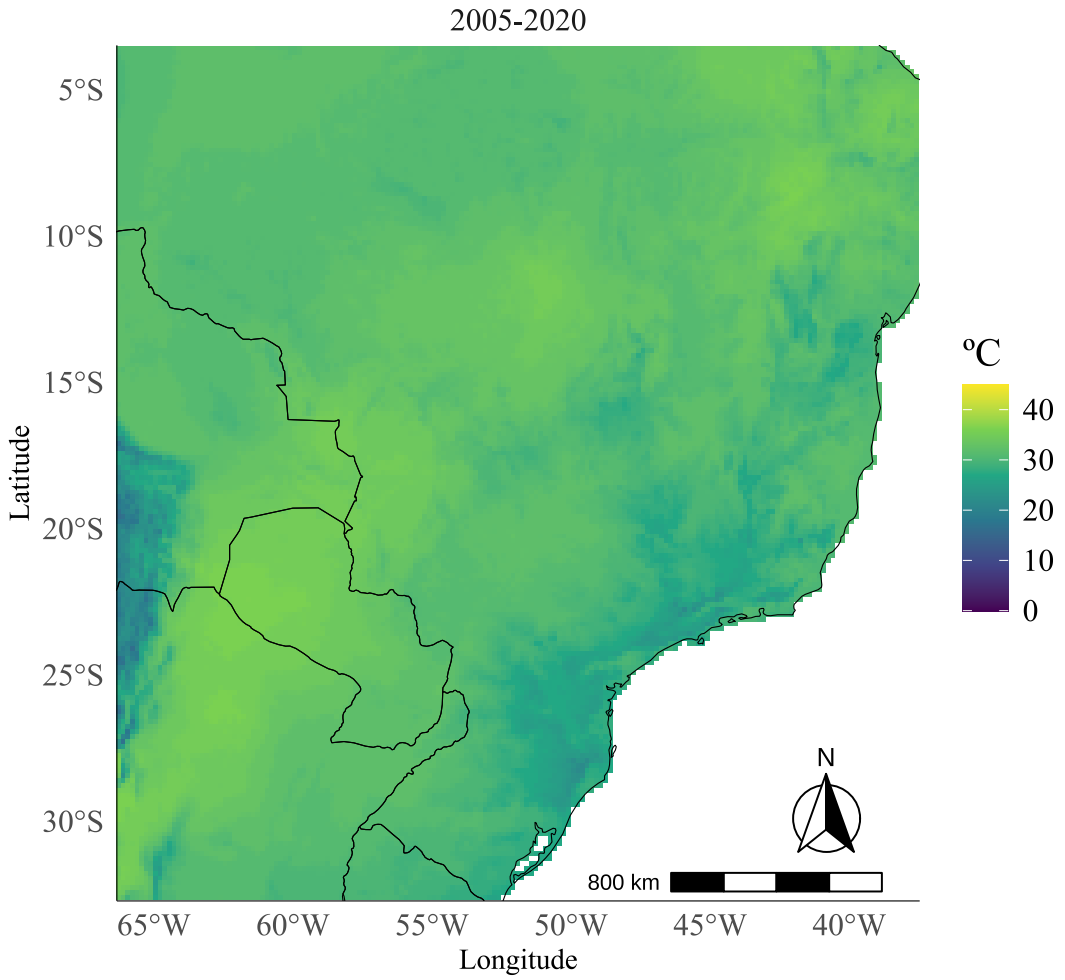

figure S6: Historical mean maximum temperature for the period 2005-2020.