INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

GENÔMICA DA ADAPTAÇÃO E VULNERABILIDADE FRENTE ÀS MUDANÇAS CLIMÁTICAS EM LAGARTOS OMBRÓFILOS NA AMAZÔNIA

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Manaus, Amazonas

Agosto, 2023

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 04 dias do mês de agosto do ano de 2023, às 15h00min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Fabricius Maia Chaves Bicalho Domingos**, da Universidade Federal do Paraná – UFPR, a Drª. **Jéssica Fenker**, do Museums Victoria - Austrália e a Drª. **Mariana Mira Vasconcellos**, da Universidade de São Paulo – USP, tendo como suplentes o Dr. Rafael de Fraga, da Universidade Federal do Oeste do Pará – UFOPA e o Dr. Alexandre P. Almeida, da Universidade Federal do Ceará – UFC, sob a presidência da orientadora, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **ANDRÉ YVES BARBOZA MARTINS**, intitulado: **"GENÔMICA DA ADAPTAÇÃO E VULNERABILIDADE FRENTE ÀS MUDANÇAS CLIMÁTICAS EM LAGARTOS OMBRÓFILOS NA AMAZÔNIA"**, orientado pela Drª. Fernanda de Pinho Werneck, do Instituto Nacional de Pesquisas da Amazônia – INPA e coorientado pelos Dr. Josué Anderson R. Azevedo, do Instituto Nacional de Pesquisas da Amazônia – INPA e Drª Renata Magalhães Pirani, da University of California, Los Angeles – UCLA.

Após a exposição, o(a) discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☑ APROVADO (A) ☐ REPROVADO (A)

☑ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, a presente ata foi lida, lavrada e assinada pelos membros da Comissão Examinadora.

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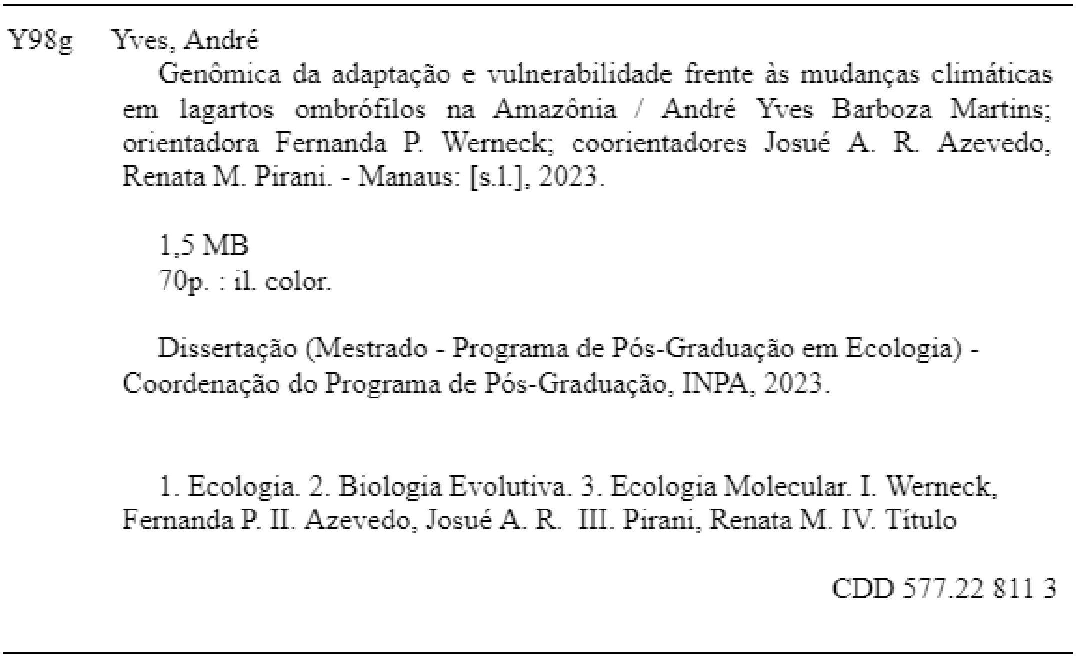

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Sinopse: Estudou-se o potencial adaptativo ao clima e o risco de extinção frente às mudanças climáticas em uma espécie de lagarto florestal amplamente distribuída na floresta amazônica, *Gonatodes humeralis*. Utilizou-se de uma abordagem eco-evolutiva e ferramentas genômicas, investigando o potencial de adaptação local e a resposta das populações desse lagarto frente à iminente catástrofe climática global, predita para os próximos 50 – 100 anos.

Palavras-chave: Amazônia; biodiversidade; ecologia molecular; lagartos; mudanças climáticas.

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“*Se vi mais longe, foi por estar de*
pé sobre ombros de gigantes”

- Isaac Newton

RESUMO

A variação genética existente entre táxons viventes reflete uma história prolongada de diversificação e mecanismos adaptativos em resposta às mudanças climáticas e alterações da paisagem, resultado de processos históricos e contemporâneos que contribuíram para a formação e estabelecimento da biodiversidade. Compreender como as espécies e populações podem ser afetadas ou responder às mudanças climáticas globais pode fornecer informações valiosas para estratégias de conservação diante dos impactos iminentes. Aqui, usamos uma abordagem espacialmente explícita que integrou dados genômicos, de ocorrência e ambientais para investigar como uma espécie de lagarto umbrófilo está ou estará localmente adaptada ou ameaçada às condições climáticas atuais e diante das mudanças climáticas futuras. Encontramos nove populações diferentes em toda a Amazônia com uma quantidade considerável de mistura genética. As análises de associação genoma-ambiente recuperaram 56 regiões de polimorfismo único (SNPs – *Single Nucleotide Polymorphism*) candidatas a estarem sob seleção e adaptação climática, com frequências alélicas recuperando um gradiente leste-oeste na paisagem adaptativa, mostrando diferenças importantes ao longo do espaço geográfico. Nosso índice de paisagem adaptativa evidenciou os processos evolutivos subjacentes, onde as populações que mostram sinais de adaptação climática local podem lidar melhor com a mudança ambiental ao enfrentar as mudanças climáticas futuras por meio de seleção natural e resgate genético. A previsão do deslocamento genômico apresenta um padrão contrastante, com as porções sul e leste da Amazônia apresentando valores elevados de vulnerabilidade às mudanças climáticas futuras. Nossos resultados destacam a importância de considerar contextos espacialmente explícitos com uma ampla cobertura amostral na avaliação do papel desempenhado pelos gradientes ambientais nos padrões de adaptação climática local e vulnerabilidade climática em lagartos e paisagens amazônicas.

Palavras-chave: Amazônia; biodiversidade; *Gonatodes humeralis*; ecologia molecular; lagartos; mudanças climáticas.

ABSTRACT

Adaptation genomics and climate change vulnerability in ombrophilous amazonian lizards

The extant genetic variation among present-day taxa reflects a protracted history of diversification and adaptive mechanisms in response to climate change and landscape alterations, thereby exemplifying the outcome of both historical and contemporary processes to the formation and establishment of biodiversity. Understanding how species and populations might be affected or respond to global climate change can provide valuable information for conservation strategies in the face of impending impacts. Here, we use a spatially explicit context multi-framework approach to investigate how a lizard species is or will be adapted or threatened to current climate conditions and in the face of future climate change. We found nine different populations across Amazonia with a considerable amount of admixture. Genome-environment association analyses recovered 56 candidate SNPs to climatic adaptation, with allele frequencies recovering an east-to-west gradient in adaptive landscape, showing important differences across geographic space. Our adaptive landscape index showed a better interpretation of underlying evolutionary processes, where populations showing signs of local climatic adaptation may deal better with environmental change when facing future climate change through natural selection and genetic rescue. Genomic offset predicts a contrasting pattern, with the south and east portions of Amazonia presenting elevated values of vulnerability to future climate change. Our findings highlight the importance of considering spatially explicit contexts with large sampling coverage in evaluating the role played by environmental gradients on the patterns of local climate adaptation and climatic vulnerability in Amazonian lizards and landscapes.

Keywords: Amazon; biodiversity; *Gonatodes humeralis*; molecular ecology; climate change.

SUMÁRIO

INTRODUÇÃO GERAL

A diversidade genética de táxons atuais representa uma longa história de diversificação e respostas adaptativas às mudanças climáticas e alterações da paisagem no passado (Riddle, 2019). Dessa forma, o que vemos hoje pode ser considerado como um produto de processos históricos e contemporâneos que moldam a biodiversidade. Mudanças climáticas recentes, aceleradas por ações antrópicas, são amplamente reconhecidas pela iminente catástrofe para a biodiversidade global (Scheffers et al., 2016). As rápidas alterações do clima produzem novas pressões seletivas sobre as populações (Hoffman e Sgro, 2011), às quais elas podem ou não sobreviver. De fato, extinções locais devido às mudanças climáticas e ambientais já têm sido amplamente documentadas em diferentes grupos taxonômicos ao redor do planeta (Wiens, 2016), e estas podem se tornar ainda mais frequentes com a intensificação prevista do aquecimento global nas próximas décadas (IPCC, 2014, IPBES, 2019) e sinergias com alterações no uso da terra e desmatamento (Nobre et al., 2016, Longobardi et al., 2016). Tudo isso traz à tona a importância de entender como as espécies e populações naturais serão impactadas ou poderão responder às mudanças climáticas globais e, assim, encontrar suporte para traçar políticas públicas que possam favorecer a persistência dos organismos frente aos impactos iminentes.

Nos trópicos a situação não é diferente, sendo que a região é prevista para sofrer consequências mais drásticas relacionadas às mudanças climáticas nos próximos anos (e.g. Huey et al. 2009, Dillon et al., 2010, Llewelyn et al., 2016, Wiens, 2016). Nessa região, tanto as mudanças climáticas quanto eventos associados, como desmatamento, perda de hábitat e queimadas permanecem como as maiores ameaças à biodiversidade local (Malhi et al., 2008, Pereira et al., 2019), com impactos também em nível mundial (Werth e Avissar, 2002, Cheng et al., 2013). Ainda que em menor magnitude se comparado às regiões de maior latitude, o aquecimento nos trópicos poderá ter consequências mais deletérias, visto que essa é justamente a região onde se concentra a maior parte da biodiversidade global (Deutsch et al., 2008). Dentre os organismos considerados sob maiores riscos de extinção devido às mudanças climáticas, os répteis ocupam posição de destaque (Sinervo et al., 2010, Urban, 2015, Winter et al., 2016, Pontes-da-Silva et al., 2018). Por serem organismos ectotérmicos, a temperatura corporal dos répteis reflete as variações térmicas do ambiente em que vivem (Angilletta, 2009), o que explica estes serem considerados em diversos estudos como o alvo de maior impacto negativo advindo das mudanças climáticas (e.g. Deutsch et al., 2008, Dillion et al., 2010, Huey et al., 2012).

Dentre os répteis, muitos estudos evidenciam o impacto negativo das mudanças climáticas em Lepidosauria (lagartos, serpentes, anfisbênias e tuataras) (e.g. Mitchell et al., 2008, Huey et al., 2009, Sinervo et al., 2010, Diele-Viegas e Rocha, 2018, Pontes-da-Silva et al., 2018) e advogam pelo uso de abordagens que melhor integrem dados genéticos, ecológicos, ambientais e climáticos para melhor entender e traçar estratégias contra esse risco iminente (e.g., Sheu et al., 2020). Alguns autores argumentam que lagartos de florestas tropicais estariam entre as espécies mais ameaçadas, uma vez que eles já estariam vivenciando temperaturas corporais estressantes ao longo das últimas décadas, chegando próximas as temperaturas máximas críticas (CTmax) as quais estão adaptados (Huey et al., 2012). Acredita-se que as espécies termoconformadoras florestais, ativas em baixas temperaturas corporais e mais intolerantes ao incremento das temperaturas ambientais, estariam sob riscos ainda maiores ao aquecimento global (Huey, 2009, Sinervo et al., 2010). Ainda assim, existe uma lacuna de conhecimento no que diz respeito aos aspectos ecológicos e de história de vida desses organismos que possam determinar as bases da vulnerabilidade e possíveis respostas às alterações ambientais, essenciais para entender melhor os impactos das mudanças climáticas sobre essas espécies. Para mitigar os impactos negativos das mudanças climáticas e construir estratégias de conservação a longo prazo, é fundamental entender como diferentes espécies irão reagir às pressões ambientais.

Existem três formas principais pelas quais uma espécie ou população pode escapar da extinção local causada por mudanças climáticas. Primeiro, seria mudando sua distribuição geográfica buscando habitats favoráveis, de acordo com seus requerimentos fisiológicos e a dinâmica espacial das alterações ambientais (Lenoir e Svenning, 2014). Esse tipo de resposta depende diretamente da capacidade de dispersão de cada espécie, da velocidade das mudanças climáticas e da presença de hábitats adequados que permitam a dispersão e permanência da espécie (Lenoir e Svenning, 2014, Waldvogel et al., 2020). Outro aspecto importante é que ajustes nos padrões de distribuição das espécies podem ocasionar mudanças na composição das comunidades biológicas, o que pode ter impactos variáveis sobre os ecossistemas em questão e mudanças em interações ecológicas (e.g. competição) (Parmesan e Yohe, 2003, Sales et al., 2020). Em segundo lugar, as espécies poderiam sobrepujar os efeitos deletérios através da plasticidade fenotípica (definida como variação fenotípica produzida por um genótipo em diferentes condições ambientais), desde que as mudanças ambientais não ultrapassem seus limites fisiológicos (Riddell, et al., 2018, Waldvogel et al., 2020). Assim, alguns fenótipos poderiam facilitar processos adaptativos e a persistência das espécies mesmo em cenários de alterações ambientais futuras (Kelly, 2019, Fox et al., 2019). De fato, alguns estudos têm buscado responder como a plasticidade fenotípica poderia operar no cenário atual de grandes mudanças antropogênicas (e.g., Chevin et al., 2010, Crispo et al., 2010, Zhang et al., 2015, Kelly, 2019, Jarrold et al., 2019, Norin e Metcalfe, 2019), mas ainda faltam abordagens integrando a plasticidade de múltiplos atributos na habilidade dos indivíduos de se ajustarem (Riddell et al., 2018). Por fim, as espécies podem evitar a extinção através da evolução adaptativa, ocasionada por seleção natural. Mudanças nas condições ambientais podem resultar em seleção local atuando sobre as populações, especialmente em espécies com ampla distribuição ao longo de gradientes ambientais, as quais vivem sob diferentes pressões ecológicas (Hoffman e Sgro, 2011, Waldvogel et al., 2020).

Mesmo com os cenários mencionados acima, espécies e populações podem não ter tempo suficiente e a variação genética adaptativa para alcançar nenhuma dessas possibilidades (Diniz-Filho e Bini, 2019). Consequentemente, espécies e populações que não responderem das maneiras supracitadas estarão fadadas a um expressivo declínio populacional ou mesmo eventos de extinção local ou total (Sinervo et al., 2010, Hoffman e Sgro, 2011, Waldvogel et al., 2020). Em sua maioria, as avaliações de vulnerabilidade frente a mudanças climáticas são testadas utilizando modelos de nicho associados a projeções futuras para a distribuição das espécies com base em condições climáticas (Helmuth et al., 2014, Pacifici et al., 2015, Foden et al., 2019). Ainda assim, poucos trabalhos incluem as possíveis respostas supracitadas em estudos de vulnerabilidade e predições adaptativas, o que dificulta uma análise mais apurada sobre os verdadeiros impactos das mudanças climáticas em populações de diversos grupos taxonômicos.

Análises de associação genoma-ambiente (GEA – Genome Environment Association analysis) tem se tornado uma importante ferramenta para estudos de adaptação local em populações que ocupem habitats heterogêneos (e.g. Rellstab et al., 2015). As GEA identificam regiões potencialmente adaptativas do genoma com base na associação entre os dados genéticos com representação genômica e as variáveis ambientais (Forester et al., 2016, Capblancq e Forester, 2021). Dessa forma, ao mapear a variação genética adaptativa selecionada pelo clima é possível identificar populações que possam estar pré-adaptadas para enfrentar as alterações climáticas e assim escapar da extinção local (Razgour et al., 2019). Diversos métodos já foram propostos para implementar análises de GEA, e abordagens integrativas tem se mostrado bastante úteis em estudos assim nos últimos anos. Por exemplo, Bay et al. (2018), integraram dados genômicos e ambientais para identificar variação genômica associada ao clima em uma espécie de pássaro migratório e estudar sua adaptação local frente a cenários de mudanças climáticas. Assim, foi possível mapear a vulnerabilidade genômica da espécie, definida como a dissimilaridade entre a variação genômica atual estimada na relação genoma-ambiente modelada ao longo de populações atuais e a predita para o futuro (Bay et al., 2018). Consequentemente, Bay et al. (2018) puderam mapear espacialmente quais populações seriam mais afetadas nos cenários futuros e quais já estariam possivelmente experienciando declínios populacionais por mudanças recentes. Em uma abordagem um pouco diferente, Razgour et al. (2019) também avaliaram a vulnerabilidade climática de populações de duas espécies de morcegos na Europa. Nesse caso, a variação genética adaptativa foi utilizada para inferir a persistência das populações no futuro através da distribuição atual e potencial dispersão ao longo da paisagem de indivíduos climaticamente adaptados.

Um organismo que representa um sistema apropriado para examinar sinais de adaptação local associada a gradientes ambientais é a espécie de lagarto *Gonatodes humeralis* (Sphaerodactylidae) (Figura 1), ou popularmente conhecido como lagartixa-da-mata, um lagarto diurno, florestal e tido como a menor espécie do gênero (Vitt et al., 1999). Com ampla distribuição na Amazônia, *G. humeralis* habita diversos tipos de ambientes florestais, ao longo de um extenso gradiente climático (Ribeiro-Júnior, 2015). Além disso, *G. humeralis* faz parte de um grupo funcional de organismos (lagartos umbrófilos tropicais) previsto para estar sob maior vulnerabilidade frente às alterações climáticas globais (Huey et al, 2009, Sinervo et al 2010). Isso faz da espécie um excelente sistema para investigar variação genômica e adaptação climática local (Hohenlohe et al., 2010, Bay et al., 2018, Prates et al., 2018), e soma-se ao fato de, no presente momento, ainda não existirem estudos de genômica e adaptação com esta ou outras espécies que apresentem ecologias semelhantes. Além disso, Pinto et al. (2019) ao apresentarem um estudo filogeográfico para a espécie, constataram que existe uma estruturação genética neutra para as populações em três grupos principais, um em Trinidad, um a oeste e outro a leste da bacia Amazônica, mas que essa estrutura populacional oeste-leste corresponde de fato a uma espécie de ampla distribuição geográfica na bacia Amazônica. Tal padrão foi também corroborado por análises de superfícies de migração genética (Pirani et al., 2019). Assim, tais estudos facilitam a compreensão dos impactos da evolução da paisagem sobre processos neutros de diversificação (i.e., deriva genética e fluxo gênico) e estabelecem o arcabouço genético e biológico para que processos adaptativos possam ser investigados em maior profundidade.

Figura 1. Indivíduo macho da espécie *Gonatodes humeralis* (lagartixa-da-mata) registrado em Porto Trombetas, PA, Brasil. (Foto: Henrique C. Costa).

Dentro desse contexto, no presente estudo busquei avaliar o papel das características climáticas do ambiente em gerar padrões de diversidade genômica potencialmente adaptada ao clima e, com base nas relações ambiente-genoma inferidas, avaliei os potenciais de adaptação e os riscos de extinção local frente à cenários de mudanças climáticas globais em *Gonatodes humeralis*. Mais especificamente, busquei responder duas questões principais: 1) Como a variação genética (neutra e adaptativa) está distribuída e caracterizada ao longo da distribuição do lagarto *Gonatodes humeralis?* 2) Como as predições futuras de mudanças climáticas vão impactar a vulnerabilidade de

G. humeralis através da dissimilaridade inferida entre a relação genoma-ambiente no presente e a predita para o futuro? Para responder a essas perguntas, utilizei uma abordagem que integra dados genômicos de representação reduzida (double digest Restriction site Associated DNA sequencing – ddRADSeq) de populações naturais dessa espécie de lagarto florestal ombrófilo, amplamente distribuído na Amazônia sob uma perspectiva eco-evolutiva. Primeiramente, investiguei a estrutura genética neutra das populações de *Gonatodes humeralis* ao longo do espaço geográfico. Em seguida, realizei varreduras no genoma, buscando por regiões de polimorfismo único (*Single Nucleotide Polymorphism* - SNPs) obtidas a partir do ddRADSeq para inferir sua relação com as variáveis climáticas que melhor expliquem a variação genética atual, encontrando assim populações climaticamente adaptadas. Por fim, realizei análises de associação genoma-ambiente integradas com projeções futuras para calcular a vulnerabilidade das populações de *G. humeralis* frente às mudanças climáticas globais.

Uma vez que regiões periféricas da distribuição das espécies usualmente representam zonas de tensão ecológica e fisiológica com pressões ambientais seletivas mais intensas e condições mais estressantes para as populações (Pironon et al., 2017), espera-se que a proximidade do ecótono Amazônia/Cerrado mostre alguma correlação na distribuição das populações climaticamente adaptadas ao longo da Amazônia. Assim, o gradiente entre o centro e a periferia da distribuição de uma espécie pode mostrar correlação com a estrutura genética em suas populações, o que pode ser influenciado tanto por dinâmicas populacionais quanto seleção natural (Kark et al, 2008; Pironon et al., 217). Por outro lado, a distribuição de populações climaticamente adaptadas pode seguir uma estruturação espacial em manchas, ao longo de diferentes ambientes florestais contínuos ou isolados na Amazônia, ou até mesmo uma estrutura leste-oeste, como reportado geneticamente por Pinto et al. (2019) e Pirani et al. (2019). A identificação de regiões importantes para a manutenção das populações, através do fluxo gênico, entre indivíduos climaticamente adaptados e populações mal adaptadas se mostra importante em escala local e regional para a adoção de planos de conservação e manejo das espécies na Amazônia, uma vez que indivíduos climaticamente adaptados podem resgatar populações do declínio por meio da migração, através do resgate evolutivo (Diniz-Filho e Bini, 2019, Razgour et al., 2019, Waldvogel et al., 2020).

OBJETIVO

O objetivo geral desta dissertação foi avaliar as relações entre variação ambiental e a diversidade genômica potencialmente adaptada ao clima, assim como inferir o impacto da adaptação local nas estimativas dos riscos de extinção frente à cenários de mudanças climáticas globais em populações do lagarto *Gonatodes humeralis*, amplamente distribuído na Amazônia.

Capítulo único

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1 INTRODUCTION

The standing genetic diversity of current taxa illustrates a long history of diversification and adaptive processes to climate change and landscape shifts (Riddle, 2019), representing the consequences of both historical and contemporary processes shaping biodiversity. Yet, the acceleration of human-induced global climate change (GCC) is now widely recognized for causing a forthcoming catastrophe to global biodiversity (Scheffers et al., 2016). Rapid shifts in climate can cause new selective pressures upon the organisms (Hoffman and Sgro, 2011), which they may or may not be able to overcome. In fact, local extinctions due to climate and environmental changes have already been documented in several taxa across the globe (e.g., Wiens, 2016). As global temperatures are projected to rise in the coming decades, combined with escalating land use changes and deforestation (IPCC, 2021, Nobre et al., 2016, Longobardi et al., 2016, IPBES, 2019), the occurrence of extinction events may intensify.

Within the scenario above, there are three main ways in which natural populations from a given species can escape from local extinction caused by GCC: (i) shifting its geographic distribution, tracking suitable habitats according to its physiological demands via dispersal corridors (Lenoir and Svenning, 2014, Waldvogel et al., 2020); (ii) through phenotypic plasticity, that is, the phenotypic variation created by one genotype in different environmental conditions, as long as the environmental changes do not exceed the species' physiological limits (Riddell, et al., 2018, Waldvogel et al., 2020); or (iii) through adaptive evolution, driven by natural selection (Razgour et al., 2019, Waldvogel et al., 2020). Adaptive evolution is especially important for widely distributed species that experience environmental gradients and varying ecological pressures, as environmental changes can result in local adaptation within populations (Hoffman and Sgro, 2011, Waldvogel et al., 2020). Although such different responses can buy time and eventually avoid local extinctions (Fox et al., 2019), species and populations might not have enough time and genetic variation to achieve either of these possibilities (Diniz-Filho and Bini, 2019). Consequently, populations without the ability to cope or respond in some manner might face expressive population declines or even local extinction (Sinervo et al., 2010, Hoffman and Sgro, 2011, Waldvogel et al., 2020).

Generally, forecasts of climate vulnerability are inferred using niche modeling, either through correlative or mechanistic approaches (Helmuth et al., 2014, Pacifici et al., 2015, Foden et al., 2019). With analytical advances, the use of genomic data becomes crucial to infer local adaptation and climate vulnerability (Kardos et al., 2021, Forester et al., 2022) and therefore better inform global climate change forecasts of non-model organisms (e.g., Bay et al., 2018, Razgour et al., 2019, Capblancq et al., 2020). Genome-Environment Association (GEA) analyses have become an important tool in local adaptation studies in populations occupying heterogeneous habitats (e.g., Rellstab et al., 2015). GEA uses associations between genetic data and environmental variables to identify potential adaptive variation across the DNA (Forester et al., 2016). This information can highlight populations that may be able to avoid local extinction due to climate change, vulnerable populations, as well as point out important geographic regions for conservation planning (Razgour et al., 2019). For example, local adaptation, which can be measured by the match between adaptive genetic variation and environmental variation, has an important role in conferring higher survival and reproduction in local environments and is key to preparing populations for challenging climates (Meek, et al., 2023).

Altogether, understanding how species and populations might be affected or respond to global climate change can provide valuable information for conservation strategies in the face of impending impacts (Urban, 2015, Meek et al., 2023). For instance, genomic offset, defined as the amount of mismatch (dissimilarity) between current and future genotype-environmental relationships (Bay et al., 2018) can help identify populations that may experience loss of genetic diversity due to environmental or human pressures. Genomic offset reflects a potential shift in the adaptive optimum induced by climate change (Capblancq et al., 2020, Capblancq and Forester, 2021) and it is frequently referred also as genomic vulnerability (Bay et al., 2018), risk of non-adaptedness (Rellstab et al., 2016), or maladaptation (Capblancq et al., 2020).

Across the tropics, biodiversity crises due to climate change can be even more severe, since this region harbors most of the global biodiversity (e.g., Deutsch et al., 2008, Huey et al. 2009, Dillon et al., 2010, Llewelyn et al., 2016, Wiens, 2016). In this region, both climate change and associated events, such as deforestation, habitat loss and wildfires are the greatest threats to local species (Malhi et al., 2008, Pereira et al., 2019) and global biodiversity patterns (Werth and Avissar, 2002, Cheng et al., 2013). Ectothermic organisms across the tropics often figure as having high vulnerability and extinction risks (Sinervo et al., 2010, Urban, 2015). In this context, our focal species is the widely distributed Amazonian gecko *Gonatodes humeralis* (Sphaerodactylidae). The species inhabits several forested environments across an extensive climatic gradient (Ribeiro-Júnior, 2015). Besides, *G. humeralis* is a thermoconformer forest lizard, meaning that individuals do not actively thermoregulate and as such the species is part of a functional group predicted to be under high vulnerability due to GCC (Huey et al., 2009, Sinervo et al., 2010). Although widespread, the species present signals of genetic structure across Amazonia (Pinto et al., 2019, Pirani et al., 2019). However, former studies did not take into consideration adaptive events at the populational level nor integrated those into future forecasts.

Herein we employ an integrative eco-evolutionary approach using genomic data from natural populations of *G. humeralis* to evaluate the role of genomic diversity potentially adapted to climate on local adaptation and the extinction risks facing climate change. We addressed two main questions: 1) How is the genetic variation (both neutral and adaptive) distributed and arranged across the distribution range of *Gonatodes humeralis*? 2) Will climate change lead to a mismatch between current and future genome-environmental relationships in *G. humeralis*, impacting its vulnerability? We expect to find a more refined population genetic structure than previous studies, since we employ a broader geographic and genomic sampling. Also, we expect to encounter the determinants of the genetic variation in the adaptive landscape for *G. humeralis*, following an climatic gradient across Amazonia. We predict more admixture in the eastern portion of Amazonia due to the more dynamic nature of this region (Ávila-Pires et al., 2012, Pinto et al., 2019), but also that GCC impacts would be more severe in the western portion of Amazonia, since it has a more stable climate (Cheng et al., 2013). By using a genome-environmental association (Genomic Offset) and considering future scenarios of climate change in Amazonia we expect to map and recover an accurate assessment of climatic vulnerability for *G. humeralis* across its distribution range (Bay et al., 2018, Razgour et al., 2019).

2 METHODS

2.1 Geographic and genomic sampling

We sequenced genomic data from 194 specimens of *Gonatodes humeralis* sampled from several localities across the Amazonia (Figure 1), the same geographic coverage of Pirani et al. (2019). The complete list of samples and scientific collections vouchers are provided in Supplementary Table S1. For each individual, genomic DNA was extracted from muscle or liver fragments, and preserved in 100% ethanol, using the Qiagen DNeasy Blood and Tissue Kit. Two reduced representation libraries were constructed with the samples through ddRADSeq – double digest restriction associated DNA sequencing – approach, following the protocol established by Peterson et al. (2012). In summary, double-digested DNA with ligated unique barcodes for each individual was pooled and 350–450 bp fragments sizes were selected using Pippin Prep (Sage Science). For a complete description of the genomic library preparation and DNA sequencing process, see Pirani et al. (2019).

In order to de-multiplex and quality filter the genomic data, we used the Ipyrad v.0.9.68 pipeline (Eaton and Overcast, 2020) to perform a de-novo genome assembly and call for single nucleotide polymorphisms (SNPs). The main filtering steps in Ipyrad were adjusted for the following parameters: 5% of maximum low-quality bases in a read, minimum read length of 100bp, minimum samples per locus for output of 108, representing 66% or two-thirds of all individuals, maximum number of SNPs per locus of 20%, and maximum number of indels per locus of 5. For the remaining parameters, we used the program defaults. We removed from the dataset 22 individuals with less than 600,000 reads and the other three that did not pass the filtering steps, remaining with 169 individuals. Before all downstream analyses (sNMF, GEA and Genomic Offset), we used VCFtools v. 0.1.13 (Danecek et al., 2011) to filter out singletons and include SNPs present in at least 95% of individuals by minor allele frequency (MAF = 0.05), to avoid count sequencing errors (Ahrens et al., 2018) and to select one SNP for read to reduce linkage disequilibrium. We also filtered to remove four samples with more than 20% of missing data per individual and per locus. After all the aforementioned steps our final dataset was composed of 165 individuals of *G. humeralis*, with 36.915 unlinked SNPs and 17.25% of missing data, and that was the dataset we used in all downstream analyses (see Supplementary Table S2 for details).

2.2 Population genetic structure

To evaluate the underlying neutral population structure of *Gonatodes humeralis*, we estimated the number of genetic clusters (k) along with its distribution using the Sparse Nonnegative Matrix Factorization (sNMF) v. 1.2 (Frichot et al., 2014), which defines the number of clusters and admixture coefficients based on SNP data. We tested k = 1-15, with 100 replicates (α =100) for each k, and the best k was the one with the lowest cross-entropy value inferred by the sNMF (Frichot et al., 2014). The robustness of the results was verified by testing four different values of alpha regularization parameter (10, 100, 1000, 10000) recommended by the program. The sNMF analysis was performed in R v. 4.1.3 (R Core Team, 2022) with the package "LEA" v. 2 (Frichot and François, 2015).

2.3 Genome-environmental association analyses

To identify possible loci under climatic selection (candidate SNPs), we performed genome scans using genome-environmental association (GEA) approaches. These analyses test correlations between genome (allele frequencies in multiple loci) and environmental variables along the distribution of our samples. As environmental predictors in the GEA analyses, we used bioclimatic variables from the Climond database (available at www.climond.org – Kriticos et al., 2012). We first chose the variables based on their importance for our biological system - *Gonatodes humeralis* - and the expectations concerning environmental pressures upon natural populations (e.g., minimum, maximum and seasonality of temperatures and precipitation - Razgour et al., 2019, Román-Palacios and Wiens, 2020) and geographic variation across Amazonia. Afterwards, we tested the variance inflation factor (VIF) to estimate how much of the variance is inflated due to multicollinearity between the selected environmental variables (Dorman et al., 2013), and we removed two variables that presented multicollinearity. Subsequently, we performed a model selection based on a RDA analysis (Capblancq and Forester, 2021). We retained the following six bioclimatic variables: temperature seasonality (Bio_4), mean daily maximum air temperature of the warmest month (Bio_5), mean daily minimum air temperature of the coldest month (Bio_6), precipitation amount of the driest month (Bio_14), precipitation seasonality (Bio_15) and mean monthly precipitation amount of the warmest quarter (Bio_18). We then extracted the values of each bioclimatic variable from the collection sites of our samples, used herein.

We ran two different GEA analyses to infer associations between environmental predictors and allele frequencies in our dataset. We chose to run two distinct complementary methods to minimize false positives and false negatives in our genome scan as well as to achieve a more powerful selection of candidate SNPs (Forester et al., 2018, Capblancq and Forester, 2021). First, we ran a Redundancy Analysis (RDA – Lasky et al., 2012, Capblancq and Forester, 2021), which investigates how groups of loci covary in response to the multivariate environment (e.g., Razgour et al., 2019, Capblancq et al., 2018, Varas-Myrik et al., 2022). RDA is able to detect processes resulting from weak multilocus signs (Forester et al., 2016 and 2018), being an efficient tool to evaluate and forecast genome environmental associations (Capblancq and Forester, 2021). We used a PCA of all SNPs to disentangle the effects of neutral and adaptive genetic variation, where we used the first three PCs (60% of the variation) as conditioning variables to account for neutral population structure. Additionally, we applied a partial redundancy analysis (pRDA) to our data, in order to decompose the contribution of climate, neutral population structure and geography in explaining genetic variation (allele frequencies) (Capblancq and Forester, 2021). We used the functions rda() and rdadapt() (Capblancq et al., 2018) to perform RDA genome scans and to extract the Q-values and select the SNPs with false discovery rate smaller than 0.05, respectively.

Second, we ran a Latent Factor Mixed Model (LFMM – Frichot et al., 2013), which investigates correlations between environmental and genomic variation across the landscape, while levels of neutral population structure, from the previous sNMF analysis, are considered to define the best number of latent factors in the analysis. LFMM computes z-scores and p-values to quantify the strength of associations and which are also informative when compared among environmental factors while accounting for low rates of false positives and false negatives (Rellstab et al., 2015). Further, LFMM is good at detecting weak selection and works very well with complex hierarchical neutral genetic structures and polygenic selection (Frichot et al., 2013, de Villemereuil et al., 2014). It also has been extensively used in recent empirical studies (e.g., Prates et al., 2018, Ruegg et al., 2018, Razgour et al., 2019, Gugger et al., 2020). After running, we checked the LFMM histograms and corrected the p-values by the GIF (Genomic Inflation Factor), extracted the Q-values, and identified the outlier loci using a threshold of FDR (False Discovery Rates) < 0.05.

Last, we looked for overlap between SNPs detected by both RDA and LFMM methods and combined them into a single dataset of candidate SNPs. For the downstream analysis, we used only SNPs detected by both methods.

2.4 Adaptive landscape

Once we found the set of candidate adaptive loci, we calculated the adaptive genetic similarity across the landscape with the adaptive index (Capblancq and Forester, 2021). To do so, we first ran a new RDA with only the candidate SNPs (outlier loci) and used the scores of the RDA axes to predict the adaptive index along the landscape for each environmental pixel, using the following formula:

$$Adaptive\ Index = \sum_{i=1}^{n} a_i b_i$$

where a is the climatic variable score (RDA loading), b is the standardized value for this particular variable at the focal pixel and i refers to one of the n different variables used in our RDA model (Steane et al., 2014, Capblancq and Forester, 2021). The adaptive index provides an estimate of genetic dissimilarity in all pixels on the landscape as a function of the environmental predictors' values at that exact site (Capblancq and Forester, 2021). We limited our predictive landscape on the map using a minimum convex polygon, based on our sampling points, plus a buffer of three degrees, thus mapping the adaptive index across the species' geographic range.

2.5 Genomic offset and climate vulnerability

We applied the genomic offset to investigate which populations of *G. humeralis* are under major vulnerability to future climate change. We assumed that populations with a greater genomic offset index would be the most vulnerable ones. Because they would be under strong selective pressure and, possibly, would not be able to change their genetic composition rapidly enough to track the environmental change and adaptive optimum shift in the future. We measured the genomic offset through Euclidean distances between the current genetic dissimilarity, estimated from the Adaptive Index, and the ones predicted in the future, for each pixel. In a nutshell, higher values of genomic offset indicate higher vulnerability to environmental change while lower values indicate lower risk (Capblancq and Forester, 2021).

For future forecasts needed to measure the genomic offset, we used the A1B and A2 climate scenarios, which differ in their greenhouse gas emissions and socioeconomic assumptions (IPCC, 2021). The A1B scenario represents a balanced approach, estimating a temperature increase of 1.7–4.4◦C by the end of the 21st century, with greenhouse gas emissions peaking in the mid-21st century. The A2 scenario portrays a future with higher greenhouse gas emissions and fewer efforts to mitigate them, forecasting a 2.0–5.5◦C temperature increase. Although not directly equivalent, the A1B scenario aligns with the moderate-emission RCP4.5 scenario, while the A2 scenario is more comparable to the high-emission RCP8.5 scenario. These scenarios provide contrasting outlooks for future climate conditions and allow for a comprehensive assessment of potential impacts on species' adaptation and vulnerability. Then we mapped the genomic offset for 2050 and 2100, under these aforementioned scenarios. We did not include a milder climatic scenario because of its virtual impossibility, since it requires we had broken off greenhouse gasses emission a few of years ago (Raftery et al., 2017).

3 RESULTS

3.1 Population genetic structure

The sNMF analysis recovered as the best-fit model nine geographically structured populations (K = 9) across the distribution range of *Gonatodes humeralis* (Figure 2A). The analysis also showed high levels of admixture among several of these populations (Figure 2C), mostly along the northeastern populations. However, there is low or non-admixture in western and southwestern Amazonian populations. Likewise, there are one isolated populations (single localities) in northern Amazonia (pink cluster in Figure 2B), and another two isolated near the Amazonia-Cerrado ecotone.

3.2 Genomic Environmental Association

The result of the RDA variable importance indicated that the six bioclimatic variables retained in the analyses were important in explaining the genetic variation structure in *G. humeralis* (Table 1). In general, three precipitation and three temperature variables were significantly correlated with genetic variation in *Gonatodes humeralis* across its distribution range. However, the most important variable was the mean monthly precipitation amount of the warmest quarter (Bio 18 – F = 18.55), followed by the mean daily minimum air temperature of the coldest month (Bio 06 – F = 4.3). Further, the pRDA results showed that climate, geographic distance, and neutral population structure explained 4%, 1% and 10% of the genomic variation in our data, respectively.

RDA-only results (GEA) recovered 451 candidate SNPs under environmental selection while LFMM-only results recovered 492 candidate SNPs. The overlap between RDA and LFMM results identified 56 candidate SNPs under environmental selection associated with bioclimatic gradients. The new RDA ran only with the overlapped candidate SNPs revealed putative signals of local adaptation across the Amazonian climatic gradient for *G. humeralis*, as well as how variables correlate among themselves (Figure 3 – R2 = 0.28). The first two axes accounted for 80% of the explained variation. Most of the variation is accumulated in the first axes (RDA1 = 54% of variance) where allele frequencies were most associated with low precipitation in the warmest months (Bio18 and negative RDA1 scores) or with elevated precipitation seasonality (Bio15 and positive RDA1 scores). Positive scores in the second axes (RDA2 = 26% of variance) were related to temperature seasonality across the landscape.

3.3 Adaptive landscape

With the adaptively enriched genetic space - RDA with candidate SNPs only - (Figure 3), we were able to extrapolate the RDA axes scores across the landscape in the entire range of *G. humeralis* (Figure 4) using the Adaptive Index. The adaptive landscape shows how the RDA1 predicted scores, which account for most of the accumulated variation (54% of variance), contrast in an east-western gradient, from positive RDA scores in eastern Amazonia to negative RDA1 scores in western Amazonia. There is an increase in the adaptive-genetic dissimilarity from the western to eastern Amazonia, highlighting distinct adaptive landscapes across climate gradients in Amazonia. Likewise, the adaptive gradient shown by the RDA2 index, differentiated western Amazonian areas, characterized by more precipitation and annual climatic stability, to the south and eastern portions of this domain, generally characterized by a drier climate. Together, both RDA axes reveal adaptive dissimilarities across the range of *Gonatodes humeralis* in Amazonia related to bioclimatic variables of precipitation and temperature (Figure 4). Most of the explanation in the first axes relies on variables of precipitation while in the second axes, temperature.

3.4 Genomic offset

The genomic offset, or the estimated mismatch between current and predicted genome-environment relationships derived from the adaptive index showed the vulnerability under climate change across the *G. humeralis* species range. Accordingly, our model predicts disparate patterns, both for 2050 and 2100, with low to moderate values of genomic offset in the south and east portions of Amazonia and elevated values, so higher vulnerability, in the central-western portion of Amazonia (Figure 5). We can certainly observe an increase in vulnerability for 2100 compared to 2050, with several areas presenting the highest levels of genomic offset in central and western Amazonia.

For the extreme scenario (Figure 5 – 2100 maps), our model predicts an increased level of genomic offset, raising the vulnerability across Amazonia, especially along the aforementioned areas. Conversely, south and eastern populations seem to be at lower risk in the future since they present lower levels of genomic offset (light colors on the map).

4 DISCUSSION

Our findings elucidate the genomic-environment relationships for a widespread Amazonian gecko, providing a risk assessment in the face of future climate change as well as an estimate of the current adaptive landscape across the most biodiverse and complex tropical rainforest. The genome-environment analyses revealed a set of putative SNPs under climate selection, using six selected bioclimatic variables as predictors. To account for the underlying neutral population structure and also better understand the population history of *G. humeralis*, we identified nine genetically distinct populations across different regions of Amazonia. Eastern Amazonia populations harbor distinct levels of genetic admixture, while populations located in western and southwestern

Amazonia show a clearer pattern of isolation. Although some population genomics studies have recently accessed the extent of local adaptation in the Neotropics, most of them have addressed tree species as the main system (e.g., Collevatti et al., 2019, Leal et al., 2021, Vieira et al., 2022). This is the first time that the role of local adaptation is accounted for in forecasts of responses to changing climates on ectothermic Amazonian organisms, supposedly under higher vulnerability to climate change. Accordingly, our results on local adaptation show a distinctive pattern across Amazonia, highlighting how different climatic gradients shaped the adaptive landscape of *G. humeralis* across its range. Likewise, the predictive genomic offset showed that, in both 2050 and 2100 scenarios, populations from central and western Amazonia would be under higher risk of extinction events due to future climate change. The distinctive pattern we found of genomic offset shows how different populations within the same species might be more or less vulnerable to future environmental changes. Incorporating this information into risk assessments can enhance the prospects of species and population survival.

4.1 Population Structure

The east-western population structure pattern we observed for *Gonatodes humeralis* resembles the findings of previous studies with different molecular and geographic sampling designs (e.g., Ávila-Pires et al., 2012, Pinto et al., 2019, Pirani et al., 2019). However, the nine populations we recovered depict a much more detailed degree of population differentiation and structure than former studies (Pinto et al., 2019), which used a sparse sampling across the species range and recovered two populations within the Amazon Basin (one at 'eastern Amazonia' and one at 'western Amazonia'). We believe that differences in genetic markers used (sanger vs ddRADSeq) and reduced geographic sampling coverage across Amazonia in previous studies may account for such differences. For example, Pinto et al. (2019) sampled only 31 individuals from 13 localities, while we sampled 165 from 37 localities (see methods session). A denser sampling, both in terms of individuals and localities, may have resulted in more geographically structured populations, avoiding the so-called K = 2 conundrum (Janes et al., 2017), and is more in line with what would be expected from the species' biological traits of low vagility and poor disperser (Vitt et al., 1997, Ávila-Pires et al., 2012). Our denser sampling recovered a more refined population structure, with a general northeast to southwest pattern with increased structure across the species’ range and decreasing levels of admixture accompanying the same direction (Figure 1).

We found strong genetic differentiation between populations geographically close to each other (Figure 2), which is consistent with the species' low vagility (Ávila-Pires et al., 2012), but also a weak signal of isolation (high admixture). For example, populations at the extreme northeastern of the species distribution in the lower Tocantins River (blue and purple, Figure 2) are close to each other but were assigned to very distinct clusters. Furthermore, there are isolated single populations with little or no admixture at all (pink and green in Figure 2). Conversely, admixture seems to be widespread through populations at the central-eastern portion of the species range, which could be related to the species center-of-origin (Pinto et al., 2019), where genetic diversity tends to accumulate over time (Kimura, 1983). Population structure may change over time, with multiple historical events leaving signals currently detectable in the data (Lawson et al., 2018).

Explaining admixture is not a trivial task. Several historical demographic events, even discordant ones, may cause the admixture pattern we see nowadays and many of those might have occurred in Amazonia. Different regions went through different historical processes and generated a landscape complexity that can be interpreted as a consequence of those multiple processes that shaped current Amazonian biodiversity (Hoorn et al., 2022, Cracraft et al., 2020). For example, historical expansion and retraction events may have favored the presence of strong admixture signal across eastern Amazonia, a region closer to the transition zone with Cerrado and Caatinga ecoregions and historically more unstable regarding the climate (Cheng et al., 2013, Silva et al., 2019). Likewise, the role played by rivers as primary or secondary barriers to gene flow might also have influenced the pattern of admixture we see in our results (e.g., Alfaro et al., 2015, Godinho and Silva, 2018, Pirani et al., 2019). Geographic contact in headwater regions might have prevented isolation between populations from occurring, since the rivers may no longer act as effective barriers to gene flow (Weir et al., 2015), favoring admixture in those regions. Further, broad admixture zones in Amazonia can come out from secondary contact following lineage divergence (Barrera-Guzmán et al., 2022), where the disappearance attenuation of physical barriers that hinder gene flow can promote admixture between genetically distinct populations (Musher et al., 2022).

4.2 Local adaptation

Our results showed that genetic variation was significantly correlated with the six selected environmental variables (Table 1). Regarding candidate SNPs, the adaptive genetic variation was strongly correlated with precipitation amount in the warmest season (Bio_18, Figure 3). Moreover, we can assume that precipitation and temperature are important and relevant features to explain the genetic variation (neutral and adaptive) and result in patterns of local adaptation across the range of *G. humeralis*. The 56 putative SNPs we found from both GEA approaches to be under climate selection, reveal the existence of local adaptation in *G. humeralis* across Amazonian landscapes or a spatial variation in fitness. The historical establishment of environmental gradients within Amazonia and at its transition to other biomes (e.g., the Amazonia-Cerrado ecotone) can explain the local adaptation and adaptive landscape patterns we found. Further, more recent environmental changes caused by human action could act now as synergetic climatic selective pressures upon the organisms. For example, southern Amazonia presents a relatively long dry-season length (DSL), a pattern that has a trend to increase further in the late 21st Century (Fu et al., 2013). When combined with human-induced fires and land use (Salazar et al., 2007, De Faria et al., 2017), this increasing DSL can have an influence in the adaptive index of *G. humeralis* across that region. Besides, changes in the Amazonian vegetation during the Pleistocene, especially in the southern region (Mayle et al., 2000), may play a role in explaining the adaptive landscape pattern found (south-to-north). This occurred when forest retractions towards the equator took place due to climatic fluctuations (Ayres and Clutton-Brock, 1992, Hafer and Prance, 2002, Hafer, 2008), which is also supported by the diversification timing found by Pinto et al. (2019) for the same focal species.

The adaptive-enriched RDA model we employed captured 80% of the variation across two axes, indicating strong signals of local adaptation. Precipitation seasonality appears as a strong predictor for the candidate SNPs we found, with SNP frequencies associated with low levels of this variable (Figures 3 and 4), which shows us a sign of local adaptation towards regions with more constant rain rather than markable seasonality. These are the characteristics of western Amazonia, which was precisely the region with less admixture in clustering analysis (Figure 2C), highlighting low levels of gene flow between these populations and their eastern counterparts, and possibly explaining local adaptation results. Likewise, western populations exhibit SNPs associated with higher rainfall during the warmest season, consistent with the greater precipitation levels found in western Amazonia (Cheng et al., 2013). In conclusion, we see that accounting for both neutral and adaptive genetic diversity can improve our interpretation of underlying evolutionary processes on a geographic scale across Amazonia.

4.3 Adaptive landscape and future genomic offset

As we mapped the adaptive index across the landscape, we were able to assess the scale and pattern of local adaptation of *G. humeralis* in Amazonia (Figure 4). The spatial projection of the adaptive variation provides a better understanding of potential climate adaptation to unsampled areas within the species distribution (Gugger et al., 2021), revealing regions where patterns of local adaptation differ from the background genetic variation. Our results show a consistent gradient pattern in the adaptive optimum from areas close to the Cerrado-Amazonia transition (eastern to south) to central and western Amazonia, with remarkable differences in the adaptive index (positive to negative scores). Interestingly, our results present an east-west difference in the adaptive index for Amazonia, which is a common direction of biodiversity patterns turnover in this biome (e.g., Pinto et al., 2018).

The adaptive landscape of *G. humeralis* provides valuable information to include in plans and actions toward conservation and management strategies for the survival of the species' (and potentially other taxa from similar functional groups - i.e., thermoconformer and ombrophilous tropical ectotherms) facing climate change (Aitken and Whitlock, 2013, Fitzpatrick and Keller, 2015, Gugger et al., 2021). According to future scenarios, not only will the temperature rise but also rainfall patterns are expected to change (Dai, 2013, Marengo et al., 2011, IPCC, 2021). As we have shown, precipitation and temperature variables were significantly important in explaining the patterns of local adaptation in *G. humeralis* across Amazonia. Consequently, the aforementioned changes will likely have a negative effect on populations that are currently adapted to a given climate, imposing new selective pressures upon individuals that they may not be able to cope with under future scenarios. One way to avoid local extinctions in changing climates and preserve both wide genetic variation and genomic regions putatively under climate selection would be the use of adaptive index information across the landscape to propose connectivity via assisted gene flow between populations (Hoffmann et al., 2021, Chen et al., 2022, Meek et al., 2023). Given the advances in population genomics, assisted gene flow has emerged as a viable strategy for enhancing population resilience by leveraging adaptive genetic variation (Fitzpatrick and Funk, 2019, Hohenlohe et al., 2020). Also, these results can guide propositions of ecological forested corridors, considering the distributional areas that could enable the species' natural dispersion, and prevent local climate-driven extinctions (Littlefield et al., 2019).

According to our results, and accounting for the existence of an east-western gradient in the adaptive landscape index, it is reasonable to suggest that some *G. humeralis* populations may have the ability to cope with the impacts of climate change, especially those in eastern Amazonia. Nonetheless, populations in western Amazonia may not be able to survive, as their eastern counterparts, if novel adaptive variation does not arise through de novo mutation or migration (Bay et al., 2018, Razgour et al., 2019). The main reason for this is the significant disparity in adaptive optimum in the west (Figure 4), coupled with the potential impact of future changes in temperature and precipitation patterns. Moreover, as expected, we see an increase in vulnerability for 2100, when carbon emissions are not likely to be reduced, with more areas presenting prominent genomic offset levels.

The genomic offset predicts the overall future genomic change required in a population to maintain the standing genome environment associations under climate scenarios. Apparently, *Gonatodes humeralis* populations in central and western Amazonia are under greater threat, considering the higher values of genomic offset for those regions. Although populations in these regions are well adapted to current conditions (Figure 4), the predicted environmental change across the landscape will possibly disrupt the genome-environment relationships in the future, requiring more genomic change than they can afford, which might possibly lead to local extinctions. On the other hand, some populations nested in western Amazonia are at lower or at least attenuated risk, considering the levels of genomic offset in that region (yellowish color in Figure 5). One explanation for this would be that this region will change less of its environmental conditions in the future, reducing the need for genomic change and thus buffering the struggle of populations to persist there.

Our results predict a high value of genomic offset along the distribution range of another forest gecko, *Gonatodes tapajonicus*, which is currently the only threatened lizard species in Amazonia (Vulnerable in the IUCN Red List and Endangered in the Brazilian Red List of Threatened Species) (Silveira et al., 2021, ICMBio, 2018 respectively). *Gonatodes tapajonicus* is known only from some records along the east bank of Rio Tapajós basin and face several human-induced threats (Rodrigues, 1980, Sturaro and Avila-Pires, 2011, Silveira et al., 2021). Our study with *G. humeralis* can act as a baseline for future studies regarding climate change vulnerability and adaptive potential with *G. tapajonicus*, which has a more restricted distribution and vulnerability. So, a better understanding of adaptation patterns for this species can help to design action strategies for its conservation, based on eco-evolutionary aspects of a congener (*G. humeralis*).

Molecular data gathered across populations and species (e.g., neutral and adaptive genetic diversity, gene flow, genomic vulnerability, heterozygosity, inbreeding, hybridization) may help to build important strategies for conservation, providing valuable sources of information for biodiversity maintenance (Nielsen et al., 2022). Considering the threats to biodiversity in the Anthropocene, forest lizards (thermoconformers, ombrophilous) stand out among the most endangered organisms (Huey et al., 2009, Sinervo et al., 2010, Urban, 2015, Teixeira et al., 2022). Therefore, studies addressing molecular patterns and processes involved in population structuring and local adaptation at multiple scales become important tools for improving risk assessments and strategies for conservation of these organisms under current global changing scenarios (Urban et al., 2016, Forester et al., 2022, Nielsen et al., 2022).

4.4 Conclusions and perspectives

This is the first population genomics investigation of a Neotropical lizard species that uses a integrative approach to understand how local adaptation can affect climate change vulnerability on a large Amazonian spatial scale. Our findings highlight the importance of considering spatially explicit contexts with large sampling coverage to evaluate the role played by environmental gradients in selecting patterns of local climate adaptation. Besides, the focus on fairly wide distributed populations, in opposition to extremely narrow ones, is of biological interest given that processes that operate at small populations, such as genetic drift and mutation load may prevent local adaptation from buffering the effects of climate change (Meek et al., 2023). Genomic climate vulnerability is an important component of risk assessments and can help construct new opportunities for investigation and push forward the frontier in eco-evolutionary research and conservation genetics (Forester et al., 2022). Populations showing true signs of local adaptation may deal better with environmental change when facing future climate change through natural selection and genetic rescue (Razgour et al., 2019, Capblancq et al., 2020). However, despite being an experimental field of research in evolutionary ecology and population genomics, the detection of local adaptation is presently a trending topic that is likely to undergo further methodological and interpretational advancements in the coming years (Csilléry et al., 2018, Capblancq and Forester, 2021). Future investigation should focus on evaluating the potential of using eco-evolutionary data in creation of new protected areas and how much of the adaptive potential is covered by the extant protected areas and indigenous lands across the biome. The potential of using lizards as a model for eco-evolutionary questions is supported in our study, and Amazonia harbors hundreds of them, living in the most different sorts of environments throughout the biome. The need and feasibility of further strategies such as assisted gene flow through genetic rescue and validating the predictions of adaptive loci through common garden experiments for non-model organisms on a broader geographic scale could also be the focus of new investigations throughout Amazonia.

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7 FIGURES AND CAPTIONS

Figure 1: Genomic sampling distribution of *Gonatodes humeralis* across South America (adapted from Olson et al., 2001). Blue lines represent the main rivers of South America. The map is displayed on an equal-area Behrman projection. Photo: Rodrigo Tinoco.

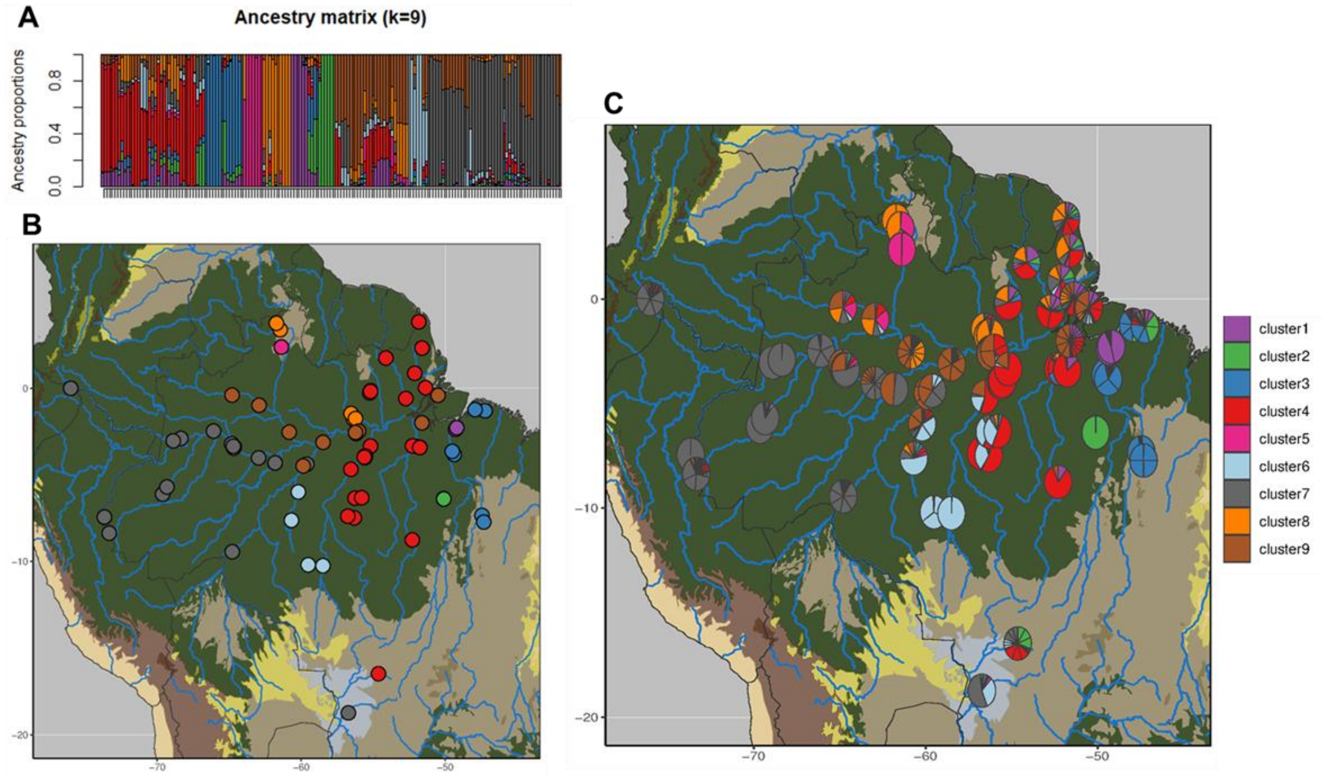

Figure 2: Population structure and assignment of *Gonatodes humeralis* across Amazonia and transitional biomes; A) Barplot from sNMF analysis, showing high admixture and nine population clusters; B) Population assignment across the studied species range; C) Pie chart with admixture proportions among clusters (K = 9). Maps are displayed on an equal-area Behrman projection.

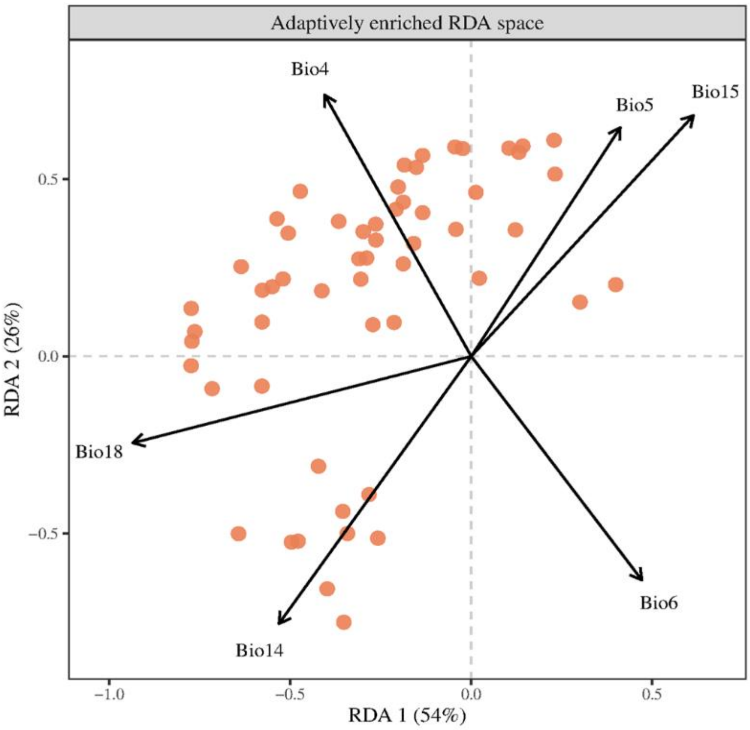

Figure 3: Adaptively enriched RDA-biplot (candidate SNPs only) showing the association between putative adaptive loci (orange dots) and bioclimatic variables from Climond as drivers of local adaptation, as well as the correlation among variables.

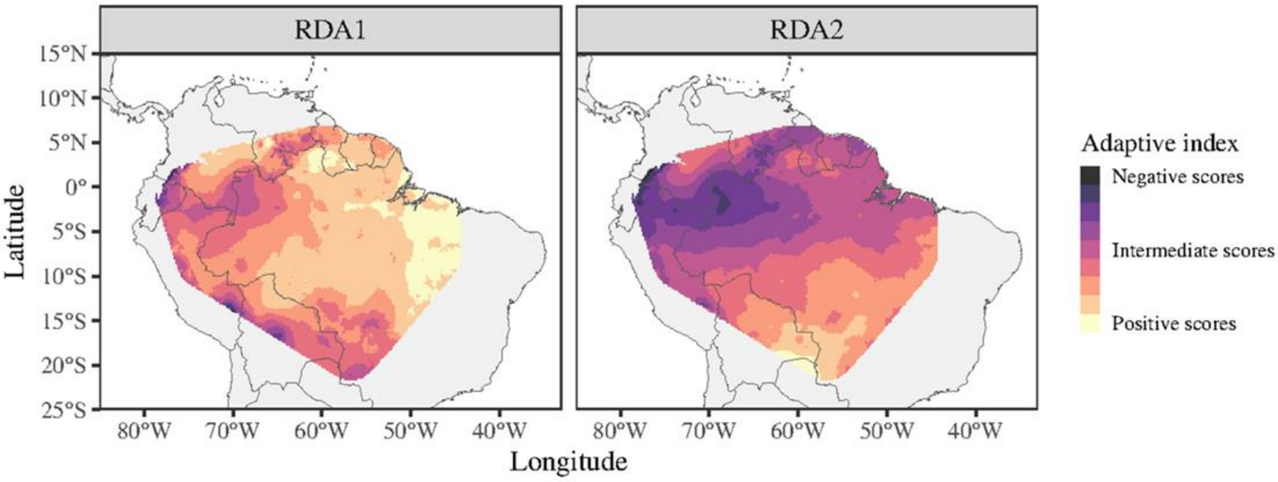

Figure 4: Adaptive landscape inferred by the predicted genetic similarity derived from an extrapolation of RDA axes with the adaptive index scores as a spatial projection across the range of *Gonatodes humeralis*. Similar colors across the landscape represent regions with populations adapted to similar conditions.

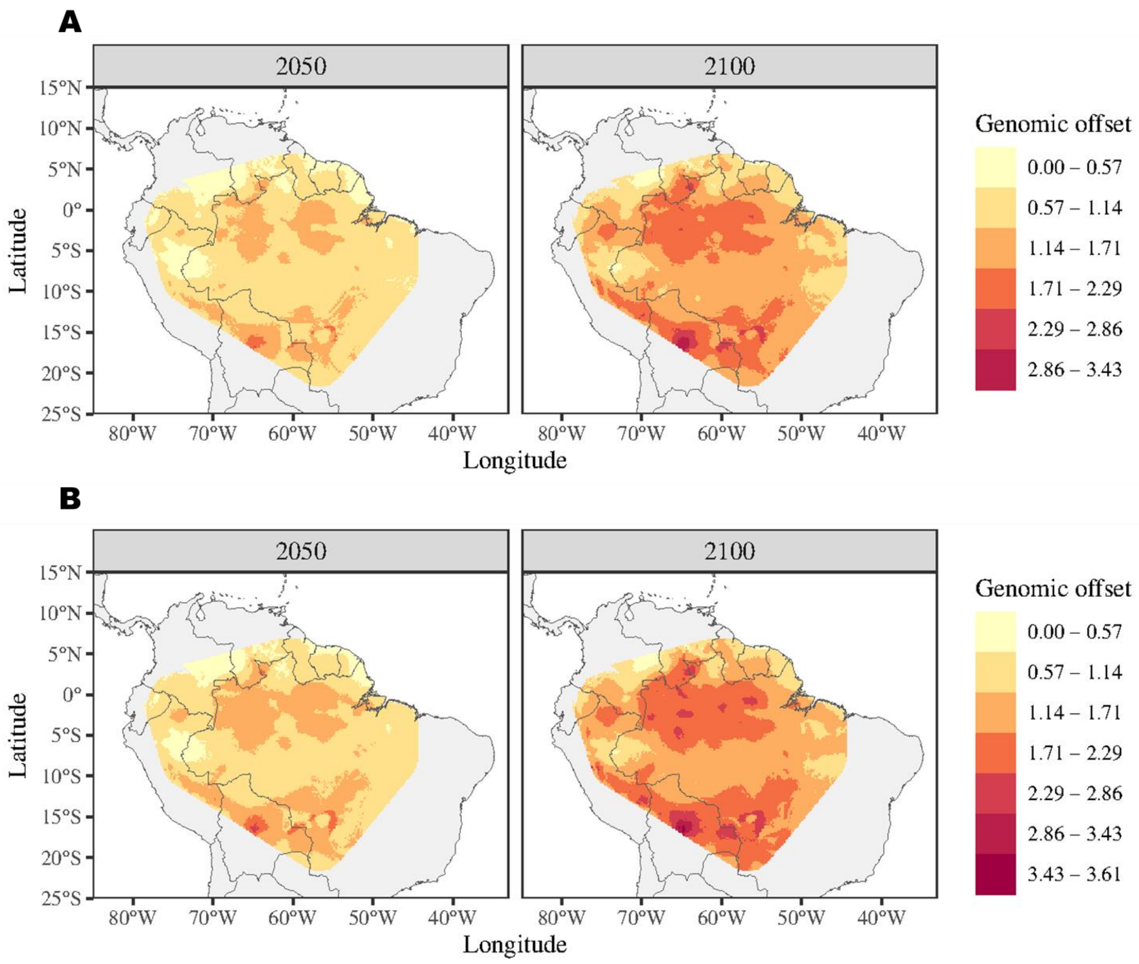

Figure 5: Predicted genomic offset for *Gonatodes humeralis* across its distribution range in Amazonia using the projections for the years 2050 and 2100 under A) an intermediate emission scenario (A1B) and B) an extreme emission scenario (A2). Dark red colors represent more vulnerability.

Table 1. RDA climatic variables selection results. Bioclimatic abbreviations represent: bio_18 - mean monthly precipitation amount of the warmest quarter, bio_6 - mean daily minimum air temperature of the coldest month, bio_05 - mean daily maximum air temperature of the warmest month, bio_04 - temperature seasonality, bio_15 - precipitation seasonality and bio_14 - precipitation amount of the driest month. Df = degrees of freedom; AIC = Akaike Information Criteria.

	R2.adj	Df	AIC	F	Pr(>F)
bio_18	0.10	1.00	1506.74	18.55	0.002
bio_6	0.11	1.00	1504.42	4.30	0.002
bio_5	0.13	1.00	1503.25	3.12	0.002
bio_4	0.14	1.00	1502.27	2.91	0.002
bio_15	0.15	1.00	1501.56	2.64	0.002
bio_14	0.15	1.00	1500.83	2.64	0.002
All variables	0.15	-	-	-	-

8 SUPPLEMENTARY MATERIALS

Local adaptation and vulnerability to climate change in a widespread Amazonian Forest lizard

André Yves, Josué A. R. Azevedo, Renata M. Pirani, Fernanda P. Werneck

Supplementary Material

List of scientific collections assessed:

INPA-H - Herpetology Collection at the Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil)

LSU - The collection of reptiles and amphibians of the Louisiana Museum of Natural History (Baton Rouge, United States)

MNCN - Colección de Anfibios Y Reptiles at the Museo Nacional de Ciencias Naturales (Madrid, Spain)

MPEG – Coleção Herpetológica Osvaldo Rodrigues da Cunha, deposited at Museu Paraense Emilio Goeldi at the Museu Paraense Emílio Goeldi (Belém, Brazil)

USP - Universidade de São Paulo (São Paulo, Brazil)

Supplemental Tables

Table S1. Individual level sampling information for *Gonatodes humeralis* used in this study. * specimens removed from downstream analysis.

Voucher	Locality	Latitude	Longitude
MPEG/1476*	Almeirim	-1.1911	-52.6478
MPEG/2374*	Almeirim	-0.6906	-52.8192
USP/977116	Aripuana	-10.2406	-58.4911
USP/977403	Aripuana	-10.1883	-59.5122
MPEG/ACP 026	Juruti	-2.6094	-56.1961
MPEG/ACP 064	Juruti	-2.4717	-56.0122
MPEG/ACP 446	Oriximiná	-1.7731	-56.3706
MPEG/ACP 580	Oriximiná	-1.7731	-56.3706
MPEG/AOM 089	Fonte_Boa	-2.4686	-66.0836
MPEG/AOM 091	Fonte_Boa	-2.4686	-66.0836

Voucher	Locality	Latitude	Longitude
MPEG/AOM 092	Fonte_Boa	-2.4686	-66.0836
MPEG/AOM 093*	Fonte_Boa	-2.4686	-66.0836
MPEG/AOM 095	Fonte_Boa	-2.4686	-66.0836
MPEG/AOM 099	Fonte_Boa	-2.4686	-66.0836
MPEG/AOM 108	Tefé	-3.3794	-64.6408
MPEG/AOM 117	Tefé	-3.4498	-64.6848
MPEG/AOM 131	Coari	-4.0146	-62.9550
MPEG/AOM 134	Coari	-4.0146	-62.9550
MPEG/AOM 135	Coari	-4.0146	-62.9550
MPEG/AOM 136	Coari	-4.0146	-62.9550
MPEG/AOM 137	Coari	-4.0146	-62.9550
MPEG/AOM 139	Coari	-4.0146	-62.9550
MPEG/AOM 185	Borba	-4.4803	-59.8617
MPEG/AOM 186	Borba	-4.4803	-59.8617
MPEG/AOM 187	Borba	-4.4803	-59.8617
MPEG/AOM 189	Borba	-4.3786	-59.6119
MPEG/AOM 190	Borba	-4.3786	-59.6119
MPEG/AOM 202	Itacoatiara	-3.1181	-58.4819
MPEG/AOM 203	Itacoatiara	-3.1181	-58.4819
MPEG/AOM 204	Itacoatiara	-3.1181	-58.4819
MPEG/AOM 205	Itacoatiara	-3.1181	-58.4819
MPEG/AOM 206	Itacoatiara	-3.1181	-58.4819
USP/BM 572	Altamira	-8.7498	-52.2862
USP/BM 580	Altamira	-3.3228	-52.2748
USP/BM 581	Altamira	-3.3228	-52.2748
USP/BM 710	Altamira	-3.3426	-52.0777
MPEG/BML 011	Vitoria_do_Xingu	-3.4178	-51.7572
MPEG/BML 012*	Vitoria_do_Xingu	-3.4147	-51.7614
MPEG/BML 036	Vitoria_do_Xingu	-3.4147	-51.7614
MPEG/BML 038	Vitoria_do_Xingu	-3.4083	-51.7556
MPEG/BML 1092*	Vitoria_do_Xingu	-3.4017	-51.7356
MPEG/BML 1247	Vitoria_do_Xingu	-3.4154	-51.7657
MPEG/CN 1545	Almeirim	1.7447	-54.1197
MPEG/CN 1653*	Almeirim	1.9686	-55.5508
MPEG/CN 738	Alenquer	-0.2628	-55.2439
MPEG/CN 753	Alenquer	-0.1356	-55.1817
MPEG/CN 808	Alenquer	-0.1775	-55.1800
USP/ESTR00049	Estreito	-7.3333	-47.4500
USP/ESTR00182	Estreito	-7.3333	-47.4500
USP/ESTR0492	Estreito	-7.7213	-47.3215
USP/ESTR0766	Estreito	-7.7213	-47.3215
USP/ESTR0874	Estreito	-7.7213	-47.3215

Voucher	**Locality**	**Latitude**	**Longitude**
USP/ESTR0886	Estreito	-7.7213	-47.3215
USP/FSFL 1018	Corumbá	-18.7310	-56.7233
MPEG/GRLF 119	Viseu	-1.3006	-47.2319
MPEG/GRLF 120	Viseu	-1.3006	-47.2319
MPEG/GRLF 16	Viseu	-1.2099	-46.1782
MPEG/GRLF 199*	Viseu	-1.2333	-47.9278
MPEG/GRLF 200	Viseu	-1.2333	-47.9278
MPEG/GRLF 8	Viseu	-1.2104	-46.1777
USP/INPA - H 18441*	Aripuanã	-7.6187	-60.6799
USP/INPA - H 18442*	Aripuanã	-7.6179	-60.6796
USP/INPA - H 18443	Aripuanã	-7.6179	-60.6796
USP/HJ0008	Porto_Velho	-9.4333	-64.7842
USP/HJ0079	Porto_Velho	-9.4333	-64.7842
USP/HJ0108	Porto_Velho	-9.4333	-64.7842
USP/HJ0140	Porto_Velho	-9.4333	-64.7842
USP/HJ0141	Porto_Velho	-9.4333	-64.7842
USP/HJ0202	Porto_Velho	-9.4333	-64.7842
INPA/HT.4544	Barcelos	-0.3925	-64.7979
INPA/HT.4854*	Itapuana	-3.3445	-55.1841
INPA/HT.4855	Itapuana	-3.3445	-55.1841
INPA/HT.4898*	Itapuana	-3.3455	-55.1967
INPA/HT.4917	Itapuana	-3.3459	-55.1868
INPA/HT.4979	Itapuana	-3.3364	-55.1884
INPA/HT.4999*	Itapuana	-3.3353	-55.2015
INPA/HT.5141	Taquera	-1.4580	-56.5385
INPA/HT.5186	Taquera	-1.4580	-56.5385
INPA/HT.5224*	Taquera	-1.4024	-56.4178
MPEG/JOG 499	Itaituba	-7.4811	-56.3169
MPEG/JOG 513	Itaituba	-6.3414	-56.2631
MPEG/JOG 517	Itaituba	-6.3158	-55.7978
MPEG/JOG 655*	Itaituba	-6.3158	-55.7978
MPEG/JUR 1111	Juruti	-2.4717	-56.0122
MPEG/JUR 237	Juruti	-2.5475	-56.2256
MPEG/JUR 359*	Juruti	-2.4531	-56.1528
MPEG/JUR 59*	Juruti	-2.4717	-56.1558
USP/LG1177	Aripuanã	-10.1883	-59.5122
USP/LG1178	Aripuanã	-10.1883	-59.5122
LSU/LSU_12589	Cuyabeno	0.0000	-76.0000
LSU/LSU_12603	Cuyabeno	0.0000	-76.0000
LSU/LSU_12636	Cuyabeno	0.0000	-76.0000
LSU/LSU_12637	Cuyabeno	0.0000	-76.0000
LSU/LSU_12638	Cuyabeno	0.0000	-76.0000

Voucher	Locality	Latitude	Longitude
LSU/LSU_12639	Cuyabeno	0.0000	-76.0000
MPEG/M1R11	Oriximiná	-1.7439	-56.2281
MPEG/M1R8	Oriximiná	-1.7439	-56.2281
MPEG/MAR 1488*	Afuá	-0.4037	-50.4964
MPEG/MAR 1498	Afuá	-0.4037	-50.4964
MPEG/MAR 1527*	Afuá	-0.4037	-50.4964
MPEG/MAR 1530	Afuá	-0.4037	-50.4964
MPEG/MAR 169	Portel	-1.9936	-51.6153
MPEG/MAR 617	Portel	-1.9936	-51.6153
MPEG/MAR 673	Portel	-1.9936	-51.6153
MPEG/MAR 688	Portel	-1.9936	-51.6153
MPEG/MAR 987*	Portel	-1.9936	-51.6153
MPEG/MAR 992	Portel	-1.9936	-51.6153
USP/MBS 008	Serra_do_Divisor	-8.3600	-73.3300
USP/MBS 013	Serra_do_Divisor	-8.3600	-73.3300
USP/MBS 020*	Serra_do_Divisor	-8.3600	-73.3300
USP/MBS 028	Serra_do_Divisor	-8.3600	-73.3300
USP/MBS 029*	Serra_do_Divisor	-8.3600	-73.3300
USP/MBS 036*	Serra_do_Divisor	-8.3600	-73.3300
MNCN/ADN 6177*	Bolívia	-14.3367	-68.0992
USP/MRT 4436	Barcelos	-0.9747	-62.9242
USP/MRT 4437*	Barcelos	-0.9747	-62.9242
USP/MRT 6263	Serra_do_Navio	0.0333	-51.3667
USP/MRT 6323	Serra_do_Navio	0.0333	-51.3667
USP/MRT 6324	Serra_do_Navio	0.0333	-51.3667
USP/MSH 10213	Anavilhanas	-2.5333	-60.8333
USP/MSH 10214	Anavilhanas	-2.5333	-60.8333
USP/MSH 10215	Anavilhanas	-2.5333	-60.8333
USP/MSH 10216	Anavilhanas	-2.5333	-60.8333
USP/MSH 10218	Anavilhanas	-2.5333	-60.8333
USP/MSH 10229*	Anavilhanas	-2.5333	-60.8333
MPEG/MSH 12015	Igarapé_Miri	-2.3693	-49.2813
MPEG/MSH 12016	Igarapé_Miri	-2.3693	-49.2813
MPEG/MSH 12017	Igarapé_Miri	-2.3693	-49.2813
MPEG/MSH 12018	Igarapé_Miri	-2.3693	-49.2813
MPEG/MSH 12023	Igarapé_Miri	-2.2773	-49.1997
MPEG/MSH 12027	Igarapé_Miri	-2.2773	-49.1997
MPEG/MSH 12102	Breu_Branco	-3.8186	-49.3735
MPEG/MSH 12103	Breu_Branco	-3.8186	-49.3735
MPEG/MSH 12104	Breu_Branco	-3.8186	-49.3735
MPEG/MSH 12107	Breu_Branco	-3.6395	-49.5124
MPEG/MSH 12110	Breu_Branco	-3.6370	-49.5114

Voucher	Locality	Latitude	Longitude
MPEG/MSH 12112	Breu_Branco	-3.6370	-49.5114
MPEG/MSH 12376	Carajás	-6.3972	-50.1042
MPEG/MSH 12427	Carajás	-6.3975	-50.1198
MPEG/MSH 12503	Carajás	-6.3942	-50.1049
MPEG/MSH 12556	Carajás	-6.3650	-50.1169
MPEG/MSH 12565	Carajás	-6.3647	-50.1170
MPEG/MSH 12626	Carajás	-6.3877	-50.1003
MPEG/MSH 9175	Itaituba	-7.3783	-56.7642
MPEG/MSH 7636	Almeirim	-0.5908	-52.7358
MPEG/MSH 7869	Almeirim	-0.5908	-52.7358
MPEG/MSH 8065	Itaituba	-4.6742	-56.5478
MPEG/MSH 9792	Jutaí	-6.1094	-69.6214
MPEG/MSH 9798	Jutaí	-5.6936	-69.3192
USP/MTR 13826	Serra_do_Navio	0.8667	-52.1167
USP/MTR 18574	Itapuru	-4.3079	-61.8159
USP/MTR 18680	Itapuru	-4.3079	-61.8159
USP/MTR 18689	Itapuru	-4.3111	-61.8168
USP/MTR 18690*	Itapuru	-4.3078	-61.8153
USP/MTR 18703	Itapuru	-4.3056	-61.8134
USP/MTR 18705	Itapuru	-4.3060	-61.8134
USP/MTR 20457	Tepequém	3.3807	-61.4544
USP/MTR 20641	Tepequém	3.3807	-61.4544
USP/MTR 20835	Tepequém	3.7548	-61.7175
USP/MTR 20851*	Tepequém	3.7548	-61.7175
USP/MTR 20919	Tepequém	3.7548	-61.7175
USP/MTR 20920	Tepequém	3.7548	-61.7175
USP/MTR23035	Serra_do_Maroquinha	2.3905	-61.3788
USP/MTR23042	Serra_do_Maroquinha	2.3836	-61.3756
USP/MTR23049	Serra_do_Maroquinha	2.3779	-61.3756
USP/MTR23067	Serra_do_Maroquinha	2.3905	-61.3788
USP/MTR23095	Serra_do_Maroquinha	2.3905	-61.3788
USP/MTR23154	Serra_do_Maroquinha	2.3779	-61.3756
USP/MTR 24063*	Oiapoque	3.8355	-51.8333
USP/MTR 24064	Oiapoque	3.8355	-51.8333
USP/MTR 24153	Oiapoque	3.8355	-51.8333
USP/MTR 24269	Oiapoque	2.3216	-51.6109
USP/MTR 28051	Serra_do_Divisor	-7.4431	-73.6577
USP/MTR 28054	Serra_do_Divisor	-7.4431	-73.6577
USP/MTR 28134	Serra_do_Divisor	-7.4301	-73.6616
USP/MTR 28205	Serra_do_Divisor	-7.4458	-73.6576
USP/MTR 28222	Serra_do_Divisor	-7.4334	-73.6611
USP/MTR 28307	Serra_do_Divisor	-7.4312	-73.6617

Voucher	Locality	Latitude	Longitude
USP/MTR 36103	Tefé	-2.8909	-68.3527
USP/MTR 36493	Tefé	-3.0339	-68.8838
USP/MTR 36909	Tefé	-3.1997	-64.8226
USP/MTR 36947	Tefé	-3.3455	-64.7112
MPEG/PRMT 552	Aveiro	-3.9224	-55.5942
MPEG/PRMT 554	Aveiro	-3.9224	-55.5942
MPEG/PRMT 575	Aveiro	-3.9111	-55.5325
MPEG/PRMT 702	Aveiro	-4.0069	-55.5760
MPEG/PRMT 704	Aveiro	-4.0069	-55.5760
MPEG/PRMT 723	Aveiro	-3.9731	-55.6193
USP/RRT 31	Rondonópolis	-16.4713	-54.6371
USP/RRT 34	Rondonópolis	-16.4713	-54.6371
USP/RRT 39	Rondonópolis	-16.4713	-54.6371
USP/VOGT 2081	Aripuanã	-5.9833	-60.2000
USP/VOGT 2082*	Aripuanã	-5.9833	-60.2000
USP/VOGT 2083	Aripuanã	-5.9833	-60.2000

Table S2. Processing information and ipyrad summary statistics for specimens sequenced. Raw reads refers to the total reads produced during Illumina sequencing; post-filtering reads are those that remained after filtering for quality; total clusters are the number of homologous sequences clusters created with the post-processing reads; mean depth is the mean depth of coverage of a cluster. Heterozygosity estimation (H) and error estimation (E) were estimated across clusters, and consensus sequences were created for each cluster. Variable and invariable DNA sites were summed across all loci (Total sites), and the percentage of polymorphic sites (% poly) is presented. Consensus sequences were clustered across specimens, and loci that passed filtering parameters were included in the final data matrix (Final loci). *specimens with low number of reads (<600).

Voucher	raw reads	reads passed filter	clusters total	clusters hidepth	H	E	reads consens	loci in assembly
G_hum_LG1177_ArMtBr	2475426	2459448	241060	87918	0.008848	0.001833	83639	43372
G_hum_MSH12018_ImPaBr	2021624	2006147	255586	90040	0.010651	0.002191	85134	43324
G_hum_ACP026_JuPaBr	2018064	1994372	244595	88513	0.010705	0.00186	83776	43266
G_hum_MSH12565_CaPaBr	1994337	1972084	249317	89185	0.009173	0.002033	84689	42444
G_hum_LSU12636_CuSuEc	1935873	1921119	232090	81872	0.008419	0.002154	77928	43414
G_hum_MTR36947_TfAmBr	1904163	1889138	218631	80912	0.010504	0.001854	76782	43805
G_hum_MSH12016_ImPaBr	1880702	1863827	243726	89209	0.010872	0.002132	84313	43009
G_hum_HT5186_TaPaBr	1866138	1848870	238061	89810	0.01119	0.002219	84779	42328
G_hum_MSH12015_ImPaBr	1857468	1841301	241789	86030	0.01072	0.002071	81481	42845
G_hum_MSH12104_BbPaBr	1829843	1815699	227620	87453	0.009385	0.001939	82918	42320
G_hum_AOM187_BoAmBr	1792968	1773427	239739	86729	0.010842	0.002039	81993	42712
G_hum_MSH12107_BbPaBr	1770814	1758288	234557	84268	0.009568	0.001937	79840	42161
G_hum_MTR28222_SdAcBr	1763687	1751381	224787	81096	0.009444	0.001915	77108	43502
G_hum_AOM117_TfAmBr	1695298	1683633	224961	79280	0.010056	0.001926	75176	43323
G_hum_MTR28054_SdAcBr	1694014	1679195	234006	79615	0.00908	0.002112	75708	43134
G_hum_MSH12027_ImPaBr	1692948	1679316	245315	82824	0.010603	0.001987	78230	42093
G_hum_MTR20641_MaRrBr	1686754	1670698	220399	79336	0.010587	0.002096	75249	42833
G_hum_MSH12017_ImPaBr	1681808	1667921	234053	81010	0.010386	0.001928	76628	41845
G_hum_ESTR0492_EsMaBr	1653601	1640539	220534	75745	0.008261	0.002092	71971	41855
G_hum_BM572_AtPaBr	1653103	1639340	221147	80357	0.011471	0.002074	75963	42700

G_hum_AOM091_FbAmBr	1649565	1621377	244466	82014	0.009939	0.002284	77527	41825
G_hum_977116_JuMtBr	1620990	1605567	244992	74618	0.009337	0.002191	70864	41717
G_hum_MTR36493_SpAmBr	1611367	1591610	215149	75916	0.009276	0.002286	72144	42935
G_hum_AOM134_CoAmBr	1606762	1587188	229021	81869	0.010635	0.00189	77305	41837
G_hum_AOM131_CoAmBr	1599551	1568249	250307	76868	0.010704	0.002037	72493	41252
G_hum_M1R8_OxPaBr	1594303	1579873	233626	80518	0.011076	0.002424	75890	41411
G_hum_MSH12112_BbPaBr	1591715	1577827	218748	79191	0.010017	0.002163	74943	41262
G_hum_AOM139_CoAmBr	1579738	1559734	230312	77016	0.010197	0.002013	72950	41566
G_hum_MSH12427_CaPaBr	1518690	1498696	223636	77103	0.009338	0.00216	73111	40552
G_hum_HJ0079_PrRoBr	1509855	1499200	201089	76425	0.00968	0.002022	72600	42484
G_hum_LG1178_ArMtBr	1507829	1496035	206194	74426	0.0093	0.00202	70877	41989
G_hum_LSU12639_CuSuEc	1504359	1493025	199103	75224	0.010545	0.001018	71405	11344
G_hum_MSH12503_CaPaBr	1503137	1483083	224675	78399	0.009271	0.002282	74193	40422
G_hum_MSH12626_CaPaBr	1497791	1484810	210526	77976	0.008796	0.002224	73917	40582
G_hum_AOM203_ItAmBr	1491371	1472303	227454	76421	0.01211	0.002094	72063	40725
G_hum_AOM137_CoAmBr	1480039	1463918	219624	74999	0.010414	0.001929	70902	40955
G_hum_GRLF200_CaPaBr	1479189	1460637	227329	78082	0.010114	0.002429	73748	40065
G_hum_LSU12637_CuSuEc	1477682	1459725	221734	74293	0.009175	0.002215	70694	41629
G_hum_ACP580_OxPaBr	1473452	1451066	234014	78021	0.011769	0.002308	73290	39853
G_hum_MTR18705_PuAmBr	1467120	1447141	214813	75673	0.01138	0.00201	71489	42205
G_hum_MAR617_CxPaBr	1466198	1450486	230059	76564	0.012139	0.002351	71950	40896
G_hum_GRLF8_ViPaBr	1462830	1448096	219368	78294	0.009949	0.00223	74082	40081
G_hum_MAR688_CxPaBr	1458887	1446075	226551	78268	0.011848	0.002117	73571	40851
G_hum_LSU12638_CuSuEc	1455617	1444547	199052	75315	0.009401	0.002223	71709	42064
G_hum_MSH12023_ImPaBr	1455512	1443803	228466	77384	0.010399	0.00234	72960	40813
G_hum_MTR20920_TeRrBr	1440853	1426353	204319	75940	0.010724	0.002176	71905	41656
G_hum_GRLF16_ViPaBr	1438750	1428706	215436	77806	0.009809	0.002292	73572	40443
G_hum_PRMT704_AvPaBr	1431237	1411750	250093	74305	0.011258	0.002359	69905	40107
G_hum_HJ0141_PvRoBr	1427135	1416576	199318	75279	0.009707	0.001971	71463	41903

G_hum_MTR36103_CaAmBr	1425894	1414274	201600	73091	0.008918	0.00201	69620	42315
G_hum_MSH12556_CaPaBr	1424291	1409365	205094	76306	0.009114	0.002334	72315	39827
G_hum_AOM092_FbAmBr	1423965	1406960	217932	75472	0.010184	0.002195	71268	40669
G_hum_HJ0008_PvRoBr	1398152	1384063	208769	74252	0.009328	0.002115	70469	41495
G_hum_ESTR00049_CaMaBr	1396052	1381457	214546	74270	0.008682	0.00222	70442	40193
G_hum_HT5141_TaPaBr	1386095	1373990	212510	72669	0.009873	0.002199	68770	39248
G_hum_AOM089_FbAmBr	1384031	1371953	205165	73008	0.009718	0.001919	69123	40362
G_hum_MTR28051_SdAcBr	1360416	1348793	201581	72181	0.009183	0.002129	68513	41815
G_hum_MTR28205_SdAcBr	1354706	1343832	201843	72124	0.009498	0.002197	68520	41772
G_hum_AOM204_ItAmBr	1332841	1314132	220685	71329	0.012542	0.002311	66956	38951
G_hum_PRMT552_AvPaBr	1323045	1303318	237108	70984	0.011117	0.002358	66659	38891
G_hum_MTR23042_SmRrBr	1320102	1306352	201601	70538	0.010744	0.00222	66817	41029
G_hum_PRMT723_AvPaBr	1304950	1289070	220724	72255	0.011035	0.002405	67925	38460
G_hum_MRT4436_BaAmBr	1304604	1291363	212342	72117	0.011215	0.002259	68072	39091
G_hum_MTR23049_SmRrBr	1299887	1290529	188843	66067	0.010811	0.00248	62368	39019
G_hum_AOM095_FbAmBr	1298972	1282152	203317	70231	0.010353	0.002029	66344	39325
G_hum_MTR20835_TeRrBr	1298892	1286474	202970	69647	0.010424	0.001958	65999	40209
G_hum_PRMT575_AvPaBr	1293855	1276671	232168	70749	0.01153	0.002183	66527	38134
G_hum_ACP064_JuPaBr	1292434	1274609	221213	68057	0.011427	0.002179	64104	38233
G_hum_MSH1975_NpPaBr	1269477	1249038	232023	69178	0.009239	0.002428	65033	37473
G_hum_MTR20457_MaRrBr	1266381	1251654	195360	70725	0.009388	0.002279	67067	40074
G_hum_AOM205_ItAmBr	1265113	1252047	201178	69202	0.011734	0.002184	65052	38477
G_hum_JOG499_ItPaBr	1264347	1245431	229847	66502	0.00937	0.002297	62713	36878
G_hum_MSH10218_AnAmBr	1263946	1252816	202118	70630	0.012239	0.002393	66488	39609
G_hum_BML038_VxPaBr	1257181	1238184	232665	65812	0.012252	0.002302	61600	37037
G_hum_AOM190_BoAmBr	1247532	1235555	199000	70418	0.011083	0.002337	66388	38664
G_hum_BM581_AtPaBr	1241574	1231430	192763	68198	0.011886	0.0025	64323	39974
G_hum_HT4917_ItPaBr	1234062	1222256	199400	68025	0.011393	0.001958	64177	39624
G_hum_MTR20919_TeRrBr	1227228	1216478	189762	70145	0.010758	0.002291	66312	39729

G_hum_AOM202_ItAmBr	1218477	1206696	198131	67611	0.012778	0.002135	63628	37732
G_hum_CN753_AlPaBr	1217287	1207312	199219	69738	0.010764	0.002446	65515	37498
G_hum_MRT6263_MaApBr	1215708	1203919	198943	69256	0.012735	0.002518	65167	39237
G_hum_JUR1111_JuPaBr	1201683	1185806	213486	67534	0.012644	0.002279	63228	36988
G_hum_AOM099_FbAmBr	1198183	1182373	221318	63163	0.009687	0.002074	59648	36370
G_hum_JUR237_JuPaBr	1193919	1179419	210339	66003	0.011598	0.002284	62016	37523
G_hum_MTR23035_SmRrBr	1184179	1170726	189711	67585	0.011371	0.002235	63744	39027
G_hum_ESTR0874_EsMaBr	1168723	1160143	192524	65262	0.008701	0.002297	61943	38409
G_hum_MSH7869_AlPaBr	1162698	1148403	204896	64504	0.011522	0.002414	60566	36322
G_hum_HJ0108_PvRoBr	1159898	1149767	193327	64310	0.009405	0.002281	61074	38769
G_hum_MSH12110_BbPaBr	1159344	1147793	197153	64819	0.010618	0.002248	61041	36560
G_hum_MSH10216_AnAmBr	1151919	1143963	197767	66342	0.012625	0.002468	62229	37956
G_hum_MTR23095_SmRrBr	1150211	1136587	208301	63172	0.01091	0.002296	59682	38110
G_hum_JOG513_ItPaBr	1148168	1138911	238925	60798	0.012141	0.003072	56708	33793
G_hum_MSH10215_AnAmBr	1146951	1137391	187357	67136	0.012906	0.002244	63145	38477
G_hum_MTR36909_TfAmBr	1141258	1131717	190041	64791	0.01112	0.002134	61337	39493
G_hum_MAR1530_AfPaBr	1139703	1125887	218982	61490	0.011351	0.002582	57691	35191
G_hum_FSFL1018_CoMtsBr	1138599	1129741	180330	65609	0.009216	0.002483	62132	36812
G_hum_GRLF120_BoPaBr	1138547	1127414	200073	63756	0.009658	0.002467	60099	36013
G_hum_RRT39_RoMtBr	1135806	1122445	194832	61392	0.008103	0.002258	58470	35832
G_hum_AOM135_CoAmBr	1131424	1113847	217632	59696	0.011597	0.002256	56143	34775
G_hum_AOM189_BoAmBr	1126034	1110338	195661	63313	0.011383	0.002367	59510	36304
G_hum_HT4979_ItPaBr	1119737	1107606	190024	64634	0.01133	0.002278	60817	37926
G_hum_MAR673_CxPaBr	1119541	1109965	212049	62490	0.012353	0.002464	58436	36095
G_hum_ESTR0886_EsMaBr	1117448	1106730	180282	64026	0.008308	0.002288	60810	38200
G_hum_MSH12103_BbPaBr	1108405	1097367	191602	63011	0.010422	0.002227	59371	35769
G_hum_HJ0202_PvRoBr	1106722	1095310	203463	64149	0.0106	0.002248	60551	37528
G_hum_MAR169_CxPaBr	1099356	1088311	211927	59985	0.011724	0.00224	56115	35058
G_hum_MSH8065_ItPaBr	1098387	1085664	205171	62064	0.01137	0.002769	58125	35054

G_hum_ESTR0766_EsMaBr	1097769	1088036	194087	62672	0.00851	0.002605	59397	36931
G_hum_HT4855_ItPaBr	1092609	1074236	233294	56361	0.01234	0.002333	52864	34338
G_hum_MTR23067_SmRrBr	1092550	1083893	187755	63587	0.010917	0.00267	59888	37624
G_hum_PRMT702_AvPaBr	1091746	1076202	208368	61560	0.011593	0.002392	57633	34607
G_hum_BML036_VxPaBR	1086887	1070952	211387	58692	0.012235	0.002722	54932	34027
G_hum_CN1545_AlPaBr	1085726	1072285	198453	61881	0.01184	0.002666	58034	34136
G_hum_MTR23154_SmRrBr	1084025	1073576	176832	62540	0.010787	0.002356	59185	38002
G_hum_M1R11_OxPaBr	1082889	1069200	203101	59776	0.011034	0.002171	56102	34482
G_hum_AOM186_BoAmBr	1059607	1049075	199564	60178	0.011639	0.002524	56317	35049
G_hum_HJ0140_PvRoBr	1045649	1033353	187296	59989	0.010235	0.002435	56854	37137
G_hum_MSH10214_AnAmBr	1040089	1032225	174731	59573	0.012464	0.002084	56254	36327
G_hum_LSU12603_CuSuEc	1019841	1012371	172692	63168	0.009656	0.0029	59670	36916
G_hum_AOM136_CoAmBr	1016618	1005827	192137	58009	0.011565	0.002165	54332	34163
G_hum_HT4898_ItPaBr	1010924	1002580	154758	48924	0.013062	0.003312	45481	75
G_hum_BM580_AtPaBr	1009170	1001470	190594	59816	0.012351	0.002589	55968	35206
G_hum_JOG517_ItPaBr	1004832	993691	201661	56696	0.009728	0.002383	53282	32765
G_hum_MSH12102_BbPaBr	993389	981452	184655	56576	0.01008	0.00231	53277	33056
G_hum_ESTR00182_CaMaBr	991861	985303	180060	60072	0.009217	0.002485	56655	34794
G_hum_MSH9798_JuAmBr	989050	975927	192265	56727	0.010022	0.002735	53415	34704
G_hum_MTR28134_SdAcBr	985345	973768	224499	55243	0.011376	0.002733	51793	33396
G_hum_MSH7636_AlPaBr	983438	974639	187003	55408	0.010806	0.002169	52063	32617
G_hum_MTR28307_SdAcBr	980399	973361	173518	59829	0.010124	0.002401	56450	36076
G_hum_AOM185_BoAmBr	977901	968294	186883	55826	0.011753	0.002398	52246	33014
G_hum_PRMT554_AvPaBr	975034	956555	215082	51771	0.012306	0.002555	48285	30883
G_hum_BML011_VxPaBr	953003	940653	202098	52006	0.013151	0.00261	48235	30660
G_hum_BM710_AtPaBr	913984	907287	182680	54863	0.012107	0.002633	51389	33042
G_hum_1476_AlPaBr	891365	879691	170716	35018	0.016474	0.003705	31391	332
G_hum_CN738_AlPaBr	889664	881386	178834	51329	0.011844	0.00286	47878	29254
G_hum_MSH12376_CaPaBr	879793	864612	216835	43460	0.010941	0.002729	40537	25268

G_hum_VOGT2081_ArAmBr	879025	870810	178253	51532	0.012233	0.002533	48098	31212
G_hum_AOM206_ItAmBr	873067	864444	173390	49835	0.013135	0.002406	46472	29919
G_hum_HT4544_DaAmBr	854480	849143	163092	52191	0.012387	0.002633	48749	32064
G_hum_MAR992_CxPaBr	853543	845688	189155	45581	0.013371	0.002506	42241	27717
G_hum_MTR18689_PuAmBr	848606	840246	162154	52652	0.012312	0.002671	49068	31836
G_hum_MTR24064_OiApBr	843548	837449	159696	52856	0.01172	0.00269	49393	31587
G_hum_MBS020_SdAcBr	842288	828363	169827	22463	0.016398	0.001528	20324	8067
G_hum_CN808_AlPaBr	840552	831172	182662	46185	0.011387	0.00276	42979	27434
G_hum_MTR18703_PuAmBr	830113	822848	164378	50693	0.013527	0.002522	47217	30862
G_hum_MRT6323_MaApBr	807254	800044	158156	32945	0.014854	0.002022	30290	17525
G_hum_977403_ArMtBr	790568	784330	166651	47827	0.01207	0.002911	44647	28174
G_hum_MTR24269_LoApBr	786452	777580	165756	46150	0.013625	0.003026	42830	28391
G_hum_MSH9792_JuAmBr	780105	767542	208383	37669	0.012017	0.003106	34942	23634
G_hum_LSU12589_CuSuEc	763839	758366	149926	47622	0.011729	0.003111	44500	28305
G_hum_ACP446_OxPaBr	761402	751837	187562	37483	0.015375	0.00307	34153	22439
G_hum_RRT34_RoMtBr	759651	751149	157490	45918	0.009669	0.002925	43178	27996
G_hum_MRT6324_MaApBr	749697	741592	178166	40415	0.01429	0.002584	37429	25678
G_hum_MBS008_SdAcBr	743141	727197	186552	34952	0.013153	0.003231	32195	21081
G_hum_MBS028_SdAcBr	733193	722847	175456	38803	0.012532	0.003276	35899	23612
G_hum_GRLF119_BoPaBr	723005	716328	159308	40102	0.01185	0.003143	37130	23731
G_hum_MTR24153_OiApBr	711277	705572	156755	40979	0.014102	0.002993	37887	24449
G_hum_MTR18680_PuAmBr	699131	691843	150365	40727	0.014067	0.002974	37628	25640
G_hum_VOGT2083_ArAmBr	697859	692793	153243	40900	0.012263	0.002978	38007	25825
G_hum_MTR13826_SnApBr	686763	680438	221728	22549	0.018714	0.0046	20135	12887
G_hum_MAR1498_AfPaBr	680701	672514	176290	32381	0.012722	0.003276	29707	19948
G_hum_MTR18574_PuAmBr	672885	665061	157203	36714	0.014786	0.003085	33596	22917
G_hum_RRT31_RoMtBr	665992	659842	181782	31434	0.012411	0.003198	29198	19474
G_hum_AOM108_TfAmBr	665954	658693	151884	37458	0.013628	0.002852	34570	23747
G_hum_MBS013_SdAcBr	649151	630902	193929	23697	0.017395	0.003892	21217	14188

G_hum_MAR1527_AfPaBr	621476	610985	141273	21956	0.013743	0.004548	19825	26
G_hum_BML1247_VxPaBr	616819	607076	170101	25612	0.016689	0.003293	23126	15490
G_hum_H18443_ArAmBr	615393	609321	156733	29906	0.013338	0.003236	27479	17836
G_hum_MSH10213_AnAmBr	609012	604922	146947	32040	0.015527	0.003237	29113	20079
G_hum_MTR18690_PuAmBr*	574857	567382	143553	29299	0.015057	0.003257	26734	19102
G_hum_MTR24063_OiApBr*	569124	564793	168218	24513	0.015971	0.003735	22273	15325
G_hum_MTR20851_TeRrBr*	539973	534961	158014	21231	0.019744	0.003867	18898	12623
G_hum_MBS029_SdAcBr*	514723	503822	168185	15718	0.021956	0.004906	13601	9095
G_hum_BML012_VxPaBr*	510222	503361	166933	14519	0.021116	0.004875	12578	8374
G_hum_JUR359_JuPaBr*	495524	481635	170791	11151	0.025145	0.005692	9115	5905
G_hum_VOGT2082_ArAmBr*	482921	478826	141301	18390	0.019723	0.004101	16237	11006
G_hum_HT5224_TbPaBr*	457856	451911	160113	10886	0.023501	0.006349	8306	1680
G_hum_MRT4437_BaAmBr*	388372	384935	102978	14113	0.021204	0.006079	12444	11
G_hum_MAR1488_AfPaBr*	299854	293653	128840	3265	0.031286	0.008232	2400	1580
G_hum_MAR987_CxPaBr*	297565	294189	127974	3916	0.03238	0.008137	2845	1891
G_hum_AOM093_FbAmBr*	280134	277532	138982	2025	0.038544	0.011511	1330	769
G_hum_H18442_ArAmBr*	258810	254363	113859	2639	0.035965	0.009391	1800	1092
G_hum_MBS036_SdAcBr*	246466	241974	108716	2076	0.04292	0.009849	1313	776
G_hum_H18441_ArAmBr*	234737	231017	105546	2205	0.039103	0.011315	1420	896
G_hum_JOG655_ItPaBr*	85643	83575	55657	196	0.080466	0.019455	58	7
G_hum_JUR59_JuPaBr*	72901	72177	49992	182	0.07788	0.021429	47	3
G_hum_GRLF199_CaPaBr*	69655	69087	49284	148	0.059993	0.020695	36	0
G_hum_2374_AlPaBr*	49683	49312	34580	208	0.031764	0.01379	139	0
G_hum_BML1092VxPaBr*	4504	4379	3681	12	0.083547	0.030793	3	0
G_hum_HT4999_ItPaBr*	2778	2691	2504	3	0.005611	0.012112	2	0
G_hum_HT4854_ItPaBr*	2105	1932	1833	2	0.000691	0.020838	1	0

CONCLUSÃO GERAL

Neste trabalho, encontramos um conjunto de SNPs potencialmente sob seleção climática para a espécie de lagarto amplamente distribuída *Gonatodes humeralis*. Nossos resultados evidenciam a relação genoma-ambiente e o potencial evolutivo de um lagarto umbrófilo na Amazônia, por meio de populações adaptadas localmente. Investigando a estrutura populacional neutra em *G. humeralis*, identificamos nove populações geneticamente distintas em diferentes regiões da Amazônia, sendo que populações do leste da Amazônia apresentaram níveis distintos de estruturação genética, enquanto as populações localizadas no oeste e sudoeste da Amazônia apresentam um padrão mais claro de isolamento. De acordo com nossos resultados sobre adaptação local, mostramos um padrão distintivo em toda a Amazônia, destacando a forma como diferentes gradientes climáticos moldaram a paisagem adaptativa de *G. humeralis* ao longo de sua distribuição. Da mesma forma, a predição genômica mostrou que, nos cenários futuros de 2050 e 2100, as populações do centro e oeste da Amazônia estariam sob maior risco de sofrer eventos de extinção devido às mudanças climáticas. Novamente, o padrão distinto que encontramos de vulnerabilidade genômica mostra como diferentes populações da mesma espécie podem ser mais ou menos vulneráveis a mudanças climáticas e ambientais. Incorporar essas informações nas avaliações de risco pode melhorar as perspectivas de sobrevivência das espécies e populações.

O estudo apresentado aqui é uma das primeiras investigações de genômica populacional de espécies de lagartos neotropicais que utiliza uma abordagem multidisciplinar para entender como padrões de adaptação local podem afetar a vulnerabilidade frente às mudanças climáticas em uma grande escala espacial na floresta Amazônica. Nossos resultados destacam a importância de considerar contextos espacialmente explícitos com ampla cobertura de amostragem na avaliação do papel desempenhado pelos gradientes ambientais nos padrões de adaptação climática local. Identificar os níveis de adaptação local em populações naturais pode fornecer informações interessantes sobre a diferenciação populacional em espécies com ampla distribuição, que não são raras na escala amazônica. Além disso, o foco em populações bastante grandes, em oposição a populações extremamente pequenas, é de interesse biológico, uma vez que processos que operam em populações pequenas, como a deriva genética e a carga mutacional, podem impedir que adaptação local proteja os efeitos das mudanças climáticas.

Em relação às estratégias de conservação e manejo, investigações futuras devem se concentrar na avaliação do potencial de utilização de dados eco-evolutivos na criação de novas áreas protegidas, fluxo gênico assistido por resgate genético, monitoramento de populações e suas tendências demográficas e validação das previsões de loci potencialmente adaptativos por meio de experimentos de jardim comum para organismos não-modelo em uma escala geográfica mais ampla. Além disso, a vulnerabilidade climática genômica, como apresentamos aqui, é um componente importante das avaliações de risco e pode ajudar a construir novas oportunidades para investigação e avançar a fronteira na pesquisa eco-evolutiva e genética da conservação.

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