



UNIVERSIDADE FEDERAL DO AMAZONAS - UFAM
INSTITUTO DE CIÊNCIAS BIOLÓGICAS - ICB
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA – PPGZOO



**Os efeitos das alterações ambientais sobre a distribuição e fenótipo de
um lagarto partenogenético na Amazônia Central**

Lucas Rosado Mendonça

Manaus, Amazonas

Junho/2023



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um lagarto partenogenético na Amazônia Central**

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Dissertação apresentada à Universidade Federal do Amazonas como parte dos requisitos para obtenção do título de Mestre pelo Programa de Pós-Graduação em Zoologia.

Manaus, Amazonas

Junho/2023

Ficha Catalográfica

Ficha catalográfica elaborada automaticamente de acordo com os dados fornecidos pelo(a) autor(a).

M539e Mendonça, Lucas Rosado
Os efeitos das alterações ambientais sobre a distribuição e
fenótipo de um lagarto partenogenético na Amazônia Central /
Lucas Rosado Mendonça . 2023
75 f.: il. color; 31 cm.

Orientador: Marcelo Gordo
Coorientadora: Fernanda de Pinho Werneck
Coorientador: Josué Anderson Rêgo Azevedo
Dissertação (Mestrado em Zoologia) - Universidade Federal do
Amazonas.

1. Emergência climática. 2. Espécie neonativa. 3. Ecofisiologia
termal. 4. Morfologia. 5. Plasticidade fenotípica. I. Gordo, Marcelo.
II. Universidade Federal do Amazonas III. Título

*“Por toda parte a natureza fala com o homem
numa voz que é familiar à sua alma”*

Alexander von Humboldt

Agradecimentos

Agradeço imensamente aos meus pais, Sr. Aristides e Dona Teresa, que do jeito deles me deram o suporte que eu precisava. Ao meu irmão, Daniel, pelo companheirismo.

Agradeço a minha companheira, Letícia Sena, pelo apoio quando decidi ficar a mais de 1000 km de distância; que foi sempre paciente e amorosa nos momentos de dificuldade; que me ajudou durante os experimentos; que gastou até mesmo quando não deveria para ir à Manaus me encontrar. Obrigado.

Sou imensamente grato aos meus amigos, Alexander T. Mônico, Esteban D. Koch e Igor Y. Fernandes por todo suporte e amizade em Manaus. Chegar e me manter na cidade sem a ajuda de vocês teria sido muito mais difícil. Muito obrigado pelos ensinamentos e conversas, boa parte do que aprendi sobre a Amazônia é graças a vocês.

Agradeço aos meus companheiros de casa, Bryan C. Martins e Silionamã P. Dantas. Dentre todas minhas experiências em república, essa com toda certeza foi a mais tranquila e proveitosa. Dividir o espaço com vocês foi um imenso prazer. A cada conversa era um peso a menos nas costas e uma injeção de motivação, essenciais para passar por esse período de uma forma mais tranquila. Aprendi muito, e se meu doutorado tiver linhas taxonômicas foi graças a vocês (e ao Alexander também *hehehe*).

Agradeço aos amigos que fiz durante o processo, Alessandra Rodrigues, Brena S. Gonçalves, Cláudia Souza, Eliza R. Costa, Erasmo Andrade, Leandro Moraes, Pedro Taucce e Vanessa Braga. Muito obrigado pelas conversas, pelos ensinamentos, pelas risadas e pelo apoio.

Agradeço a todos os meus amigos do Herpeto em Foco, pelo apoio e ajuda ao longo dos anos, por mais que eu tenha me afastado um pouco do projeto e não tenha conseguido contribuir efetivamente.

Agradeço aos meus amigos, em especial ao Gleydson Emílio, Marcelo Dias, Luana Coutinho e Ubiratã Souza, pelas conversas, apoio e ensinamentos. Mesmo a distâncias vocês todos têm e tiveram papel importante durante minha trajetória.

Agradeço aos professores que tive a oportunidade de conhecer durante o processo, André Andrade, Adrian Garda, Cíntia C. Frische, Fabrício B. Baccaro, Fabrícus Domingos, Igor Kaefer, Ronis Da Silveira e Sérgio H. Borges, sendo em campo ou em sala, formal ou informalmente.

Agradeço a Fernanda Werneck pelas oportunidades dadas a mim para conhecer as diferentes Amazôniaas. Tenho muito ainda para conhecer, mas aprendi imensamente com o que vi e vivi. Muito obrigado.

Agradeço ao Fabrício B. Baccaro e Marcos R. Rosado pela ajuda durante as análises e *scripts*. Trabalhar no R às vezes pode ser bem estressante. Muito obrigado.

Por fim, mas não menos importante, agradeço ao PPGZOOOL-UFAM e aos meus orientadores, Fernanda Werneck, Josué Azevedo e Marcelo Gordo, pelo ensinamento e orientação. Agradeço em especial ao Josué, que antes mesmo de me ter como orientado já me dava todo suporte que podia quanto as análises e construção da dissertação.

A todos que me ajudaram de alguma forma, seja em uma análise, nas coletas, na companhia ou tendo uma simples conversa, meu muito obrigado.

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Resumo

Diferentes mudanças ambientais podem levar diferentes populações ao vórtice de extinção, reduzindo sua variabilidade genética através do isolamento e diminuição populacional, impedindo assim seu resgate evolutivo. A modificação do habitat, como o desmatamento e a urbanização, juntamente com a mudança climática global, estão entre os impactos mais desafiadores para as espécies e geralmente exigem respostas rápidas e diferentes dos organismos. Podendo responder por meio de plasticidade fenotípica, adaptação evolutiva ou se dispersar para áreas adequadas. No entanto, espera-se que espécies com ecologias particulares, como aquelas associadas a áreas abertas ou hábitos generalistas, possam se beneficiar de mudanças ambientais expandindo suas áreas de distribuição para novas áreas disponibilizadas pela ação humana (espécies neonativas). Assim como as espécies partenogenéticas (se reproduzem sem o auxílio de machos), que possuem grande capacidade de colonização de novos ambientes. Aqui, avaliamos a variação na morfologia e preferências térmicas entre duas populações, natural e neonativa (urbana) de *Gymnophthalmus underwoodi* Grant, 1958 (Squamata: Gymnophthalmidae), um lagarto partenogenético que habita das ilhas do Caribe, a ambientes abertos e urbanos na bacia amazônica, além de prever como as mudanças climáticas podem impactar sua distribuição até 2100. Avaliamos a variação entre as populações: nativa em Bonfim, RR e neonativa em Manaus, AM; usando 16 características morfológicas e suas preferências térmicas quanto a temperatura preferencial, temperatura crítica mínima, temperatura crítica máxima e curva de desempenho locomotor. Estimamos a distribuição da espécie no presente e futuro utilizando a modelagem híbrida para obtermos assim uma resposta mais acurada, relacionando dados de distribuição da espécie, variáveis climáticas, geográficas, e ecofisiológicas como desempenho locomotor e horas de atividade. O ambiente urbano apresenta estruturas e obstáculos diferentes quando comparado ao ambiente natural aberto (ex.: estruturas de baixa impermeabilidade, estruturas com baixo albedo, lixo, etc), resultando em respostas adaptativas das espécies que ali vivem. Desta forma, encontramos que a população neonativa apresenta maior velocidade do que a população nativa, como resultado de patas traseiras e dianteiras maiores, que podem facilitar a locomoção em ambientes verticalizados e com mais obstáculos, como as cidades. Apresentam também, um ótimo desempenho locomotor em temperaturas mais altas, em possível resultado à presença de ilhas de calor. Não somente, a população neonativa apresenta menor temperatura crítica mínima, podendo assim tolerar temperaturas mais

baixas, que pode estar associado ao aumento da variação de temperatura em ambientes urbanos e ao aumento de seu tronco que proporciona maior inércia térmica. Dentre as variáveis de importância pro modelo, obtivemos: sazonalidade de temperatura, desempenho locomotor, teor de argila no solo e áreas abertas próximas a rios e cidades. As áreas de grande adequabilidade para a espécie apresentam maior distribuição ao longo dos ambientes abertos naturais (savanas, campinas, etc.) e curso dos rios Branco e Amazonas, devido à presença de bancos de areias e áreas abertas pela presença humana. Está associação aos rios e áreas abertas pode facilitar a dispersão de indivíduos pela Amazônia, através do transporte acidental em barcos e/ou rastreando ambientes em mudança e se dispersando por eles. Ainda, a espécie mostra tolerância às previsões climáticas mesmo em cenários extremos, aumentando sua distribuição em áreas abertas. Portanto, apesar de a espécie ser partenogenética e conseqüentemente ter baixo potencial para o resgate evolutivo, este é um dos poucos exemplos em que espécies de lagartos amazônicos podem se beneficiar de mudanças ambientais.

Palavra-chave: Emergência climática, Espécie neonativa, Ecofisiologia termal, Morfologia, Plasticidade fenotípica.

1. Introdução

As alterações ambientais como uso do solo, mineração, desmatamento, urbanização e mudanças climáticas globais tem levado diversas espécies a extinção, diminuindo suas populações e reduzindo sua variabilidade genética (Gibbons et al. 2000, Bickford et al. 2010, Todd et al. 2010, Lamkin e Miller 2016, IPBES 2019). As mudanças climáticas têm se acelerado e intensificado, resultando em novas previsões que apontam um aumento de 1,5 °C na temperatura global até 2030 e 5,7 °C ao final do século quando comparado a era pré-industrial (Xu et al. 2018, IPCC 2021). Conseqüentemente, diferentes respostas são observadas nos organismos, como: dispersão para locais climaticamente mais adequados ou a adaptação a novas condições ambientais através da plasticidade e/ou adaptação evolutiva (Pounds e Puschendorf 2004, Thomas et al. 2004, Wilson et al. 2005, Hoffmann e Sgrò 2011). A plasticidade permite ao organismo alterar rapidamente seu fenótipo (ex.: morfologia, fisiologia e comportamento) em resposta ao ambiente (Levis e Pfennig 2016, Snell-Rood et al. 2018). Por outro lado, as adaptações evolutivas ao nível genético podem não acontecer rápido o suficiente, em razão da magnitude e velocidade das mudanças climáticas, ou ainda serem má-adaptações (Hoffmann e Sgrò 2011, Diamond e Martin 2020). Em alguns casos a plasticidade fenotípica pode atuar também como amortecedor das mudanças, impedindo a adaptação local (Buckley et al. 2015, Fox et al. 2019).

Nos centros urbanos, as mudanças climáticas são acentuadas: formam-se ilhas de calor como consequência do aumento da temperatura das superfícies e do ar, consequência do uso extensivo de superfícies com baixo albedo (alta capacidade de reter calor) e redução de áreas cobertas por água e vegetação (Grimm et al. 2008, Hulley 2012). Com o avanço da ocupação humana, ilhas de calor já são observadas em centros urbanos na Amazônia (Souza e Alvalá 2014, Corrêa et al. 2016). Na cidade de Manaus (Amazonas), região central do bioma, a temperatura média teve aumento de 0,7°C durante o período de 1961 e 2008 (Souza e Alvalá 2014), atingindo valores próximos à média anual de 27,8°C das savanas de Roraima (Barbosa e Miranda 2004, Aguiar 2017). Em alguns casos, as adaptações às ilhas de calor podem servir como 'pré-adaptações', possibilitando que os organismos persistam no cenário de aquecimento global e ultrapassem filtros ambientais em diferentes ambientes, alcançando regiões antes indisponíveis (Borden e Flory 2021).

Organismos ectotérmicos que não conseguirem aumentar sua ingestão de alimento e/ou realocar os recursos calóricos, podem ter seu tamanho corporal reduzido

em resposta ao aumento de temperatura (Sheridan e Bickford 2011). Entretanto, em populações de lagartos que habitam ambientes urbanos têm-se encontrado tamanhos corporais e membros maiores quando comparados às não urbanas (Putman e Tippie 2020), ainda que seja possível encontrar o oposto (Sparkman et al. 2018, Putman et al. 2019, Vaughn et al. 2021). Esta variabilidade nos tamanhos corporais pode estar relacionada a diferentes estressores como às ilhas de calor, à relação presa-predador, à disponibilidade de alimento e aos poluentes presentes no ambiente (Lazić et al. 2013, Putman e Tippie 2020). Além disto, as áreas urbanas podem provocar alterações na simetria corporal, como resultado do estresse sofrido durante o desenvolvimento embrionário (Lazić et al. 2013, Olivero et al. 2021).

Modelos de distribuição de espécies são comumente usados para avaliar a resposta dos organismos às mudanças ambientais naturais e antrópicas (Pontes-da-Silva et al. 2018, Chen et al. 2021). Para isso, tem se usado principalmente os modelos correlativos, que relacionam as condições ambientais com a distribuição da espécie; e os mecanísticos, que partem de características fisiológicas da espécie (ex.: temperatura preferencial) e não somente de sua distribuição (Elith et al. 2010, Meineri et al. 2015). Contudo, o uso integrado dessas duas abordagens na construção de modelos híbridos, permite a obtenção de um modelo com maior acurácia quanto a relação da espécie com o ambiente (Kearney e Porter 2009, Elith et al. 2010, Meineri et al. 2015, Caetano et al. 2020, Tourinho et al. 2021). Com o propósito de compreender os efeitos provocados por alterações ambientais e climáticas sobre as populações de répteis, muitos autores têm utilizado de informações ecofisiológicas (Sinervo et al. 2010, Kubisch et al. 2015, Chen et al. 2021), como a temperatura preferencial, temperaturas críticas, e ótima (Taylor et al. 2020). A partir destas temperaturas é possível quantificar a vulnerabilidade da espécie às alterações climáticas, dado que esses traços representam a relação do ambiente com o organismo (Angilletta et al. 2002, Gilbert e Miles 2017). Com isso, possibilitam a obtenção do tempo de atividade da espécie, uma importante variável que pode aumentar a acurácia das predições (Caetano et al. 2020). Áreas com baixo tempo de atividade disponível impossibilitam a presença da espécie no local por não apresentarem horas com temperatura adequada o suficiente para realização de atividades básicas como forrageio e busca por parceiros reprodutivos (Angilletta et al. 2002, Angilletta 2009, Caetano et al. 2020).

As espécies especialistas são as mais afetadas pelas alterações ambientais (Cordier et al. 2021), enquanto outras espécies podem ser favorecidas por este processo,

como as espécies generalistas e de áreas abertas (Attum et al. 2006, Hoffmann e Sgrò 2011, Essl et al. 2019, Cordier et al. 2021). Algumas ainda podem rastrear as alterações ambientais e utilizá-las como corredores de dispersão, aumentando sua distribuição e atingindo áreas climaticamente favoráveis que antes estavam inatingíveis (neonativos; Essl et al. 2019). Em lagartos tem se observado alterações morfológicas (Putman e Tippie 2020, Vaughn et al. 2021), fisiológicas (Campbell-Staton et al. 2020) e comportamentais (Nordberg e Schwarzkopf 2019), devido às diferentes pressões seletivas presentes nos novos ambientes. Um caso disto é a categoria de substrato utilizado pelo organismo em determinado local, implicando diretamente na sua velocidade e sobrevivência (Tulli et al. 2012, Vanhooydonck et al. 2015, Winchell et al. 2018).

Neste processo de adaptação a um novo ambiente ou fator ambiental, o modo reprodutivo se torna uma importante característica (Orive et al. 2017, Jara et al. 2019, Partecke et al. 2020). Espécies clonais se tornam então um bom modelo para avaliar esses aspectos, como as espécies partenogenéticas verdadeiras (compostas apenas por fêmeas). Por não necessitarem de um parceiro reprodutivo, são espécies com grande capacidade para colonizar novos ambientes, principalmente em regiões de áreas marginais, áreas abertas, ilhas e áreas perturbadas, frequentemente apresentando maior área de distribuição que suas espécies irmãs sexuadas (Kearney 2005, Fujita et al. 2020). Contudo, a partenogênese pode ser custosa a longo prazo, dado que a fixação de mutações deletérias se acumula com maior facilidade — *Muller's ratchet* (Muller 1964) — além de gerarem novas combinações genotípicas mais lentamente, dificultando a adaptação a novos ambientes (Fujita et al. 2020).

Poucos são os vertebrados que se reproduzem por partenogênese (Vrijenhoek 1989), sendo os répteis Squamata (com exceção as anfisbenas) o único grupo de vertebrados que apresentam espécies com a reprodução verdadeiramente partenogenética, correspondendo a cerca de 0,6% da diversidade atual do grupo (Fujita et al. 2020). Dentre os lagartos, algumas espécies são pertencentes à família Gymnophthalmidae (Pellegrino et al. 2001, Cole et al. 2013), também conhecidos como microteídeos, apresentam pequeno tamanho corporal (comprimento rostro-cloacal — CRC, de 4 a 15 cm) e hábito semi-fossorial. A família inclui dois gêneros com espécies partenogenéticas conhecidas, *Loxopholis* e *Gymnophthalmus* (Pellegrino et al. 2001). Este último é composto por um grupo de espécies crípticas de lagartos diurnos heliotérmicos (que se aquecem sob o sol), que habitam a serapilheira de áreas abertas e

algumas áreas florestadas (Hoogmoed 1973, Avila-Pires 1995, García-Pérez e Schargel 2017, Ribeiro-Júnior e Amaral 2017).

A espécie partenogenética *Gymnophthalmus underwoodi* Grant 1958, se originou a partir da hibridização entre *G. cryptus* Hoogmoed, Cole e Ayarzagüena, 1992 e *G. speciosus* (Hallowell, 1861) possivelmente na região do Rio Orinoco, ao sul da Venezuela (Cole et al. 1990, 1993, Kizirian e Cole 1999). Este é um lagarto com CRC médio de 36 mm, com padrão corporal geral dos lagartos lacertoides (Grant 1958, Hardy et al. 1989, Recoder et al. 2018), e ciclo reprodutivo contínuo (Hardy et al. 1989). Por serem heliotérmicos, permanecem ativos preferencialmente durante os horários ensolarados e quentes do dia (Cole et al. 1990, Vitt e Zani 1998). Sua distribuição é ampla, ocorrendo na Venezuela, Ilhas caribenhas, Guiana, Guiana Francesa, Suriname e Brasil, ao longo de áreas abertas como savanas, campinaranas, campinas, áreas antropizadas e raramente em florestas (Grant 1958, Cole et al. 1990, 2013, Avila-Pires 1995, Ribeiro-Júnior e Amaral 2017, Snyder et al. 2017, Salas 2020). Ainda, novos registros de distribuição para áreas urbanas de Manaus, Amazonas (Recoder et al. 2018, Magnusson 2019) e Belém, Pará (Maciel et al. 2021) sugerem que a espécie esteja em processo de dispersão. Assim, este projeto tem por finalidade avaliar diferenças fenotípicas em traços morfológicos e na ecofisiologia termal, entre duas populações do lagarto partenogenético *Gymnophthalmus underwoodi* de áreas abertas naturais na região de Roraima e áreas urbanas em Manaus, Amazonas.

2. Objetivos

2.1 Objetivo geral

Avaliar se existem diferenças ecológicas e fenotípicas entre populações de *Gymnophthalmus underwoodi* em resposta a ocupação de novos ambientes frente as alterações ambientais.

2.2. Objetivos específicos

1. Avaliar se há diferenças funcionais nas preferências térmicas e mudanças morfológicas entre populações da área de distribuição natural nativa e populações com área de distribuição antrópica;
2. Avaliar se o ambiente urbano é um fator estressante para a espécie *Gymnophthalmus underwoodi*;

3. Avaliar a ocorrência de áreas de alta adequabilidade ambiental em direção à Amazônia Central e Oriental no presente;
4. Avaliar a distribuição geográfica de *G. underwoodi* no cenário climático futuro.

3. Conclusão

O quão plástico é a espécie *Gymnophthalmus underwoodi*? A morfologia e a ecofisiologia são plásticas o suficiente para permitir que a espécie persista e realmente prospere neste ambiente. Seus membros maiores permitem uma melhor movimentação no gradiente urbano enquanto a maior temperatura aumenta sua velocidade. Contudo, o ambiente urbano pode levar a espécie a uma armadilha evolutiva ao longo do tempo (Diamond e Martin 2020). A espécie parece ter encontrado uma área climaticamente favorável para habitar: o ambiente urbano e áreas desmatadas. Nosso modelo de distribuição de espécie sugere que este lagarto persistirá e até mesmo aumentará sua distribuição. O modelo mostra um aumento na distribuição seguindo as novas áreas abertas previstas em cenários extremos, sugerindo que *G. underwoodi* está acompanhando a mudança ambiental e não apenas se dispersando acidentalmente por barcos (Maciel et al. 2020). No entanto, esta é uma espécie partenogenética e as taxas de adaptação e plasticidade dos clones podem não ser suficientes para a espécie persistir a longo prazo (Hoffmann e Sgrò 2011, Orive et al. 2017, Fujita et al. 2020, Moreira et al. 2021). Novos estudos com dados genômicos e técnicas de transcriptômica, para avaliação dos níveis de expressão gênica sob diferentes tratamentos e mais populações podem ajudar a avaliar como a espécie se sairá no futuro e se a plasticidade fenotípica será suficiente para sua persistência.

Nosso estudo comparou vários traços funcionais em duas populações, nativa e supostamente neonativa, destacou o impacto que paisagens alteradas e ambientes urbanos podem ter em nas trajetórias ecológicas e evolutivas de organismos da Amazônia. Além disso, este é um dos primeiros passos para entender como espécies partenogenéticas podem responder às mudanças ambientais. As mudanças fenotípicas encontradas na população neonativa e seu padrão de distribuição indicam o ambiente urbano como um centro de dispersão, que pode ser utilizado pelas espécies para chegar a outras áreas (Borden e Flory 2021). Reforçando assim, o papel do ambiente urbano e desmatamento como ameaça à biodiversidade da Amazônia, não somente por reduzir as populações, mas “pré-adaptando” espécies neonativas e invasoras a outras localidades, colocando as espécies nativas em risco (Huey et al. 2009, Borden e Flory 2021).

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5. Capítulo único

Effects of urban environment and climate change on a neotropical parthenogenetic lizard

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Short title: Phenotype variation in a parthenogenetic lizard

Paper in prep. for submission in Journal of Animal Ecology.

Author guidelines available at:

<https://besjournals.onlinelibrary.wiley.com/hub/journal/13652656/author-guidelines>

Abstract

1. Habitat modification, such as deforestation and urbanization, coupled with global climate change, is among the most challenging impacts to species, and often require quick and varied responses from organisms. However, the type of reproduction is a major factor in these responses. Parthenogenetic species reproduce by cloning, and are able to colonize new environments quickly if the new environment is suitable for them. While poor genetic diversity and the accumulation of deleterious mutations can lead them to extinction over time. Therefore, how parthenogenetic species will respond to habitat modification?

2. Here, we assessed the variation in morphology and thermal traits between a natural and neonative (urban) population of *Gymnophthalmus underwoodi*, a parthenogenetic lizard that inhabits open environments within the Amazon basin. We compared the morphology of the two populations using 16 traits and assessed the urban environment as stress habitat using fluctuating asymmetry. The thermal traits were compared using preferential temperature, critical temperatures maximum and minimum, and thermal

performance curve of sprint. We also predict how changing climates might impact its distribution until 2100, through a hybrid species distribution model using ecophysiological and climatic variables, landcover, soil type and slope as predictors.

3. We provide evidence for fast phenotypic change in parthenogenetic species under anthropic factor. The neonative population shows faster sprint than the native population, as a result of the larger hind feet and fore feet, as well as higher temperature for optimal sprint performance. The neonative population shows cooler temperature to critical minimum, which may be associated with larger trunk. The distribution model shows a stronger association with open area nearby rivers and cities. This may facilitate the dispersion of individuals over the Amazon, tracking changing environments and dispersing accidentally aboard boats. The species shows tolerance to predicted climates even in extreme scenarios, increasing its distribution over open areas.

4. Despite being parthenogenetic, this is one of the few examples in which Amazonian thermoregulator lizard species may actually benefit from anthropic environmental changes. Therefore, anthropic factors may threaten Amazon biodiversity not solely by causing a population decline, but by enhancing competition between native and neonative/alien species.

Key-words: climatic emergency, morphology, neonative species, phenotype plasticity, thermal physiology.

Introduction

Ever increasing human action results in unprecedented evolutionary pressures leading species to extinction as a result of habitat loss by deforestation, introduced invasive species, urbanization, and global climate change (Gibbons et al. 2000, Bickford et al. 2010, Todd et al. 2010, Lamkin and Miller 2016, IPBES 2019). Recent climate change forecasts indicate an increase of 1.5°C in temperature by 2030 and 5.7°C by the end of the century compared to the pre-industrial era (Xu et al. 2018, IPCC 2021). Organisms can have different responses to deal with such pressures, however, we still do not have a complete understanding of whether these responses are adaptive or maladaptive (Diamond and Martin 2020). Organisms may respond through either disperse to new suitable areas or persisting in new conditions through phenotypic plasticity and evolutionary adaptation (Pounds and Puschendorf 2004, Thomas et al. 2004, Wilson et al. 2005, Hoffmann and Sgrò 2011, Meek et al. 2023). Evolutionary adaptation is

characterized by the environmental selection of locally adapted genetic variants and may require enough time and an array of adaptive genetic diversity (Hoffmann and Sgrò 2011, Levis and Pfennig 2016, Snell-Rood et al. 2018). Meanwhile, phenotypic plasticity allows the organism to change its physiology, behavior, or morphology in response to the environment (Hoffmann and Sgrò 2011, Fox et al. 2019). In that sense, phenotypic plasticity can act as a buffer to local adaptation (Buckley et al. 2015, Fox et al. 2019). These different response mechanisms to environmental change due to human activity need to be further investigated under integrated approaches and at complex natural-modified landscapes to confirm the main trend of evolutionary responses leading to species extinction (Gibbons et al. 2000, Sinervo et al. 2010, Böhm et al. 2013, Diele-Viegas et al. 2020, Cordier et al. 2021, Antonelli 2022).

Environmental differences lead to different evolutionary pressures that can result in functional variation across the distribution range of some species, such as in morphology, physiology and behavior (Vitt et al. 1997, Kohlsdorf et al. 2001, Winchell et al. 2016). Moreover, in a new environment, lizards' species might need to cross areas with different substrates, which may result in morphology changes as a consequence of the environmental filter, affecting their sprint velocities and survival (Tulli et al. 2012, Brandt et al. 2015, Vanhooydonck et al. 2015, Winchell et al. 2018, Vaughn et al. 2021). Urban landscapes represent one of these environments with different features and substrates that constrain animal locomotion (Caspi et al. 2022). Besides that, cities worldwide have developed heat islands due to the extensive use of impermeable surfaces with low albedo, high heat capacity, and reduction in forest areas (Grimm et al. 2008, Hulley 2012). The urban environment may act as an environmental filter, selecting organisms by heat tolerance, changing their body and limbs size, bilateral symmetry, physiology, and behavior through adaptations or plasticity (Lazić et al. 2013, Alberti 2015, Sparkman et al. 2018, Nordberg and Schwarzkopf 2019, Putman et al. 2019, Campbell-Staton et al. 2020, Putman and Tippie 2020, Borden and Flory 2021, Thompson et al. 2022). Regarding symmetry, pollution and other stress factors may lead to fluctuating asymmetry (FA), as a result of development instability (Palmer and Strobeck 1986, Lazić et al. 2013). Moreover, species that inhabit urban environments may use heat islands as dispersion centers to reach areas previously unavailable, tracking urban activities and moving to new areas of good thermal suitability (Essl et al. 2019, Borden and Flory 2021).

Species distribution models (SDM) are tools commonly used to assess species' response to climate change (Urban et al. 2007, Sinervo et al. 2010, Chen et al. 2011, 2021, Pontes-da-Silva et al. 2018). There are three different ways to perform a SDM: correlative model which uses distribution records and environmental variables; mechanistic model which uses ecophysiological data (e.g., preferential temperature) and microenvironment variables; and hybrid model (Elith et al. 2010, Sillero et al. 2021, 2023). Hybrid models combine correlative and mechanistic approaches (Elith et al. 2010, Meineri et al. 2015, Sillero et al. 2021, Tourinho and Vale 2023), often using ecophysiological traits, such as thermal data on hours of activity (H_a) and thermal performance curves (TPC) (Sinervo et al. 2010, Pontes-da-Silva et al. 2018, Caetano et al. 2020, Machado et al. 2023). Hours of activity correspond to the number of hours of the day in which the temperature is between the critical voluntary temperatures, which allow the individual to be able to inhabit a certain area, since the limitation in hours of activity reduce the energy gain and reproduction (Angilletta 2009, Kearney and Porter 2009). Thermal performance curve is the relationship between the organism's performance and the environmental temperatures, showing important thermal trait, such as critical temperatures and optimal temperature for performance (Angilletta et al. 2002, Angilletta 2006, Taylor et al. 2020). Frequently, hybrid models attain more accurate forecasts of species responses than correlative and mechanistic models, providing, therefore, a more complete view of species response to the environment (Kearney and Porter 2009, Elith et al. 2010, Sillero 2011, Meineri et al. 2015, Peterson et al. 2015, Tourinho and Vale 2023).

Ectotherms animals are in general more vulnerable to environmental changes, though, may change their phenotypes easier in response to new conditions (Gibbons et al. 2000, Hoffmann and Sgrò 2011, Nordberg and Schwarzkopf 2019, Diele-Viegas et al. 2020, Putman and Tippie 2020, Bodensteiner et al. 2021, Borden and Flory 2021). Reproductive modes have an important role in adaptive processes (Orive et al. 2017, Jara et al. 2019) and clonal species are interesting target groups to evaluate these effects. Parthenogenesis is the clonal reproductive mode of vertebrates and just 0.6% of the cases are true parthenogenetic species (only females) (Fujita et al. 2020). Since parthenogenesis abstains from male for reproduction, it can facilitate dispersion and therefore the establishment of new populations whenever organisms reach newly suitable areas (Kearney 2005, Hörandl 2009, Fujita et al. 2020). However, clonal reproduction may be costly in the long term. The lack of DNA-repair meiotic

mechanism and low DNA recombination can result in the increase of deleterious mutations – Muller’s Ratchet (Muller 1964) – which can lead the clones to extinction (Fujita et al. 2020, Moreira et al. 2021). Therefore, few are the species of vertebrates that exclusively use parthenogenesis as a reproductive mode (Vrijenhoek 1989). An example is the true parthenogenetic lizard, *Gymnophthalmus underwoodi* Grant, 1958 (Squamata: Gymnophthalmidae) that reproduces year-round, and sexually mature individuals lay a clutch of two eggs (Hardy et al. 1989). *G. underwoodi* is a microteiid lizard of small size and general lacertoid body shape, living as semi-fossorial organism dwelling in open areas (savannas, urban environment), forest edges and occasionally in forested areas, foraging between the leaf litter and basking in the sunlight — heliothermic (Cole et al. 1989, 1990, 2013, Vitt and Zani 1998, Alfonso and Hernandez 2017, Magnusson 2019, Salas 2020, Maciel et al. 2021). Its native distribution range is known mainly in the Amazon Forest, ranging from Amazonas, Brazil to Caribbean Islands, with records along the range (Grant 1958, Ribeiro-Júnior and Amaral 2017, Recoder et al. 2018, Salas 2020, Maciel et al. 2021) (Figure 1). As such, the species is believed to be dispersing in its latitudinal range and towards urban landscapes, and recently arrived in Manaus – AM, Belém – PA, both in Brazil, and La Habana Province, Cuba (Magnusson 2019, Salas 2020, Maciel et al. 2021).

Thus, here we aim to evaluate (1) if morphology and thermal physiology (preferential, critical, and optimal temperatures) differ between the native and neonative population to assess (2) whether the urban environment is a stress factor to the species, estimate (3) the current distribution and potential dispersion routes used to arrive in Manaus and to predict (4) the future response to climate change. Thus, we expected to enhance the acknowledgments of the effects of urbanization and climate change in neotropical parthenogenetic species.

Materials and methods

Study area & sample method

The Amazon Forest is often seen as an ocean of trees with wide rivers crossing it, however, it is much heterogeneous, composed by different phytophysiognomies, such as open areas (“Campinas”, “Campinaranas”, Savannas), “Terra Firme” and “Igapó” (flooded area) (Braga 1979, Adeney et al. 2016, de Carvalho and Mustin 2017). The campinas and campinaranas are regions with isolated small bushes and arboreal species, respectively (Adeney et al. 2016, Guimarães and Bueno 2016). Its soil presents mostly

sand content with a small clay component, and has low drainage capacity, becoming seasonally flooded in some localities (Adeney et al. 2016, Guimarães and Bueno 2016). In northern Amazonia, the savannas of Roraima are an enclave of open grasslands (“campo limpo”, “campo sujo”) with a mosaic of shrubs, scattered big trees, and forest patches (Barbosa e Miranda 2004). We collected individuals and ecological and physiological data in two localities in Brazil with contrasting environments (Figure 1): Manaus – Amazonas, (hereafter referred to as the neonative population; see Essl et al. 2019), on August 03-27, 2022, and January 16-18, 2023 during the rainy and dry season; and Bonfim – Roraima (hereafter referred to as native population), on July 17-22, 2022, during the rainy season. The precipitation between dry and rainy season are different, with general accumulated precipitation of 56.1 mm to 347 mm between them. These regions differ in temperature, in which Manaus has a mean of 27.3 °C (minimums of 23.7 °C and maximum of 34.1 °C) whereas Roraima’s savannas have a mean of 27.8 °C (maximum of 34.3 °C and minimums of 22.4 °C) (Barbosa and Miranda 2004, Corrêa et al. 2016, Aguiar 2017, INMET 2022). However, the urban region of Manaus unveiled an increase in temperature of 0.7 °C from 1961 to 2008 (Souza and Alvalá 2014) and might be hotter nowadays. The soil of Manaus and savannas of Roraima are mainly composed of clay, with some addition of sand and silt (Chauvel et al. 1987, EMBRAPA 2020).

The morphological identification was made in the field following Recoder et al. (2018) and confirmed with molecular analysis using mtDNA 16S (see below). Lizards were caught through active surveys during the hottest hours of the day (10:00 am to 14:00 pm) in open areas in Bonfim, and next to buildings or/and garden areas in Manaus (Cole et al. 1989, Vitt and Zani 1998) as these lizards were observed active in the hottest hours of the day even on hot surfaces (Cole et al. 1990). To enhance the sampling effort in Manaus, since *‘[...] on a good day of collecting, four field workers might catch a total of eight or ten of these lizards [...]’* (Cole et al. 1989), we used five pitfall traps with about four 1-liter buckets between a fence of 4 m × 30 cm (Supplementary file Figure 1).

The survey was realized under SISBIO license n. 83159-1/2022 granted to LRM and SISBIO license n° 44832-4 granted to FPW. The physiological experiments were realized under CEUA license n. 042/2020 SEI 01280.0001606/2020-88 issued to FPW.

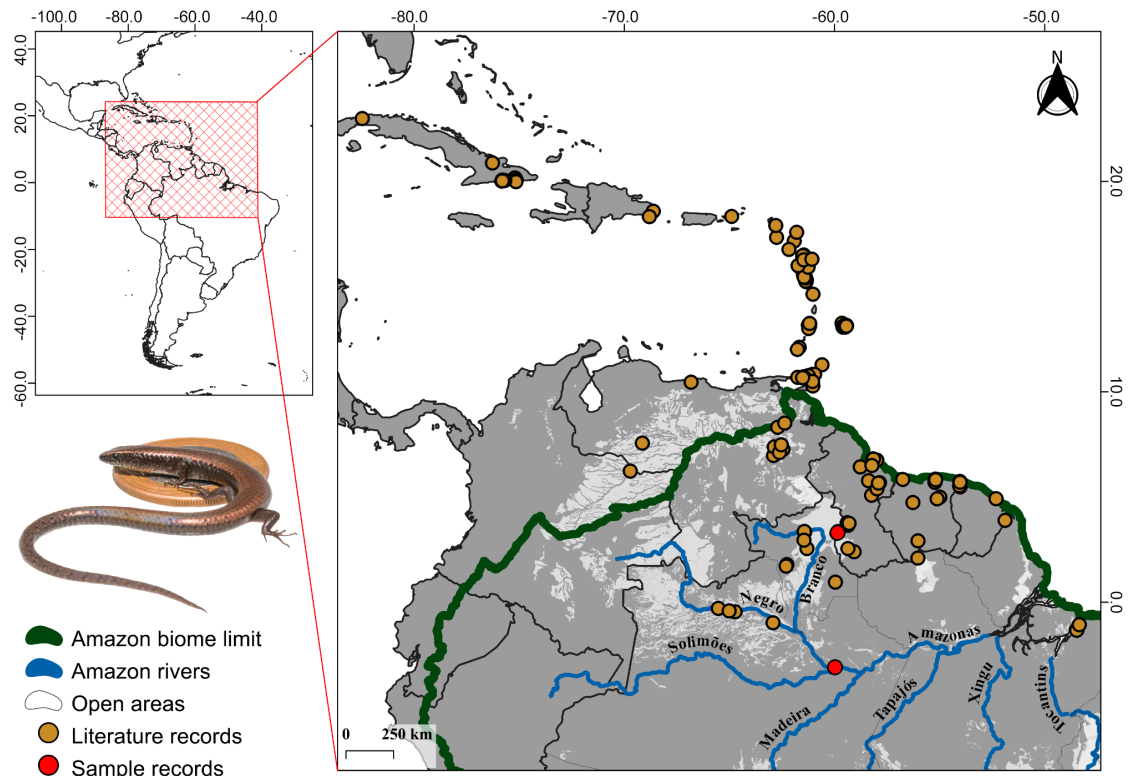


Figure 1. Distribution of *Gymnophthalmus underwoodi* shows a prevalence of records inside the Amazon biome limit (wide gray line) and in the north of Amazon/Solimões river (except for records in Belém, PA). Limits of Amazon biome, available at Mapbiomas (<https://amazonia.mapbiomas.org>). Open areas by Adeney et al. (2017). Photo: *Gymnophthalmus underwoodi* by LRM.

Genetic data

To confirm the identification of *Gymnophthalmus underwoodi* with greater accuracy, we extracted genetic samples of the mitochondrial marker 16S (± 550 bp) from tissues of tail muscle and liver of eight collected specimens from Amazonas and Roraima (Appendix 1). The DNA was extracted following Promega Wizard® Genomic DNA purification Kit. The 16S was amplified following Pellegrino et al. (2001) using primers 16SF (5'-CTGTTTACCAAAAACATMRCCTYTAGC-3') and 16SR (5'-TAGATAGAAACCGACCTGGATT-3'). The purification followed PEG 8000 protocol (Sambrook and Russel 2001) and was submitted to sequencing following BigDye Terminator 3.0 Cycle Sequencing kit (Applied Biosystems). Additionally, we used all sequences of the species available in Genbank for phylogenetic analysis, and sequences of species *Micrablepharus atticolus* Rodrigues, 1996, *M. maximiliani* (Reinhardt & Lütken, 1862) and *Calyptommatus sinebrachiatus* Rodrigues, 1991, as outgroups (Appendix 1) aligning with Geneious v7.0. To infer the phylogenetic tree, we used MrBayes v.3.2 (Ronquist et al. 2012) through the CIPRES webserver

(<http://www.phylo.org/>). The GTR+G was chosen as the best substitution model for the alignment, obtained using MrModelTest v2.4 (Nylander 2004). The Bayesian Inference (BI) was made through two independent runs of 50 million generations each, four Markov chains, and trees sampling every 5,000 generations (Recoder et al. 2018). The *burn-in* of 10% was applied using Tracer v1.7.2 and the final tree was fitted with FigTree v1.4.4.

Preferential and voluntary temperatures

The collected specimens were kept individually isolated in plastic recipients with moistened paper and without access to food during the experiments (4 days). Abstention of food was made to avoid the effects of diet on preferred temperature (T_{pref}) (Simandle et al. 2001, Abayarathna and Webb 2021). All bowls were maintained in an isolated room at air temperature of 26-30 °C and all specimens participated in all thermal tests. After collected the individuals, we started the thermal tests with T_{pref} , following to sprint performance and end with the critical temperatures.

We determined the T_{pref} using a thermal gradient made of plastic roof lining measuring 1,00 m × 1,00 m × 0,33 m, split into eight channels with a width of 12.50 cm each (Paranjpe et al. 2012) (Supplementary file Figure 2). We used a zinc plate as the base of the gradient, with ice bags at one end and 60W incandescent light bulbs covered with yellow cellophane paper at the other end (Tschanz et al. 1976, Fleishman et al. 1993, 2011). The thermal gradient ranged from 40 °C to 10 °C in each channel. The individuals were acclimated for 30 minutes inside the thermal gradient before starting the measurements. Using a small thermocouple (Omega® 5SC-TT-T-36-72 *Ready-Made Insulated Thermocouple with Kapton®*, PFA, *Glass Braid Insulation and Molded Connector*) attached to the lizards' belly with hospital tape, we recorded the lizards' body temperature every minute for 120 minutes with a data-logger (Omega® TC-08-TC-DAQ *8-Channel USB Thermocouple Data Acquisition Module*). As the core-surface temperature does not change significantly in small animals, we attached the tape to the belly instead of the cloaca to reduce the stress suffered by the specimen (Camacho et al. 2015, Diele-Viegas et al. 2018). We used the mean of the body temperatures recorded during the experiment period as the T_{pref} , the 5% percentile as voluntary minimum temperature (VT_{min}), and the 95% percentile as voluntary maximum temperature (VT_{max}) (Caetano et al. 2020, Taylor et al. 2020).

Sprint performance

After inferring the T_{pref} , we measured the sprint performance. We built a linear track with plastic roof lining measuring 1.00 m × 0.30 m × 0.30 m (Supplementary file Figure 3). To measure the performance across different substrates, the base of the track was made with two types of substrates (herein treatments): one with red clay to represent native environment (native substrate); and the other with coarse-grain sandpaper (60 grit; grains ~400 μm) to represent the street substrate in the urban environment (urban substrate). To record the sprint during the 1.0 m, we used a digital camera (Casio Exilim Ex-FH20 9.1MP) attached to a tripod about 1.30 m over the track, and we shot at 400 frames for a second. We randomly split the specimens collected at each study area into two groups, one for each treatment, and did the experiment with one lizard per turn. Each lizard ran two times for each temperature, first with body temperature at room temperature (26 – 30 °C), the second at -5 °C of the first running, and the third at +5 °C of the first running, with recovery intervals of two hours between runs in different temperatures. We classified each of the two runs as ‘good’ or ‘bad’ for further analysis. The ‘good’ run was when the lizard crossed the track with the minimum stops, and the ‘bad’ run was when the lizard returned to the start point or stopped many times. To reach the required temperature, we put the lizards inside a styrofoam box with an ice bag to the second run and with 60W incandescent light bulbs to the third run (Supplementary file Figure 4). The body temperature was measured through the cloaca using an ultrafine thermocouple connected to an automatic thermometer (Omega® HH806AU accuracy 0.3 °C). We did not use the surface temperature here to avoid measuring our own temperature, since we needed to hold the specimen for about 30 seconds to be able to measure. The sprint speed was calculated as the mean of ‘good’ run of each temperature (three different temperatures per lizard) and disregarding moments that they stopped, using Tracker v5.1.5 (available at www.physlets.org/tracker).

Critical minimum and maximum

Two hours after the last sprint performance run, we measured the critical minimum (CT_{min}) and critical maximum (CT_{max}) with the maximum being the last trait measured for each lizard. To reach these critical temperatures, we used the same equipment as for sprint performance (described above; see Supplementary file Figure 4). CT_{min} was measured when the lizard lost its righting response, whereas CT_{max} was

measured when the lizard exhibited spasms and/or lost its righting response (Taylor et al. 2020). Between tests, the lizards had four hours to rest and recover. Immediately after the temperature measurement, we restore the lizard's body temperature to normal levels using a 60W incandescent light bulb for CT_{min} and a water bath for CT_{max} . All individuals were euthanized with xylazine 2%, fixed with 10% formalin, and deposited at the Amphibians and Reptiles Collection from the Instituto Nacional de Pesquisas da Amazônia (INPA-H) at the end of the tests.

Morphological measurements

We used both the collected specimens and those deposited at the INPA-H Collection (Supplementary data). The specimens were photographed with a digital camera Nikon D3400 with a lens DX 18-55 mm 1:3.5-5.6 G equipped with a generic *close-up* filter (+2), to measure the traits using ImageJ v1.54b (Schneider et al. 2012; precision of 0.0001 mm). We measured 16 traits (Supplementary file Figure 5) including snout-vent length (SVL); head width (HW); head height (HH); head length (HL); trunk length (TRL); interbrachial-nasal length (INL); femur length (FL); tibia length (TL); hindfoot length (FTL); humeral length (HL); forearm length (FAL); tail length (TAL); pelvic girdle (PG); shoulder girdle (SG); and counted scales of the third finger of hindfoot (SHF), and third finger of forefeet (SFF) (Recoder et al. 2013, Winchell et al. 2018, Vaughn et al. 2021). Furthermore, we measured both the left (_L) and right (_R) sides of each limb to assess fluctuating asymmetry (FA) (Palmer and Strobeck 1986, Lazić et al. 2013), while for the other analyzes we used only the left side. The traits were measured twice on different days and in a different order, and remeasured those that differed by more than 10%. We used just adults in morphological analyses, and we defined them as having $SVL > 35$ mm (Hardy et al. 1989) and the development of sexual gonads.

Data analysis

All analyses were performed using R software v4.2.1 (R Core Team 2022). The scripts and supplementary data can be accessed on GitHub (<https://github.com/rosadolucas/underwoodi>).

To generate the thermal performance curve (TPC), we used a generalized additive mixed model (GAMM) (Wood 2017) with package *mgcv* v1.8 (Wood 2001). We set the extremes of the curve with the values of CT_{min} and CT_{max} as velocities equal

to zero (Taylor et al. 2020). We assessed whether morphological traits are important to sprint performance, therefore we add the morphological traits that were different between native and neonative populations, treatment and geographic distribution, as fixed factors in the model. The curve smooth was set with geographic distributions as group parameters and individuals were set as random factors. Since we had many variables, we assessed which model is the best using the package *MuMin* v1.47.1 (Bartón 2022). We selected the models with an AICc difference smaller than 2 ($\Delta < 2$), from the model with lowest AICc (Supplementary data). Graphs were made using the package *ggplot2* (Wickham, 2016). The temperature at which the lizard reached the highest performance was assumed as the optimum temperature for sprint (T_{opt}), and the thermal performance breadth as the range of temperatures where at least 80% of the maximum performance is achieved (B80; Taylor et al. 2020). CT_{min} , CT_{max} , and T_{pref} were compared between distributions (neonative \times native) using *t-tests*, and the test premises were previously assessed (Silva et al. 2022). The specimens that died in some steps of the tests were not used for thermal analyses, just for morphology.

The morphological differences between populations (neonative \times native) were assessed using a non-parametric multivariate analysis of variance (NP-MANOVA) with residual randomization in permutation procedure (RRPP; Collyer and Adams 2018) with 99999 permutations, following Telemeco and Gangloff (2020). This approach produces empirical sampling distributions from the random permutation of the residuals, reducing the chances of Type-I error and the concern between a number of variables and sample number. A principal component analysis (PCA) was used for visualization using *prcomp* and data were *z-score* standardized. The dependence of morphological trait on SVL was tested with a linear model (*lm*), and when the relationship was statistically significant the residuals of the *lm* were passed to be used in RRPP analysis.

To assess the fluctuating asymmetry (FA), we followed Lazić et al. (2013). First, we calculated an asymmetry index (AI) for all traits as the value on the right side minus on the left side ($AI = R - L$), where positive values suggest right dominance and negative values suggest left dominance. Second, we assessed trait size dependence on total body size using a linear regression between asymmetry index and SVL ($AI \sim SVL$) and the dependence on own trait size using a linear regression between asymmetry index and the average between left and right measures of each trait [$AI \sim (R + L)/2$]. Third, we assessed whether distributions have directional asymmetry (DA) or FA

through a linear mixed-effect model (LMM) with the package *nlme* (Pinheiro et al. 2023). The LMM was performed with the original data for each population for each morphological trait separately. Morphological traits were set as fixed factors between side and their interaction with specimens (side:specimen), both as fixed factors, and specimen measurements as random factor. For count of scales of hinfeet and forefeet (SFT and SFF) we used the family poisson in the package *glmmTMB* (Brooks et al. 2017). Fourth, we examined the FA between native and neonative populations using a *one-way* ANOVA with the \log_{10} -transformation of absolute values of AI ($(|\log_{10}(R_{\text{average}}) - \log_{10}(L_{\text{average}})|)$).

Inferring species distribution and extinction risks

To assess the current distribution of *Gymnophthalmus underwoodi*, infer its potential dispersion routes and its extinction risks we performed a hybrid species distribution model (Elith et al. 2010, Tourinho and Vale 2023). We chose the hybrid model since this approach has been shown as a more complete method to assess the effects of climate change on species (Pontes-da-Silva et al. 2018, Caetano et al. 2020, Tourinho et al. 2021, Tourinho and Vale 2023).

We selected four types of predictors: (1) Bioclimatic variables, available at WorldClim (<https://www.worldclim.org/>) (Fick and Hijmans 2017); (2) Soil types (percentage of clay, silt, and sand) available in Soilgrid (<https://soilgrids.org/>) (Hengl et al. 2017) for 0.0 and 5 cm depths; (3) Landcover based on Global land-use and land cover change (LUCC) (available at <https://geosimulation.cn/GlobalLUCCProduct.html>) (Li et al. 2017); (4) Slope acquired through altitude using function *terrain*; and (5) Ecophysiological variables, the hour of activity (H_a) and sprint performance. We excluded four bioclimatic variables that showed spatial anomalies in the study area (Bio07, Bio16, Bio18, and Bio19). For the remaining 15 variables left, we used variance inflation factor (VIF) with a threshold of 10 to reduce multicollinearity (Sillero et al. 2021) while changing Bio02 (Mean Diurnal Range) for Bio05 (Maximum Temperature of Warmest Month), and Bio12 (Annual Precipitation) for Bio15 (Precipitation Seasonality) since extreme are important to assess species vulnerability (Román-Palacios and Wiens 2020). The landcover was used as a continuous raster, where all forest biomes were set as 1 and grassland as 0. We used two scenarios of forest predictions in the future models, where the pessimistic scenario A2 was used for SSP5-8.5 and moderate scenario A1B for SSP3-7.0 (Sales et al. 2020). To create the

ecophysiological variables, we followed the vignette of the package *Mapinguari* (available at <https://gabrielhoc.github.io/Mapinguari.html>) (Caetano et al. 2019, 2020). We used the TPC calculated before (see Data Analysis) since this is a proxy to Darwinian fitness usually used for lizards (Angilletta 2009, Taylor et al. 2020), and hours of activity (H_a), an important predictor for assessing the effects of climate change (Angilletta et al. 2002, Sinervo et al. 2010, Caetano et al. 2020). All variables were aggregated to 2.5' (~ 5 km) spatial resolution. The correlation among all predictors was assessed using VIF (>10), resulting in the final 11 variables selected. We predicted the species distribution in two different climate change scenarios: moderate (SSP3-7.0) and extreme (SSP5-8.5); and in two different periods of time: 2060 and 2100 (Fick and Hijmans 2017, Riahi et al. 2017, IPCC 2021). To account for uncertainty, we choose four different global climate models (IPSL-CM6A-LR, MIROC6, MRI-ESM2-0, and UKESM10LL) that represent a good projection in study area (Cannon 2020).

We delimited the accessible area with a minimum convex polygon with a 500 km buffer (Elith et al. 2010, Barve et al. 2011, Mendes et al. 2020). This area almost covers the entire distribution of the genus *Gymnophthalmus*, thus covering a large variability of climate conditions available (Elith et al. 2010, Escobar et al. 2014, Sillero et al. 2021). However, we extrapolate the model to an area that ranges from latitude -90° to -45° , and longitude -10° to 25° to evaluate possible future areas of dispersion. The distribution records used were obtained through our records, literature records, GBIF (available at <https://www.gbif.org/>), and iNaturalist (available at <https://www.inaturalist.org/>), using only unique occurrences (157 total) (Supplementary data). We used an environmental filter, *EnvSample* function, that reduces environmental bias using the grid resolution of the variables (Varela et al. 2014), only with predictors selected with $VIF < 2$ (seven in total) from those 11 sets above, leaving 103 records. Additionally, we used a 10 km buffer (Castellanos et al. 2019) to reduce geographic biases, keeping 75 records.

We performed the SDM with package *ENMTML* (Andrade et al. 2020) using four algorithms: Maximum Entropy (presence and background) (Phillips 2021), Bayesian Gaussian Process (presence and pseudo-absence) (Golding 2014, Golding and Purse 2016), Random Forest (presence and pseudo-absence) (Liaw and Wiener 2002), and Support Vector Machine (presence and pseudo-absence) (Karatzoglou et al. 2004); with the final model being the ensemble of the weighted mean of Sørensen index (Leroy et al. 2018). Sørensen index uses similarity/F-measures, not using true negative (real

absence of species) to evaluate the model. This increases its discrimination capacity (distinguishing between presence and absence sites) since it is not biased by the prevalence of data (ratio between species occupancy area and study area) (Leroy et al. 2018). The choice of the four algorithms was based on their general performance in default settings and in the type of data necessary for their execution (absence and background), allowing a better ensemble (Sillero et al. 2021, Valavi et al. 2022, 2023). In addition, we performed the model using the Bioclim and generalized linear models algorithms (also available in *ENMTML*), however they did not perform well, so we excluded them from analysis. The number of pseudo-absences represents places where the species is not found but needs confirmation, and was equal to presences (presences/pseudo-absences ratio equal to 1), allocated outside a buffer of 50 km following the default parameters of the package, as well as the number of background points (10,000; points for climate sampling of environment) (Barbet-Massin et al. 2012, Andrade et al. 2020). The data partition was made using the ‘checkerboard’ cross-validation approach to reduce the spatial correlation (Roberts et al. 2017). Sørensen and TSS metrics (Allouche et al. 2006, Leroy et al. 2018), were used for model evaluation in which values close to +1 suggest a good model.

The model ensemble resulted in a threshold of 0.31 (details in Appendix 2) that was used to make a binary plot and estimate the area of occurrence. The estimated area of occurrence was calculated using the same polygon from the accessible area. The current and future binary plots were overlapped to assess which areas are considered stable, and in which areas *Gymnophthalmus underwoodi* is forecast to lose or gain ranges. Following the same process described above, we performed two other distribution models in SSP5-5.8 scenario, one without land cover and the other model without ecophysiological variables to assess which is the most limiting predictor for the species distribution.

Results

Genealogy and sample size

We collected a total of 57 individuals (29 from Bonfim, RR [native population], and 28 from Manaus, AM [neonative population]). For thermal analyses we used 36 (n = 18 to neonative; n = 18 to native) since some individuals died in the experiment (n = 2), and others did not have all limbs (n = 1) or were occasionally collected (n = 18), preventing them from being included in the experiments, in consequence of time of

collect to execution of tests. All specimens collected were attributed to *Gymnophthalmus underwoodi* by morphological inspection and Bayesian Inference which grouped all 10 specimens from the native population and 8 from the neonative population (Figure 2). As expected, all samples of *G. underwoodi* make a polytomy as a result of genetic similarity coming from a true parthenogenetic species (Cole et al. 1990, 1993, Funk and Omland 2003).

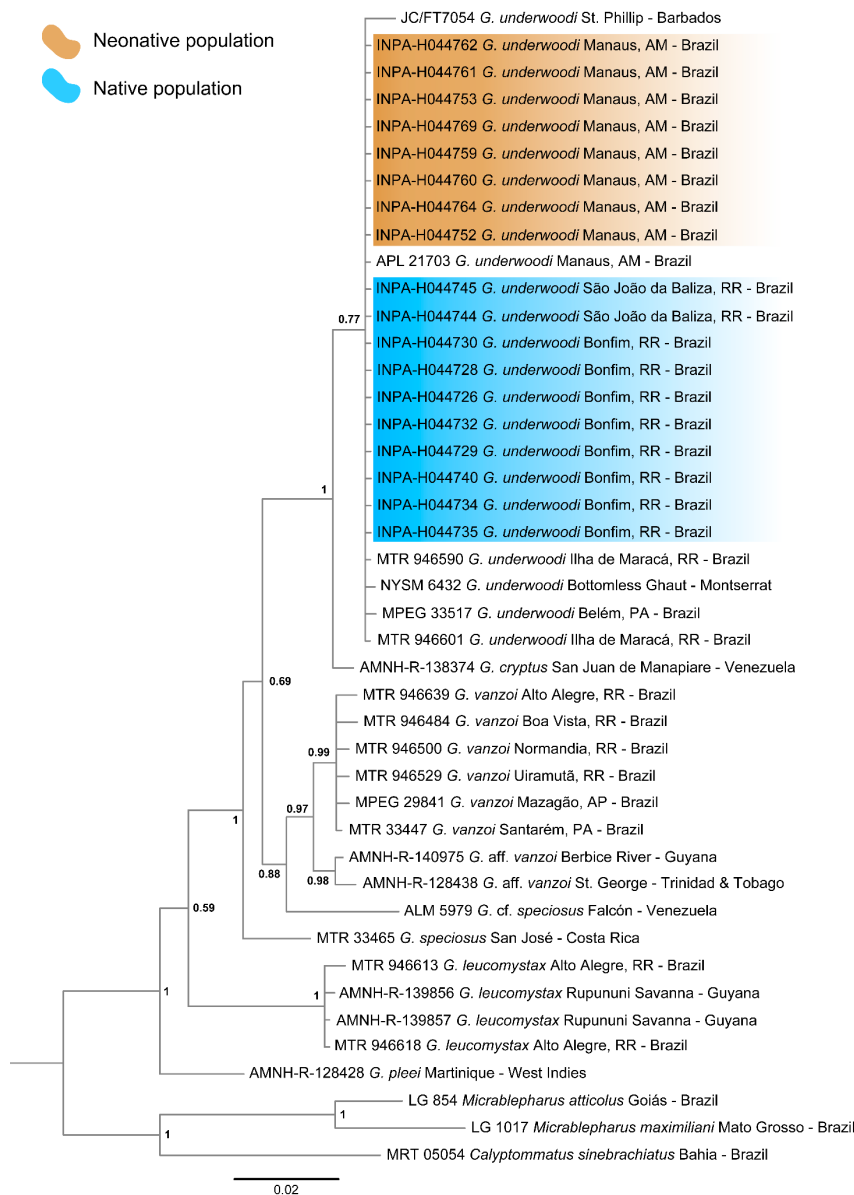


Figure 2. Bayesian Inference of mDNA 16S of *Gymnophthalmus underwoodi*. Individuals collected in the native population (blue band) and in the neonative population (brown band) are grouped with the nominal species and show very little variation as expected for parthenogenetic species.

Thermal sensitivity

The neonative population has a colder CT_{min} than the native population ($t_{34} = -4.3398$, $p\text{-value} = 0.0001$; 15.58 ± 1.20 °C and 17.65 ± 1.61 °C, respectively), but has the same values for CT_{max} ($t_{34} = 0.8055$, $p\text{-value} = 0.4261$; 45.05 ± 0.84 °C and 44.85 ± 0.57 °C, respectively). Neonative and native populations show the same T_{pref} of around 32 °C ($t_{33} = 0.8658$, $p\text{-value} = 0.3928$; 32.70 ± 1.82 °C and 32.24 ± 1.29 °C, respectively) with voluntary temperature in $VT_{min} = 30.17$ °C and $VT_{max} = 36.12$ °C for neonative and $VT_{min} = 29.7$ °C and $VT_{max} = 35.34$ °C for native. Details of t test of thermal traits are available in Supplementary file Table 1. The best model for predicting thermal performance included snout-vent length (SVL), forearm length (FAL), hindfoot length (FTL), and geographic distribution as important variables (Appendix 3 and 4) with the neonative population having greater performance than the native population (Figure 3; $p\text{-value} < 0.00005$). The neonative population has a narrow thermal performance curve (TPC), with the thermal optimal performance (T_{opt}) in higher temperatures, close to CT_{max} , whereas the native population appears to have a wider TPC (Figure 3). The thermal performance breadth (B80) follows the TPC, while the native population has a wide range (B80 = 21.95 – 40.31 °C) with T_{opt} in 32.29 ± 2.81 °C, the neonative population has a narrow range (B80 = 27.29 – 40.58 °C) with T_{opt} in 37.61 ± 0.81 °C.

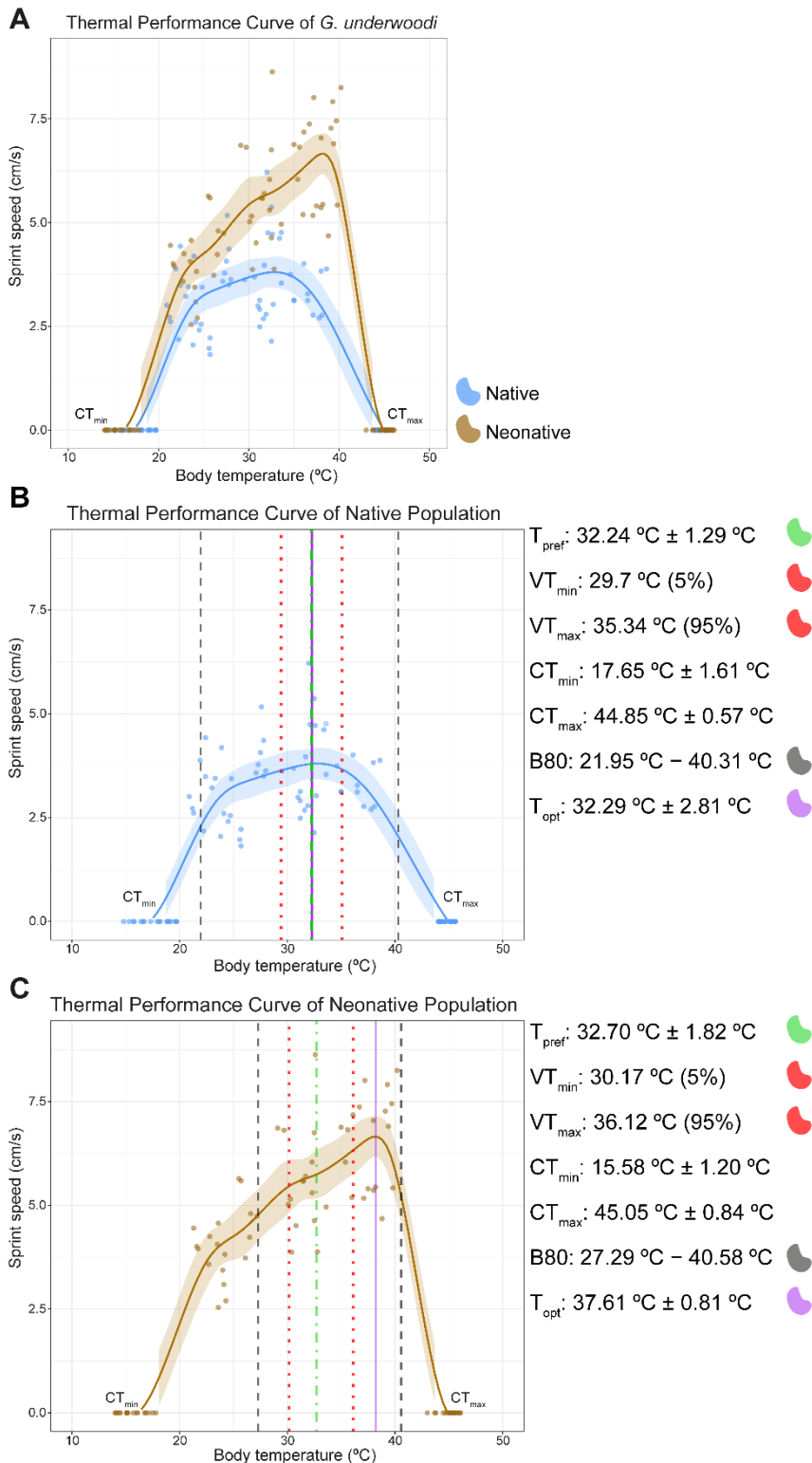


Figure 3. Thermal Performance Curve (TPC) of *Gymnophthalmus underwoodi* in native and neonative populations (A). Native population (B; blue curve) shows a wide and smaller curve with a thermal optimal (T_{opt}) nearby to the middle of the curve (purple line), at the same value of preferential temperature (T_{pref} ; green dotted line). The neonative population (C; brown curve) has a narrow and bigger curve, with a T_{opt} nearby to the critical maximum (CT_{max}) (purple line) and higher than T_{pref} (green dotted line). The native population has the T_{opt} inside the thermal voluntary limits (VT_{min} and VT_{max} ; red dotted line) whereas in the neonative population the T_{opt} is outside the VT_{min} and VT_{max} . In general, the neonative population has higher TPC but lower thermal performance breadth (B80; gray dotted line).

Morphological traits

The morphological analyses showed that there is no difference in snout-vent length (SVL) between native and neonative populations (*t-test*: $t_{54} = -0.34615$, $p\text{-value} = 0.7306$). All traits are dependent on SVL ($p\text{-value} < 0.05$) except tail length. PCA showed little overlap between neonative and native traits, with PC1 explaining 19.7% and PC2 explaining 15.3% of the variance (Supplementary files Figure 6 and Table 2). The NP-MANOVA confirms the difference in traits between native and neonative ($F_{1,47} = 6.4779$, $\text{Pr}(>F) < 0.00005$), in which the difference is in head height (HH), trunk length (TRL), interbrachial-nasal length (INL), hind foot length (FTL), forearm length (FAL), tibia length (TL), femur length (FL), scales of the third finger of hindfoot (SHF) (see Figure 4). The specimens from the neonative population are generally bigger than the native population, except for INL and FL. Details of the NP-MANOVA are available in Appendix 5 and the mean of the morphological traits is available in Appendix 6.

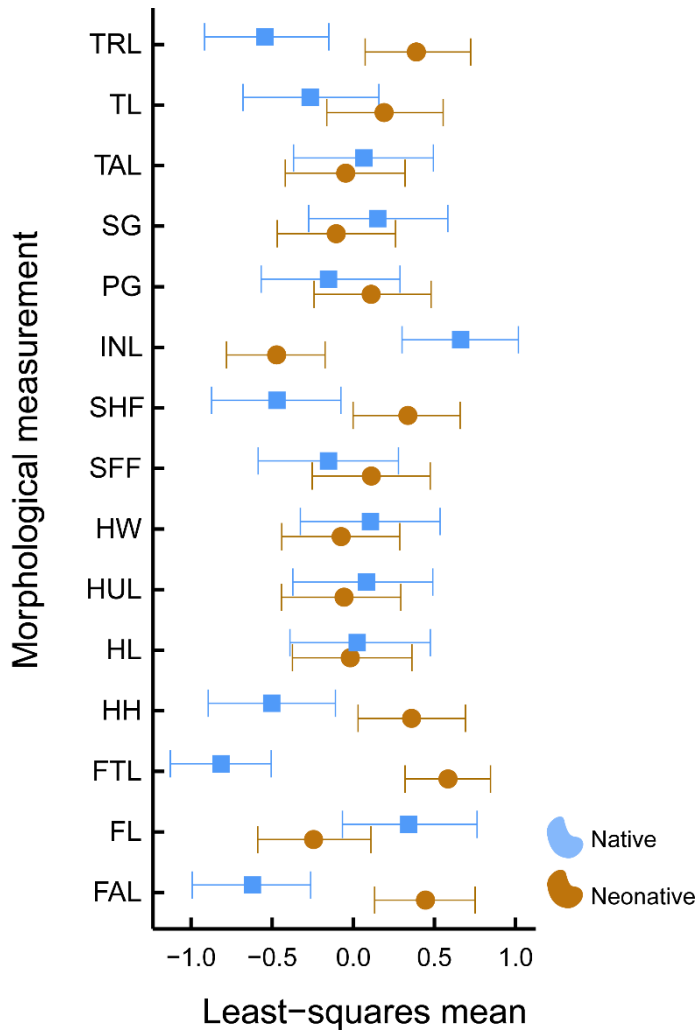


Figure 4. The least-square mean of predicted values at NP-MANOVA with residual randomization permutation procedure, of the morphological traits, analyzed between native (blue) and neonative (brown) populations. The specimens from the neonative population are mostly bigger than native in TRL, TL, HH, FTL, and FAL, except for INL and FL. Besides that, the neonative population has more scales in SFT. HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hindfoot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

The Asymmetry index (AI) did not show a relation with SVL or with trait size for all traits assessed (Appendix 7 and 8). In the model, some traits showed a degree of DA and FA in each population (Appendix 9 and 10), however, when comparing them we did not find consistency across populations nor find statistical significance for all traits (Table 1), indicating that there is no tendency for increased asymmetry in urban environments. The AI values are available in Supplementary file Table 3.

Table 1. Analysis of Variance (ANOVA) of asymmetry index (AI) between native and neonative populations. All traits assessed are equal in neonative and native populations, showing a Pr(>F) higher than 0.05. Df: degrees of freedom; FL: femur length; TL: tibia length; FTL: hindfoot length; HUL: humeral length; FAL: forearm length; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

Trait	Df	Sum Sq	Mean Sq	F value	Pr(>F)
FL	1	0.000388	0.000388	0.2449	0.6228
TL	1	0.003204	0.003204	1.9758	0.1660
FTL	1	0.001882	0.001882	2.0078	0.1627
HUL	1	0.001172	0.001172	0.9538	0.3335
FAL	1	0.000760	0.000760	0.7867	0.3794
SHF	1	0.001232	0.001232	1.3557	0.2498
SFF	1	0.001137	0.001137	0.7222	0.3995

Current and future distributions

The ensemble of SDM showed good performance (TSS = 0.70, Sørensen = 0.84; Appendix 2), and the current distribution estimated from binary models (threshold value = 0.31) of *Gymnophthalmus underwoodi* comprises an area of $\pm 1,295,742$ km². The five most important variables were (most importance > less importance): Temperature Seasonality (Bio04), Land cover, Clay content (0.0 depth), Performance of neonative population, and Isothermality (Bio03). The importance of each variable can be seen in detail in Appendix 11. The model predicts high-suitability areas next to the Atlantic coast of northern South America, the Caribbean islands, along the Amazonas and Branco rivers, and a large area in the south of Colombia (Figure 5). Future predictions (2060 and 2100) show a decline in high suitability areas and an increase of suitability in areas that nowadays are low, with an increase in the predicted area estimated from binary maps mainly in the extreme climatic scenario and with the pessimistic deforestation prediction (SSP5-8.5; Figure 6D-F and Table 2).

Table 2. Predicted area of occurrence for *Gymnophthalmus underwoodi* in current and four future scenarios. The species show a decrease of its distribution until 2100 in 38% for moderated scenarios (SSP3-7.0), whereas extreme scenarios (SSP5-8.5) with the pessimistic deforestation prediction have an increase in its distribution in 2100 (0.85%). Percentage of gain and loss reference to current distribution.

Scenario	Year	Predicted area (km ²)	Gain and loss (%)
Current	2022	1,295,742	-
SSP3-7.0	2060	1,180,537	-8.89%
	2100	791,237	-38.93%
SSP5-8.5	2060	1,201,380	-7.28%
	2100	1,306,801	+0.85%

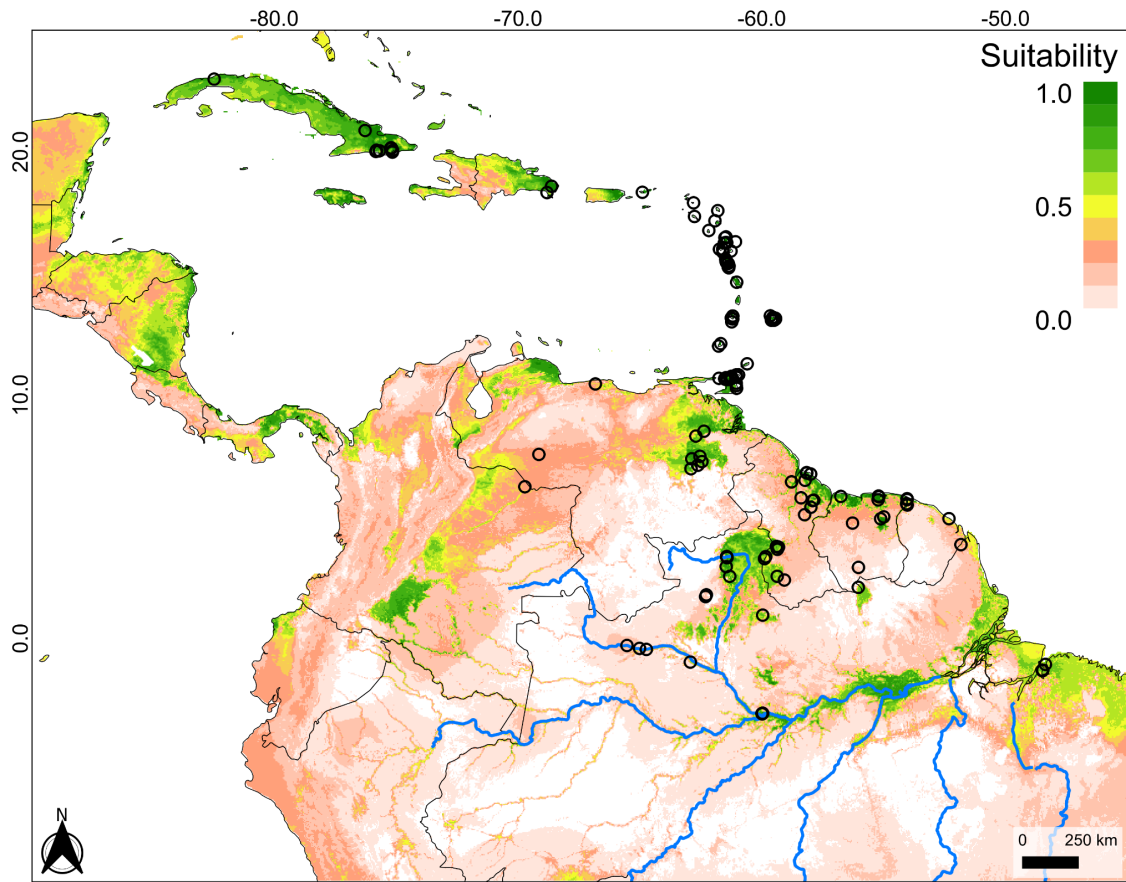


Figure 5. The current distribution of *Gymnophthalmus underwoodi* estimated from an ensemble of the weighted mean of Sørensen index from Maximum Entropy, Bayesian Gaussian Process, Random Forest, and Support Vector Machine models. The higher suitability is indicated by green color, in a continuous gradient, whereas the white color indicates the lower suitability areas. Circles represent the current distribution records of *G. underwoodi*. The blue line represent the Amazon rivers.

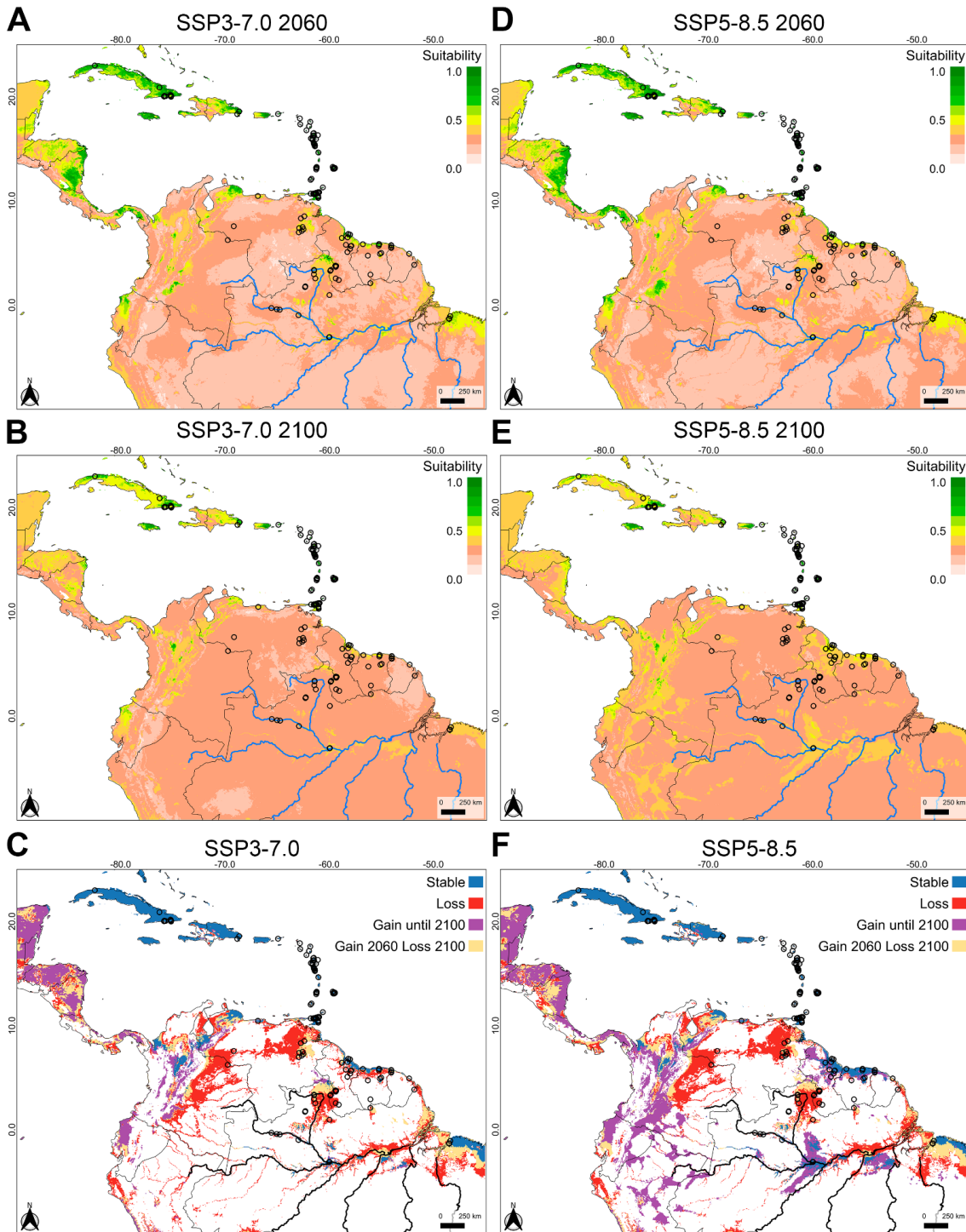


Figure 6. Species Distribution Model predicted using moderated scenario (SSP3-7.0, A-C) and extreme scenario (SSP5-8.5, D-F) of CO₂ emission in two periods 2060 (first-row) and 2100 (second-row). Binary plots (third-row) show the gain of predicted area for the extreme scenario, through overlapping of each binary plot, showing the stable areas (blue) over time, lost areas (red), areas lost in 2100 but gained in 2060 (yellow), and area gain until 2100 (purple). The blue and black line represent the Amazon rivers.

Discussion

Urban environments require species to be plastic or adapt to support the new and often stressful conditions (Donihue and Lambert 2015, Borden and Flory 2021, Lambert et al. 2021, Thompson et al. 2022), as we find for *Gymnophthalmus underwoodi*. This species dwells in open areas, which have a wide variation of temperature, and we expected to find a wide thermal curve that allows it to support this variation (Angilletta et al. 2002, Tewksbury et al. 2008). We found this pattern for the native population (Roraima), whereas the neonative population (Manaus) has a narrow thermal performance breadth (B80) in thermal performance curve (TPC), with a higher T_{opt} in warmer temperatures than the native, as probably a response to urban heat islands (Campbell-Staton et al. 2020, Borden and Flory 2021, Lambert et al. 2021).

Different mechanisms can lead to this response, and two are more likely for this parthenogenetic species. The first is transgenerational plasticity as a result of the nest site chosen by the gravid females to lay the eggs (Paranjpe et al. 2013, Sinervo et al. 2018, Fox et al. 2019, Moore et al. 2019, Caspi et al. 2022, Rossigalli-Costa and Kohlsdorf 2022). Urban environments have higher temperatures than natural environments (open areas within forest matrices included), as a result of the use of cement and other products with low albedo, which holds warmth for more time (Grimm et al. 2008, Hulley 2012, Borden and Flory 2021). The second is contextual plasticity, a change of behavior in response to the new environment (Caspi et al. 2022). Cities require that species have generalist behavior and be able to cross different barriers (Doherty et al. 2021, Caspi et al. 2022). The native habitat of *Gymnophthalmus underwoodi* is generally open, with few barriers. However, the individuals that live in cities need to climb and cross walls, and other structures, if they want to reach other areas, to explore new microhabitats as new warm surfaces, and they are able to do it (video available at <https://youtu.be/i4X32hPchQQ>; Mendonça, L. R. and Werneck, F. P. personal communication). Nevertheless, we did not find differences in speed between substrate treatments (Appendix 4), suggesting that this is not a factor leading to *G. underwoodi* adaptation to urban environments, unlike what has been found for other lizards (Winchell et al. 2016, Vaughn et al. 2021). The similarity of each substrate used in this study may have induced the absence of evidence of substrate effect. Sandpaper and clay have similar textures, and the sprint of terrestrial generalist lizards has low variation in the ground substrate (Tulli et al. 2012, Brandt et al. 2015).

CT_{\min} is generally more variable than CT_{\max} , even though the latter may change (Campbell-Staton et al. 2020, Bodensteiner et al. 2021). The changes in behavior may explain neonatives having a lower CT_{\min} than individuals from the native population, while having the same T_{pref} and CT_{\max} . The general rule is that urban environments have higher temperatures than other areas (Grimm et al. 2008). However, urban areas may have more foggy days during winter than nearby areas, reducing the solar radiation and therefore changing the thermal propriety of the microhabitat (Parris 2016). *Gymnophthalmus underwoodi* individuals inhabit garden areas close to houses and buildings, in urban environments, where the temperature is colder than in cement (Armson et al. 2012). Moreover, buildings may produce more shadows, contributing to reducing the micro-temperatures in urban areas over the day, and selecting organisms that can persist under colder environments. In the case of CT_{\max} , the urban heat island may lead to enhanced heat tolerance (Campbell-Staton et al. 2020, Lambert et al. 2021). Nevertheless, the same behavior that leads to lower CT_{\min} may buffer the higher effects of the heat island. As in the case of the burrowing habit that buffers the effects of high temperatures when reached at 5 cm depth, keeping the CT_{\max} invariable (Buckley et al. 2015, Camacho et al. 2015, Gilbert and Miles 2017).

T_{pref} did not differ between neonative and native populations. Our estimates of T_{pref} were obtained in laboratory conditions and do not account for additional effects existing in field conditions. The active body temperature of some individuals in neonative population reached 40.1 °C (LRM, personal observation), similar to that found by Cole et al. (1990). In field conditions, individuals may have fed before we caught them, resulting in higher body temperatures (T_b), which was not the case during the experiments (Simandle et al. 2001, Gilbert and Miles 2016, Abayarathna and Webb 2021). Besides that, gravid females may choose lower T_b to avoid developmental stress (Paranjpe et al. 2013, Sinervo et al. 2018), and three individuals from the neonative population had eggs, whereas others from the same locality had follicles in development. In addition, wider thermoregulatory opportunities in urban environments may act as a buffer to local adaptation, allowing the T_{pref} of neonative population to be the similar to native population (Buckley et al. 2015). Moreover, the differences between T_b and T_{pref} might suggest that the neonative population is under going an adjustment process and that T_{pref} is selected to optimize their physiological process, even though the performance of a species increases with temperature (Angilletta et al. 2002, Angilletta 2009, Nordberg and Schwarzkopf 2019, Alés et al. 2021, Caspi et al. 2022).

In some cases, individuals may not perform at 100% of their capacity, instead, they perform at lower levels to reduce energetic costs, and focus on different escape routes (Hertz et al. 1983, Huey et al. 1989, Jayne and Irschick 2000). The maintenance of body temperature is lower than the optimal temperature to sprint but inside the B80 ensures that the species will have a broader ‘safety zone’ since it is further away from CT_{max} (Martin and Huey 2008).

Gymnophthalmus underwoodi is plastic across its native and expanded ranges, not only in the thermal ecology but also in morphology. The neonative population has bigger limbs (FTL and FAL) than the native, which is linked to locomotor performance and may enhance the climbing capacity necessary in the urban environment (Losos and Irschick 1996, Melville and Swain 2000, Kohlsdorf and Navas 2012, Winchell et al. 2016, 2018, Foster et al. 2018, Rossigalli-Costa and Kohlsdorf 2022). The increase in sprint performance promoted by longer hindfoot (FTL) and forearm (FAL) may be associated with escaping behaviors from predators in the urban environment (Seligmann et al. 2003, Assis et al. 2023). In addition, the longer forearm may enhance the support during maneuverability through the rocks, trash, and other obstacles present in urban environments that are less common in natural open environments (Melville and Swain 2000, Tulli et al. 2012). Besides that, individuals of the neonative population have a longer trunk (TRL) than natives. A bigger trunk structure can be the result of the increase in food availability and the site of the nest chosen by the mother. Lower temperatures may increase development time and may increase the size of the hatch, conferring higher thermal inertia, helping the species to maintain T_{pref} during cold periods in the city, even during rainy seasons (Kingsolver and Huey 2008, Valenzuela-Sánchez et al. 2015, Noble et al. 2018, Putman and Tippie 2020). In addition, the longer TRL is associated with burrowing performance and arid environments (Grizante et al. 2012, Camacho et al. 2015), which may facilitate mobility between barriers in urban environments. In contrast, the native population shows a bigger interbrachial-nasal length (INL), and this may allow them to catch prey inside the termite mounds, the place where they were found foraging nearby (Caldwell and Vitt 1999, Mendonça, L. R. personal communication). Individuals from the native population have smaller heads than individuals from neonative population, and the increase in INL associated with other cranial structures (that were not assessed) might allow a better capacity to dig (Barros et al. 2011, Fraga et al. 2022). These significant

differences in morphology reinforce the importance of urban environments as a filter of biodiversity, leading to adaptation or plastic responses.

Both populations have some degree of fluctuating asymmetry (FA) on some of the traits measured. However, this FA does not differ between neonative and native populations. This suggests that the environmental filters that are leading the populations to new phenotypes are not very harmful, to which they possibly are adapted (Laia et al. 2015).

The SDM predicts suitable areas for the occurrence of *Gymnophthalmus underwoodi* next to the rivers, the Atlantic coast, and over the Amazonian open areas, mainly in the savanna of Roraima. Areas adjacent to rivers have a higher proportion of open areas, due to natural and anthropic disturbances, which could facilitate the dispersion of *G. underwoodi* through river banks to central (Manaus) and eastern (Belém) Amazonia. It has been proposed that the recent dispersion of *G. underwoodi* to Belém and to Caribbean islands, including Cuba, has been facilitated by accidental transport aboard boats (Alfonso et al. 2012, Alfonso and Hernandez 2017, Maciel et al. 2021), and the suitability of areas through the river banks reinforce it. This mechanism of transport has also been suggested for another species in the area (*Lepidodactylus lugubris* [Duméril & Bribon 1836]) (Hoogmoed and Avila-Pires 2015). However, another mechanism by which *G. underwoodi* could have arrived in Belém is by dispersing across the coast of Amapá, Brazil, where the model shows suitable areas, and crossing the Amazonas River using natural rafts (Hedges et al. 1992, Censky et al. 1998), as well as may use to reach the Caribbean Sea (Kizirian and Cole 1999). For the species to arrive in Manaus, they could disperse using the river banks of Branco and Negro rivers or the BR-174 road which connects Manaus, Amazonas, to Boa Vista, Roraima. Some species track environmental changes and use them to go to new suitable areas that were not previously available (Essl et al. 2019, Martins et al. 2021). We have records of *G. underwoodi* in Amazonas since 1973 in Barcelos (MZUSP31928), upper Negro river, however, the first record in Manaus, Amazonas, was in 2011 (INPA-H031306:12). This record was 34 years after the inauguration of BR-174 road, which suggests that the installation of the road allowed or facilitated their dispersion, since before it, the species was unknown in the city.

Although our forecasts show a decrease in areas with the highest values of suitability (>0.80), some scenarios show an increase in areas with enough suitability for the occurrence of the species (>0.31). The extreme scenario (SSP5.8-5) shows a gain of

suitable areas (0.85% until 2100) increasing the distribution of *Gymnophthalmus underwoodi*. The increase of the species distribution in extreme scenarios is associated with deforestation predicted by model A2 at 2100. This increase in its distribution following open areas is not unusual and was observed recently in another parthenogenetic species, *Cnemidophorus cryptus* Cole & Dessauer 1993, during the Pleistocene climatic fluctuations (Martins et al. 2021). However, the preference of *G. underwoodi* for open areas limits its real potential to dispersion. In the model without land cover, the ecophysiological predictors (H_a and TPC) are the most significant variable that increases the species' geographic distribution, and if open areas increase beyond predictions, the species' geographic distribution probably will also increase (Supplementary file Figure 7, Table 4 and 5). The increase in temperature will enhance the performance and the hours of activity (H_a) available for the species, potentially allowing it to disperse into the forest (Huey et al. 2009). *G. underwoodi* is one of the few studied reptiles' species that do not appear to be heavily threatened by recent human actions over the world (Gibbons et al. 2000, Bickford et al. 2010, Sinervo et al. 2010, Böhm et al. 2013, Diele-Viegas and Rocha 2018, Diele-Viegas et al. 2018, 2020, Pontes-da-Silva et al. 2018), and particularly in the Amazonia. This means that not any species can be used as a bio-indicator of high vulnerability or high resilience to the effects of climate change, as even closely related lizard species might have contrasting responses to changing climates (Martins 2021).

How plastic is the phenotype of *Gymnophthalmus underwoodi*? Its morphology and ecophysiology are variable and plastic enough to allow the species to persist and actually thrive in this environment. Its larger hindfoot and forearms allow for better movement in the urban gradient, while the higher temperatures increase its speed. In addition, our model suggests that this lizard will persist and even increase its distribution by 2100. The species distribution model shows an increase in distribution following the new open areas predicted in extreme scenarios, indicating that *G. underwoodi* is tracking environmental change, and not only 'taking rides' in boats to disperse. The species appears to have found an important area to inhabit, the urban environment, and at the same time, the urban environment may lead the species to an evolutionary trap over time (Diamond and Martin 2020). This is a parthenogenetic species and the adaptation rate and plasticity of the clones may not be enough for the species to persist in the long term (Hoffmann and Sgrò 2011, Orive et al. 2017, Fujita et al. 2020, Moreira et al. 2021). New studies with genomic data such as transcriptomics to

allow evaluation of gene expression levels under different treatments and more populations can help to assess how the species will perform in the future, and whether phenotypic plasticity will be enough for species persistence.

Our study compared multiple functional traits across native and supposedly neonative populations and highlighted the impact that altered landscapes and urban environments might have on the ecological and evolutionary trajectories of Amazonia organisms. In addition, this is the first step to understanding how one parthenogenetic species may respond to environmental changes. The phenotypic changes found in the neonative population and its distribution pattern indicate the urban environment as one environmental filter and center of dispersion, that can be used by them to reach other areas (Borden and Flory 2021). Therefore, the urban environment and deforestation can be a threat to Amazon biodiversity, not solely by causing a reduction in population, but also leading the species to a ‘preadaptation’ to another locality and/or filtering those species that better adapt to altered areas, increasing their potential of invasion and putting the native species in concern (Huey et al. 2009, Borden and Flory 2021).

Acknowledgements

We are thankful Brena S. Gonçalves, Bryan C. Martins, Eliza R. Costa, João M. Santos, Rafael N. Leite, Sillionamã P. Dantas and Stuart V. Nielsen for assistance with fieldwork; to Albertina P. Lima, Cintia C. Frische and Isabela Oliveira for allowing the access to areas in Manaus, AM; to Catarina, Dona Flor, Dona Preta, Francisca, Francisco, Henrique, Hélio, Josué, Marcio, Maria Sônia, Sidney, Seu Mimi, Vitor and Welinston for allowing the access to areas in Bonfim, RR; to Erasmo A Silva, Igor Y. Fernandes, Letícia C. P. Sena and Lídia F. Martins and for help in thermal experiments. We thank Marcos R. Rosado for help with R code and Fabrício B. Baccaro help with R code and statistical analysis. We are grateful to Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the fellowship granted to LRM. We also thank members of the Werneck’ lab for their comments and suggestions.

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Appendix

Appendix 1. Molecular sampling and sequences retrieved from Genbank. Specimens used in this study are in process of deposit in Genbank.

Voucher	Species	Locality	Country	16S	Reference
AMNH-R-138374	<i>Gymnophthalmus cryptus</i>	San Juan de Manapiare, Amazonas	Venezuela	AF101362	Kirizian and Cole, 1999
MTR 946613	<i>Gymnophthalmus leucomystax</i>	Alto Alegre, Roraima	Brazil	AF420715	Pellegrino et al. 2001
AMNH-R-139856	<i>Gymnophthalmus leucomystax</i>	Rupununi Savanna	Guyana	AF101363	Kirizian and Cole, 1999
AMNH-R-139857	<i>Gymnophthalmus leucomystax</i>	Rupununi Savanna	Guyana	MH732714	Recoder et al. 2018
MTR 946618	<i>Gymnophthalmus leucomystax</i>	Alto Alegre, Roraima	Brazil	MH732715	Recoder et al. 2018
AMNH-R-128428	<i>Gymnophthalmus pleii</i>	Martinique	West Indies	AF101364	Kirizian and Cole, 1999
MTR 33465	<i>Gymnophthalmus speciosus</i>	San José	Costa Rica	MH732710	Recoder et al. 2018
ALM 5979	<i>Gymnophthalmus cf. speciosus</i>	Adicora, Falcón	Venezuela	AF101367	Kirizian and Cole, 1999
JC/FT7054	<i>Gymnophthalmus underwoodi</i>	St. Phillip	Barbados	AF101369	Kirizian and Cole, 1999
APL 21703	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	MH732712	Recoder et al. 2018
INPA-H044762	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044761	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044753	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044769	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044759	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044760	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044764	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044752	<i>Gymnophthalmus underwoodi</i>	Manaus, Amazonas	Brazil	-	This study
INPA-H044745	<i>Gymnophthalmus underwoodi</i>	São João da Baliza, Roraima	Brazil	-	This study
INPA-H044744	<i>Gymnophthalmus underwoodi</i>	São João da Baliza, Roraima	Brazil	-	This study

INPA-H044730	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044728	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044726	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044732	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044729	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044740	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044734	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
INPA-H044735	<i>Gymnophthalmus underwoodi</i>	Bonfim, Roraima	Brazil	-	This study
MTR 946590	<i>Gymnophthalmus underwoodi</i>	Ilha de Maracá, Roraima	Brazil	KT254406	Goicoechea et al. 2016
NYSM 6432	<i>Gymnophthalmus underwoodi</i>	Bottomless Ghaut	Montserrat	KX866265	Snyder et al. 2017
MPEG 33517	<i>Gymnophthalmus underwoodi</i>	Belém, Pará	Brazil	MZ544022	Maciel et al. 2021
MTR 946601	<i>Gymnophthalmus underwoodi</i>	Ilha de Maracá, Roraima	Brazil	MH732711	Recoder et al. 2018
MTR 946639	<i>Gymnophthalmus vanzoi</i>	Alto Alegre, Roraima	Brazil	AF420743	Pellegrino et al. 2001
MTR 946484	<i>Gymnophthalmus vanzoi</i>	Boa Vista, Roraima	Brazil	MH732699	Recoder et al. 2018
MTR 946500	<i>Gymnophthalmus vanzoi</i>	Normandia, Roraima	Brazil	MH732705	Recoder et al. 2018
MTR 946529	<i>Gymnophthalmus vanzoi</i>	Uiramutã, Roraima	Brazil	MH732708	Recoder et al. 2018
MPEG 29841	<i>Gymnophthalmus vanzoi</i>	Mazagão, Amapá	Brazil	MZ544020	Maciel et al. 2021
MTR 33447	<i>Gymnophthalmus vanzoi</i>	Santarém, Pará	Brazil	MH732695	Recoder et al. 2018
AMNH-R-140975	<i>Gymnophthalmus</i> aff. <i>vanzoi</i>	Berbice River	Guyana	AF101366	Kirizian and Cole, 1999
AMNH-R-128438	<i>Gymnophthalmus</i> aff. <i>vanzoi</i>	St. George	Trinidad and Tobago	MH732709	Recoder et al. 2018
LG 854	<i>Micrablepharus atticolus</i>	Santa Rita do Araguaia, Goiás	Brazil	AF420718	Pellegrino et al. 2001
LG 1017	<i>Micrablepharus maximiliani</i>	Barra do Garças, Mato Grosso	Brazil	AF420730	Pellegrino et al. 2001
MRT 05054	<i>Calyptommatus sinebrachiatus</i>	Gentio do Ouro, Bahia	Brazil	AF420720	Pellegrino et al. 2001

Appendix 2. Evaluation table of Species Distribution Model for *Gymnophthalmus underwoodi*. The ensemble model was made using the weighted mean of the Sørensen index. Threshold was calculated using the Sørensen index. AUC was not used to select the best model however we chose to inform since it is a common evaluation metric. MXD: Maximum Entropy default (all features); SVM: Support Vector Machine; RDF: Random Forest; GAU: Bayesian Gaussian Process.

Algorithm	Threshold	AUC	TSS	Sørensen
MXD	0.31	0.82	0.60	0.78
SVM	0.80	0.86	0.66	0.84
RDF	1.0	0.83	0.58	0.80
GAU	0.80	0.84	0.62	0.81
Ensemble	0.31	0.86	0.70	0.84

Appendix 3. Results of the model inferred with a generalized additive mixed model (GAMM) of Thermal Performance Curve used to create the ecophysiological variables to species distribution model (SDM). FAL: forearm length; FTL: hind foot length; SVL: snout-vent length.

Trait	Estimate	Std.Error	t value	df	F	Pr(> t)
Population	1.06329	0.22974	4.628	1	21.421	7.84×10^{-06} *
FAL	0.80442	0.30456	2.641	1	6.976	0.009122*
FTL	-0.65662	0.30617	-2.145	1	4.600	0.033568*
SVL	0.05799	0.01656	3.501	1	12.260	0.000608*
Smooth terms	edf	Ref.df	F	p-value		
s(temp):neonative	7.820	9	100.70	2×10^{-16} *		
s(temp):native	5.155	9	38.33	2×10^{-16} *		

* values < 0.05.

Appendix 4. Results of the best model selected with *MuMin* and inferred with a generalized additive mixed model (GAMM) of Thermal Performance Curve. FAL: forearm length; FTL: hind foot length; SVL: snout-vent length; SFT: scales of the third finger of hindfoot.

Trait	Estimate	Std.Error	t value	df	F	Pr(> t)
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Population	1.04200	0.23171	4.497	1	20.222	$1.37 \times 10^{-05*}$
treatment	0.09826	0.13728	0.716	1	0.515	0.475216
FAL	0.83910	0.30843	2.721	1	7.402	0.007282*
FTL	-0.65826	0.30639	-2.148	1	4.616	0.033270*
SVL	0.06059	0.01696	3.573	1	12.763	0.000475*
Smooth terms	edf	Ref.df	F	p-value		
s(temp):neonative	7.835	9	101.21	$2 \times 10^{-16*}$		
s(temp):native	5.167	9	38.57	$2 \times 10^{-16*}$		

* values < 0.05.

Appendix 5. Least-square of predicted values from NP-MANOVA with residual randomization in permutation procedure. All traits were used as residual values of the linear regression between the trait and SVL in PCA. HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hindfoot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

Trait	Neonative			Native		
	Mean	95% lower confidence	95% upper confidence	Mean	95% lower confidence	95% upper confidence
HL	-0.0186	-0.3750	0.3614	0.0241	-0.3904	0.4743
HH	0.3590	0.0295	0.6917	-0.5032	-0.8936	-0.1097
HW	-0.0750	-0.4407	0.2865	0.1056	-0.3262	0.5349
TRL	0.3886	0.0731	0.7226	-0.5448	-0.9164	-0.1514
INL	-0.4722	-0.7813	-0.1739	0.6616	0.3007	1.0174
SG	-0.1052	-0.4685	0.2607	0.1503	-0.2755	0.5824
PG	0.1100	-0.2419	0.4793	-0.1528	-0.5683	0.2882
FL	-0.2448	-0.5887	0.1085	0.3415	-0.0669	0.7629
TL	0.1897	-0.1635	0.5538	-0.2657	-0.6802	0.1581
FTL	0.5835	0.3189	0.8456	-0.8155	-1.1272	-0.5057
HUL	-0.0569	-0.4430	0.2925	0.0814	-0.3729	0.4895
FAL	0.4449	0.1314	0.7511	-0.6216	-0.9924	-0.2622
SHF	0.3364	-0.0014	0.6586	-0.4706	-0.8736	-0.0768

SFF	0.1112	-0.2530	0.4739	-0.1526	-0.5860	0.2784
TAL	-0.0468	-0.4194	0.3184	0.0647	-0.3685	0.4937

Appendix 6. Table of the mean of original values of morphological traits measured. Sd: standard deviation; Se: standard error; SVL: snout-vent length; HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet. The left side is represented by _L and the right side by _R. Original data is available at (<https://github.com/rosadolucas/underwoodi>).

Trait	Distribution	N	Mean	Sd	Se
SVL	Neonative	35	40.5500	3.2548	0.5502
	Native	21	40.8900	4.0259	0.8785
INL	Neonative	28	12.6799	0.8650	0.1635
	Native	20	13.3929	1.0166	0.2273
TRL	Neonative	28	22.0621	2.2248	0.4204
	Native	20	21.5026	2.7440	0.6136
HH	Neonative	28	3.7454	0.2794	0.0528
	Native	20	3.5539	0.3527	0.0789
HL	Neonative	28	6.7392	0.5402	0.1021
	Native	20	6.7748	0.4912	0.1098
HW	Neonative	28	5.5508	0.4438	0.0839
	Native	20	5.6071	0.4750	0.1062
SG	Neonative	28	5.0078	0.4582	0.0866
	Native	20	5.0977	0.4452	0.0996
PG	Neonative	28	5.5317	0.4454	0.0842
	Native	20	5.4744	0.4874	0.1090
TAL	Neonative	28	48.5837	15.0643	2.8469
	Native	20	50.1122	11.8762	2.6556
BM	Neonative	22	0.9373	0.2713	0.0578
	Native	19	0.9247	0.2620	0.0601
FL_L	Neonative	28	4.4644	0.4013	0.0758
	Native	20	4.6115	0.3743	0.0837
FL_R	Neonative	28	4.3841	0.3153	0.0596

	Native	20	4.4840	0.3734	0.0835
TL_L	Neonative	28	3.2579	0.2828	0.0534
	Native	20	3.1369	0.2412	0.0539
TL_R	Neonative	28	3.3658	0.3297	0.0623
	Native	20	3.1763	0.2133	0.0477
FTL_L	Neonative	28	6.8120	0.3379	0.0639
	Native	20	6.3810	0.3348	0.0749
FTL_R	Neonative	28	6.8489	0.3541	0.0669
	Native	20	6.5281	0.3348	0.0749
HUL_L	Neonative	28	3.2189	0.3672	0.0694
	Native	20	3.2637	0.2006	0.0449
HUL_R	Neonative	28	3.1823	0.3162	0.0598
	Native	20	3.2374	0.1936	0.0433
FAL_L	Neonative	28	6.5710	0.3662	0.0692
	Native	20	6.2203	0.2741	0.0613
FAL_R	Neonative	28	6.5277	0.3883	0.0734
	Native	20	6.1173	0.3288	0.0735
SHF_L	Neonative	35	17.0538	0.5928	0.1002
	Native	21	16.6179	0.4967	0.1084
SFT_R	Neonative	35	17.0682	0.5925	0.1001
	Native	21	16.9048	0.6249	0.1364
SHF_L	Neonative	35	13.3881	0.6875	0.1162
	Native	21	13.3576	0.4782	0.1044
SFF_R	Neonative	35	13.4000	0.6508	0.1100
	Native	21	13.0952	0.6249	0.1364

Appendix 7. Results of analysis of variance (ANOVA) assessing the relation of asymmetry index (AI) of morphology measures with snout-vent length (SVL). HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; SFT: scales of the third finger of hindfoot; SHF: scales of the third finger of forefeet; Sd: standard deviation; Se: standard error; Df: degrees of freedom.

Trait	Df	Sum sq	Mean sq	F value	Pr(>F)
FL	1	0.1862	0.1862	2.3018	0.1323
TL	1	0.0077	0.0077	0.1510	0.6984
FTL	1	0.2090	0.2090	2.2864	0.1336

HUL	1	0.0234	0.0234	0.5389	0.4646
FAL	1	0.0997	0.0997	1.3193	0.2534
SHF	1	0.1950	0.1947	0.5318	0.4675
SFF	1	0.1500	0.1500	0.3687	0.5450

Appendix 8. Results of analysis of variance (ANOVA) assessing the relation of asymmetry index (AI) of morphology measures with trait size $(Right_{side} + Left_{side})/2$. HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; SFT: scales of the third finger of hindfoot; SHF: scales of the third finger of forefeet; Sd: standard deviation; Se: standard error; Df: degrees of freedom.

Trait	Df	Sum sq	mean sq	F value	Pr(>F)
FL	1	0.2241	0.2241	2.7839	0.0983
TL	1	0.1140	0.1140	2.2850	0.1337
FTL	1	0.2155	0.2155	2.3594	0.1276
HUL	1	0.1609	0.1609	3.8294	0.0531
FAL	1	0.2085	0.2085	2.7984	0.0974
SHF	1	0.0340	0.0345	0.0937	0.7601
SFF	1	0.0410	0.0411	0.1007	0.7516

Appendix 9. Results of the linear mixed model (LMM) assessing fluctuating asymmetry (FA) and directional asymmetry (DA) into native and neonative populations. Statistical significance of Side suggest DA whereas the interaction Side:Individual suggest FA. HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length.

Neonative					
Trait	Model	numDF	denDF	F-value	p-value
FL	Side	1	32	16.603	0.0003*
	Side:Id	60	32	2.532	0.0027*
TL	Side	1	32	10.472	0.0028*
	Side:Id	0	32	1.782	0.0391*
FTL	Side	1	32	0.359	0.5535

	Side:Id	60	32	1.449	0.1281
HUL	Side	1	32	1.694	0.2024
	Side:Id	60	32	2.072	0.0137*
FAL	Side	1	32	9.991	0.0034*
	Side:Id	60	32	1.668	0.0591
Native					
Trait	Model	numDF	denDF	F-value	p-value
FL	Side	1	22	12.060	0.0022*
	Side:Id	40	22	1.836	0.0652
TL	Side	1	22	0.841	0.3691
	Side:Id	40	22	0.990	0.5251
FTL	Side	1	22	20.185	0.0002*
	Side:Id	40	22	3.195	0.0025*
HUL	Side	1	22	2.754	0.1112
	Side:Id	40	22	0.810	0.7248
FAL	Side	1	22	5.994	0.0228*
	Side:Id	40	22	1.771	0.0772

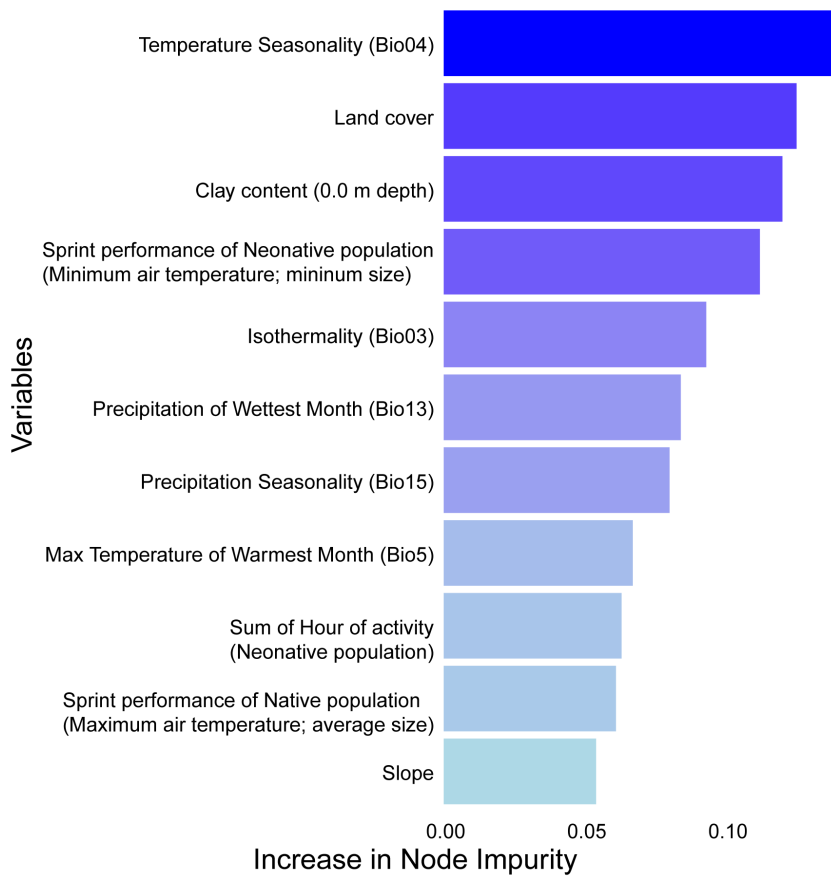
* values < 0.05.

Appendix 10. Results of the generalized linear mixed model (GLMM) with Poisson correction assessing fluctuating asymmetry (FA) and directional asymmetry (DA) into native and neonative populations. The statistical significance of Side suggests DA whereas the interaction Side: Individual suggests FA. SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

Neonative				
Trait	Model	Chisq	df	Pr(>Chisq)
SHF	Side	0.0606	1	0.8056
	Side:Id	2.7808	60	1.0000
SFF	Side	0.0000	1	1.0000
	Side:Id	4.3078	60	1.0000
Native				
Trait	Model	Chisq	df	Pr(>Chisq)
SHF	Side	0.0000	1	1.0000

	Side:Id	1.6509	40	1.0000
SFF	Side	0.0740	1	0.7855
	Side:Id	1.8363	40	1.0000

Appendix 11. Variables importance of the species distribution model performed. The Temperature Seasonality (Bio04) is the most important variable, while the Slope is the less important to the lizard *Gymnophthalmus underwoodi*.



Supplementary files



Figure 1. Pitfall traps used to collect individuals of *Gymnophthalmus underwoodi* Grant 1958, in Manaus-AM, Brazil. Photos and drawings by LRM.

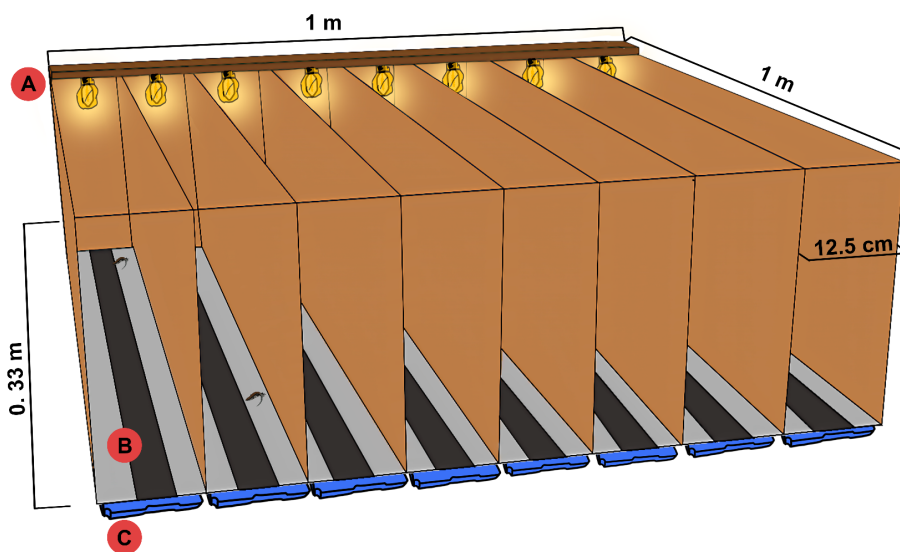


Figure 2. Structure to perform the Preferential Temperature test (T_{pref}). A: Support with 60W incandescent light bulbs covered with yellow cellophane paper; B: zinc plate with sandpaper to facilitate the mobility of individuals; C: ice bags. Drawings by LRM.

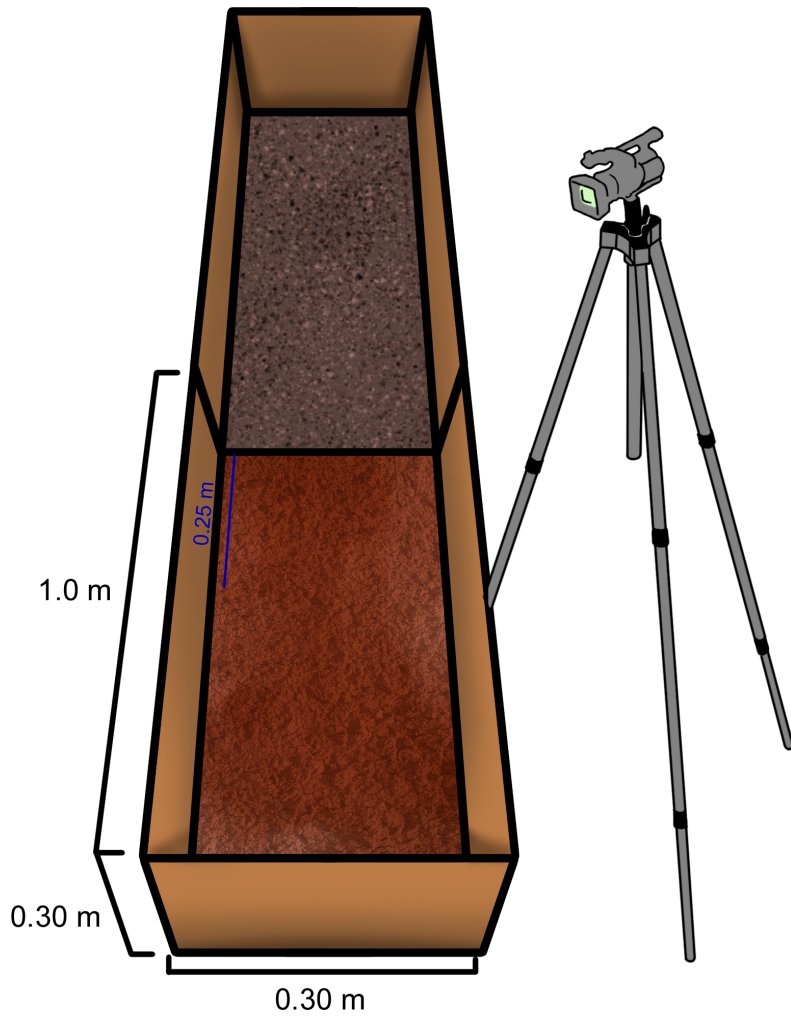


Figure 3. Structure to perform the Sprint performance. Bottom lane treatment with clay (native treatment); Upper lane treatment with sandpaper 60 grit grains $\sim 400 \mu\text{m}$ (neonative treatment). The track was split in distances of 0.25 m. Drawings by LRM.

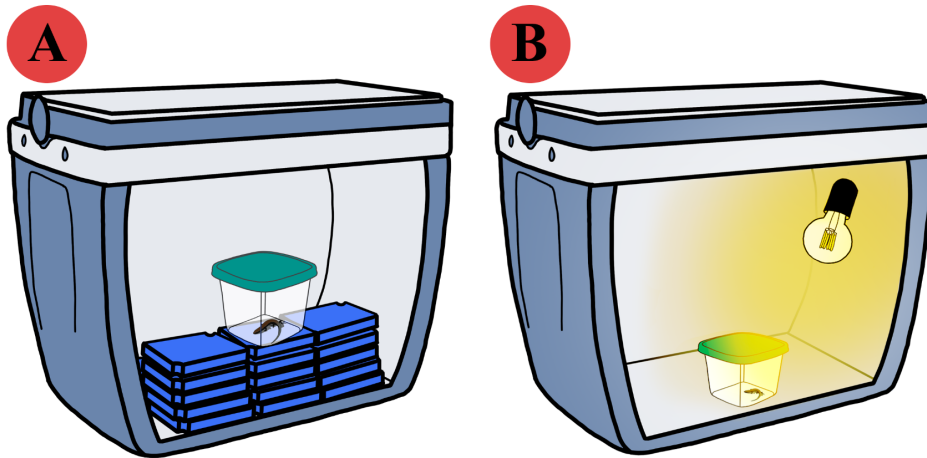


Figure 4. Structure to increase and reduce the body temperature of the individuals. A: Box with icebags to reduce the body temperature; B: Box with 60w incandescent light bulb to increase the body temperature. Drawings by LRM.

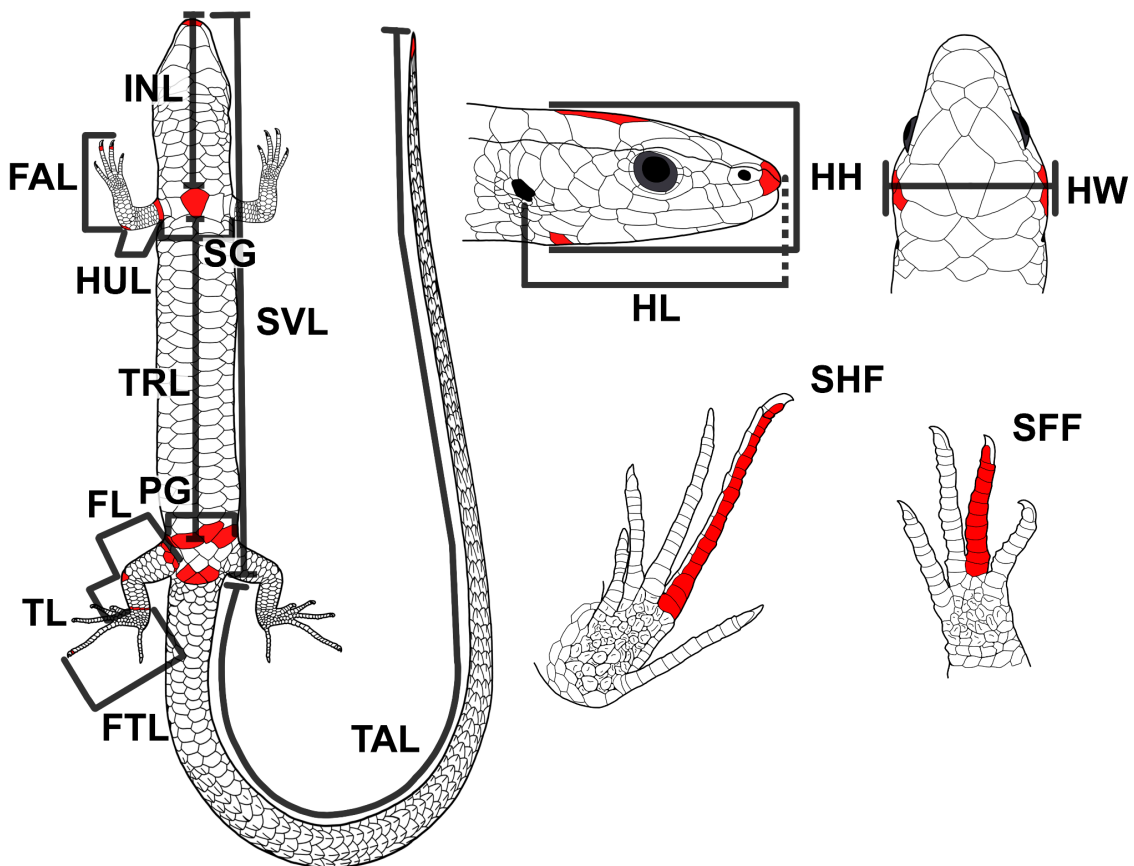


Figure 5. Morphological traits measured. HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet. Drawings by LRM.

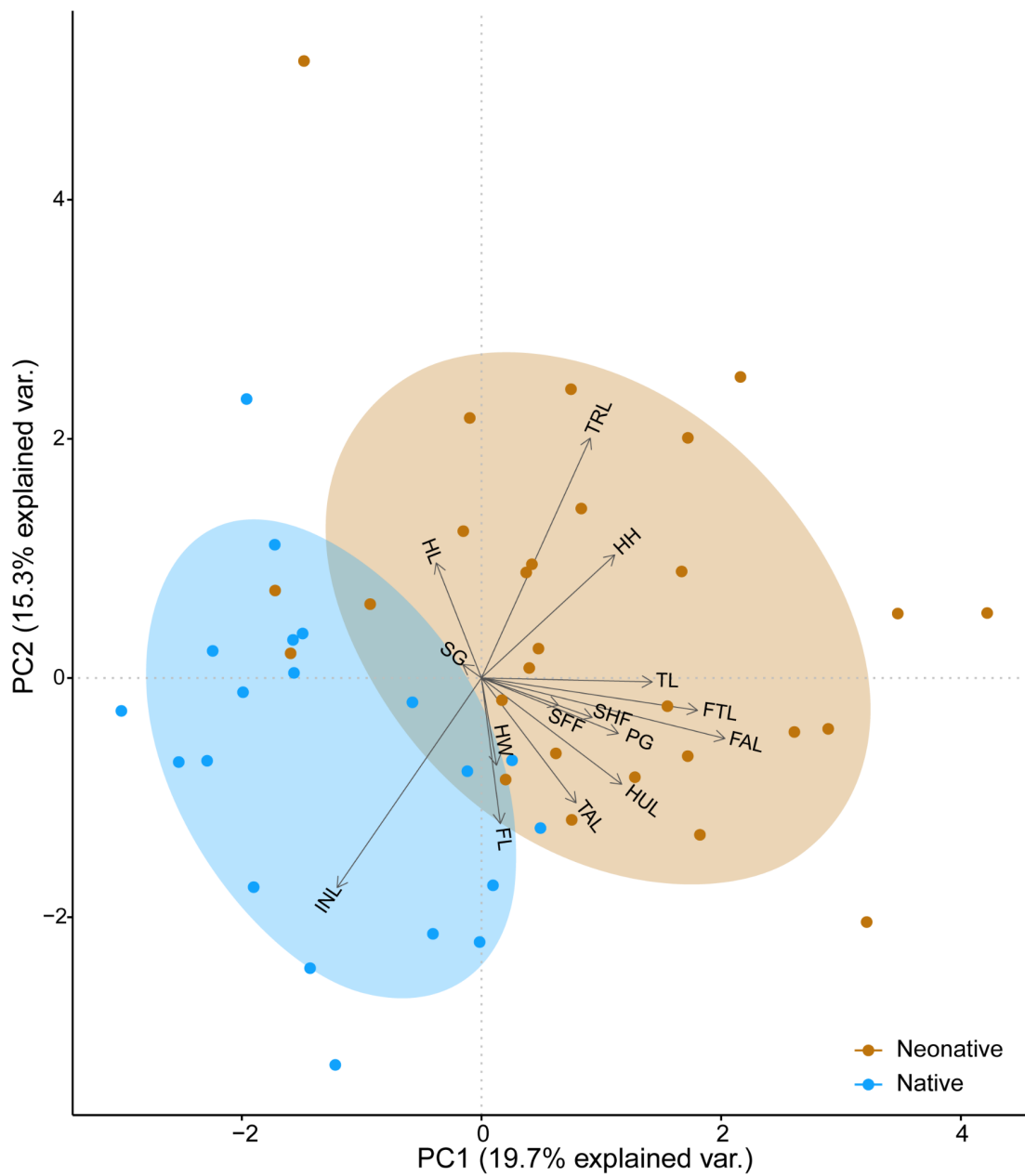


Figure 6. Principal Analysis of Components (PCA) of morphology. PC1 explains 19.7% and PC2 explains 15.3% of the variance. HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

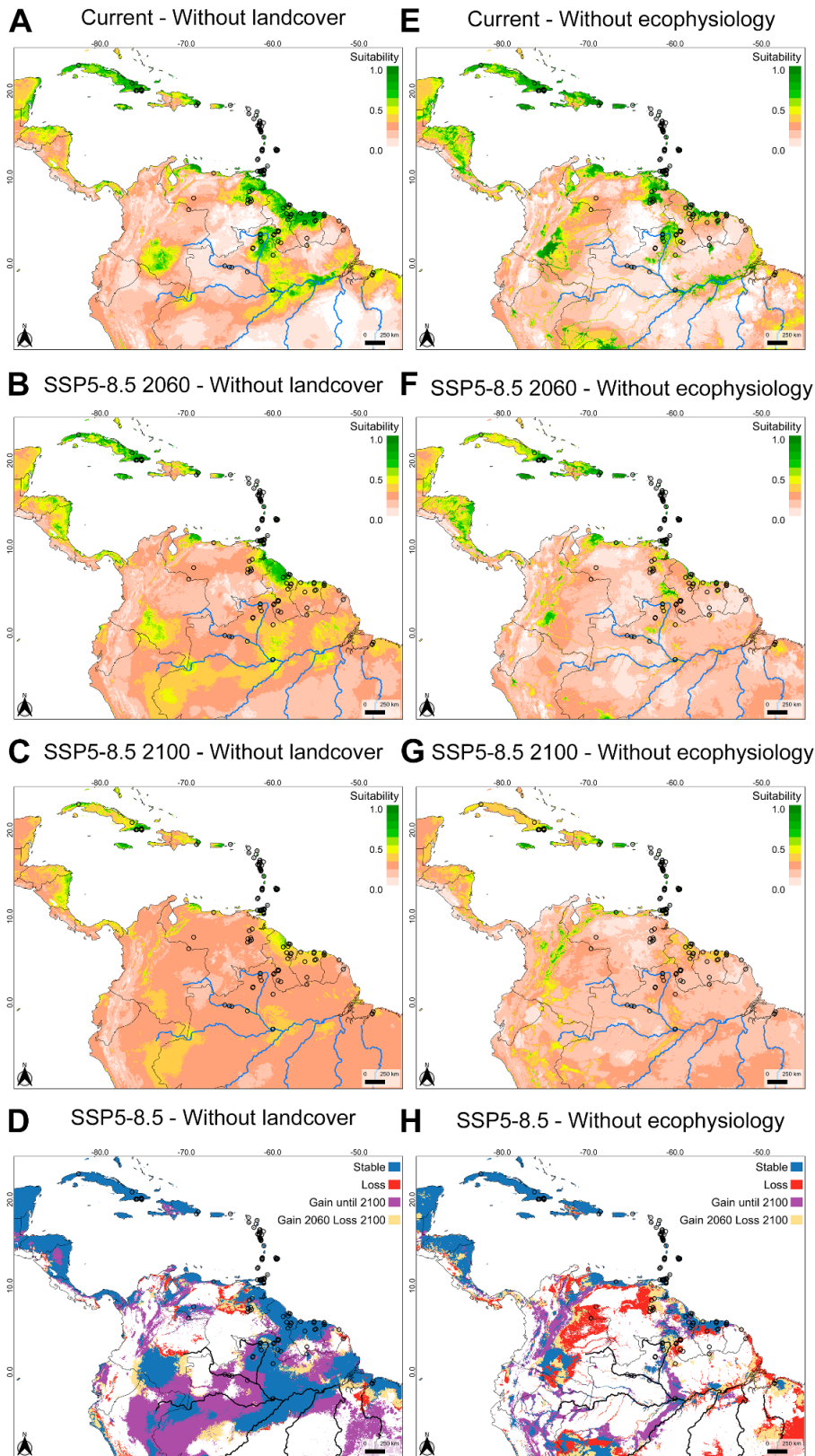


Figure 7. Species Distribution Model predicted using extreme scenario (SSP5-8.5, D-F) of CO₂ emission in two periods 2060 (second-row) and 2100 (third-row) without land cover (left column) and without ecophysiological variables (right column). First-row is the current prediction. Binary plots (last row) were made with threshold of full model (0.31) and show the gain of predicted area for the extreme scenario, through overlapping of each binary plot. The stable areas (blue) over time, lost areas (red), areas lost in 2100 but gained in 2060 (yellow), and area gain until 2100 (purple).

Table 1. Results of *t.test* of thermal traits between neonative and native populations. The normality of data was assessed using Shapiro-Wilk and LeveneTest. T_{pref} : preferential temperature; CT_{max} : critical maximum temperature; CT_{min} : critical minimum temperature.

						<i>t test</i>			
Trait	Population	N	Mean	sd	se	t	df	p-value	
T_{pref}	Neonative	18	32.7078	1.8213	0.4293	0.8658	33	0.3928	
	Native	17	32.2435	1.29866	0.3150				
CT_{max}	Neonative	18	45.0500	0.8459	0.1994	0.8055	34	0.4261	
	Native	18	44.8556	0.5772	0.1361				
CT_{min}	Neonative	18	15.5889	1.2024	0.2834	-4.3398	34	0.0001	
	Native	18	17.6500	1.6169	0.3811				
		Shapiro-Wilk		LeveneTest					
Trait	Population	W	p-value	df	F value	Pr(>F)			
T_{pref}	Neonative	0.97413	0.5661	1	0.3635	0.5507			
	Native			33					
CT_{max}	Neonative	0.9461	0.0788	1	0.5071	0.4812			
	Native			34					
CT_{min}	Neonative	0.95848	0.1929	1	2.0987	0.1566			
	Native			34					

Table 2. Values of loading of principal component analysis (PCA) of morphological traits measures. All traits except TAL were used as residual values of the linear regression between the trait and SVL in PCA. HW: head width; HH: head height; HL: head length; TRL: trunk length; INL: interbrachial-nasal length; HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; TAL: tail length; PG: pelvic girdle; SG: shoulder girdle; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet.

Trait	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
HL	-0.1546	0.3936	0.6283	0.2682	0.3561	0.2501	-0.0277	-0.0448	-0.0309
HH	0.4551	0.4211	0.4122	-0.0381	0.0974	-0.3243	0.1924	0.1677	0.1316
HW	0.0515	-0.2985	0.5631	0.5714	0.2197	-0.0182	0.1717	0.3013	-0.1059
TRL	0.3715	0.8206	-0.0974	-0.0277	0.0134	0.2408	-0.0085	0.0551	-0.0097
INL	-0.4926	-0.7172	-0.0039	-0.0172	-0.0366	-0.3192	0.0133	0.2139	-0.0406
SG	-0.0639	0.0461	0.3627	0.3576	-0.7763	0.1696	0.0986	0.1065	-0.0205
PG	0.4675	-0.1900	0.4189	0.0122	-0.4569	-0.1319	-0.1934	-0.4373	0.1918

FL	0.0646	-0.4986	0.2544	-0.0659	0.0725	0.6061	-0.3629	-0.0044	-0.1854
TL	0.5829	-0.0135	0.1279	-0.5253	-0.1034	-0.0388	0.0237	0.0137	-0.5387
FTL	0.7377	-0.1108	0.0249	0.3176	0.0128	-0.3292	-0.3648	0.0375	-0.0221
HUL	0.4788	-0.3636	-0.0730	-0.2837	-0.1379	0.4204	0.3971	0.2201	0.3332
FAL	0.8313	-0.2071	-0.1748	-0.0187	0.0778	-0.0328	-0.0623	0.3638	0.0204
SHF	0.3779	-0.1353	-0.5356	0.5550	0.1809	0.1791	-0.2064	-0.1043	0.1191
SFF	0.2632	-0.0937	-0.3773	0.5031	-0.0746	0.0223	0.5322	-0.2839	-0.3142
TAL	0.3229	-0.4273	0.3554	-0.2054	0.4312	-0.0254	0.2605	-0.4072	0.1141

Table 3. The mean values of the asymmetry index ($AI = R - L$). The negative values refer to the Left side and the positive values refer to the Right side. HUL: humeral length; FAL: forearm length; FL: femur length; TL: tibia length; FTL: hind foot length; SHF: scales of the third finger of hindfoot; SFF: scales of the third finger of forefeet; Sd: standard deviation; Se: standard error.

Trait	Population	N	Mean	Sd	Se
FL	Neonative	31	-0.11274	0.26161	0.04699
	Native	21	-0.13405	0.23912	0.05218
TL	Neonative	31	0.09403	0.23288	0.04183
	Native	21	0.03167	0.16735	0.03652
FTL	Neonative	31	0.01968	0.21633	0.03885
	Native	21	0.14762	0.32902	0.07180
HUL	Neonative	31	-0.03161	0.19011	0.03414
	Native	21	-0.05500	0.14996	0.03272
FAL	Neonative	31	-0.11032	0.22729	0.04082
	Native	21	-0.09381	0.28149	0.06143
SHF	Neonative	31	0.00000	0.51640	0.09275
	Native	21	0.33333	0.65828	0.14365
SFF	Neonative	31	0.03226	0.70635	0.12686
	Native	21	-0.19048	0.51177	0.11168

Table 4. Evaluation table of Species Distribution Model for *Gymnophthalmus underwoodi* in the extreme scenario without land cover and ecophysiological variables. The ensemble model was made using weighted mean of Sørensen index. Threshold was calculated using Sørensen index. AUC was not used to select the best model, however we chose to inform since it is a common evaluation metrics. MXD: Maximum Entropy default (all features); SVM: Support Vector Machine; RDF: Random Forest; GAU: Bayesian Gaussian Process.

SDM	Algorithm	Threshold	AUC	TSS	Sørensen
Without land cover variable	MXD	1.00	0.79	0.46	0.75
	SVM	0.55	0.79	0.59	0.80
	RDF	0.57	0.80	0.43	0.76
	GAU	0.54	0.76	0.41	0.76

	Ensemble	0.29	0.80	0.41	0.75
Without ecophysiology variable	MXD	1.00	0.77	0.53	0.74
	SVM	0.37	0.75	0.51	0.75
	RDF	0.60	0.78	0.51	0.76
	GAU	0.36	0.74	0.51	0.75
	Ensemble	0.39	0.76	0.54	0.76

Table 5. Predicted area of occurrence for *Gymnophthalmus underwoodi* in current and extreme future scenario without land cover and ecophysiological variable. The species show an increase of its distribution until 2100 in both scenarios. Percentage of gain and loss in reference to current distribution. The threshold to estimate the area was 0.31, the threshold of full model.

Scenario	Year	Predicted area (Km²) without land cover variable	Predicted area (Km²) without ecophysiological variable
Current	2022	1,876,676.11	1,511,290.90
SSP5-8.5	2060	3,916,782.07 (+108%)	1,819,202.09 (+20%)
	2100	4,286,336.53 (+128%)	1,794,473.49 (+18%)