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Tese de Doutorado

Desenvolvimento direto em anuros: Aspectos ecológicos e evolutivos

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DESENVOLVIMENTO DIRETO EM ANUROS: ASPECTOS ECOLÓGICOS E EVOLUTIVOS

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RESUMO

Forças seletivas moldaram a evolução de novas formas, comportamentos e características dos anfíbios ao longo de milhares de anos. Assim ocorreu o surgimento dos modos reprodutivos especializados, como o desenvolvimento direto. Nesta tese, reúno as principais hipóteses e potenciais forças seletivas relacionadas à evolução do desenvolvimento direto em anuros (Capítulo I). Em uma escala espacial fina, avalio as relações entre a ocorrência dessas espécies com fatores bióticos (composição filogenética e diversidade funcional) e abióticos (clima e topografia) em comunidades locais da Mata Atlântica e discuto as ideias e hipóteses evolutivas relacionadas a esse modo reprodutivo (Capítulo II). Em uma escala espacial mais ampla, testo a relação e a importância desses fatores para a ocorrência de anfíbios de desenvolvimento direto em comunidades do Novo Mundo e verifico como essas relações variam de acordo com os distintos biomas dessa região (Capítulo III). Por fim, examino a distribuição de espécies com esse modo reprodutivo do gênero *Ischnocnema* na Mata Atlântica e avalio o papel das áreas protegidas em garantir a proteção dessas espécies em cenários futuros de mudanças climáticas (Capítulo IV). No primeiro capítulo, aponto para as múltiplas hipóteses e potenciais forças seletivas que levaram a evolução do desenvolvimento direto. Os resultados do capítulo II vão de encontro a essas hipóteses, uma vez que testo e demonstro uma maior influência da umidade, sazonalidade da temperatura e diversidade funcional na estruturação e ocorrência de anuros de desenvolvimento direto em comunidades locais de anuros da Mata Atlântica. Já no terceiro capítulo, demonstro a importância da história evolutiva para a ocorrência do desenvolvimento direto em biomas tropicais do Novo Mundo, enquanto para os biomas temperados verifico uma maior influência de fatores abióticos (temperatura e umidade). No último capítulo, verifico que, apesar de bem representadas pelas áreas protegidas, muitas espécies do gênero *Ischnocnema* poderão sofrer reduções significativas em suas áreas de distribuição. Demonstro assim a importância das áreas protegidas para o futuro dessas espécies com modo reprodutivo extremamente especializado. Esses resultados fornecem importantes contribuições para o entendimento da evolução do desenvolvimento direto em anfíbios, além do potencial impacto positivo para a conservação do grupo.

Palavras-chave: Anfíbios; áreas protegidas; conservação; desenvolvimento embrionário; evolução; mudanças climáticas; Mata Atlântica; Novo Mundo

ABSTRACT

Selective forces have shaped the evolution of new forms, behaviors, and characteristics of amphibians over thousands of years. This gave rise to specialized reproductive modes, such as direct development. In this thesis, I gather the main hypotheses and potential selective forces related to the evolution of direct development in anurans (Chapter I). On a fine spatial scale, I assess the relationships between the occurrence of these species and biotic factors (phylogenetic composition and functional diversity) and abiotic factors (climate and topography) in local communities of the Atlantic Forest. I discuss evolutionary ideas and hypotheses related to this reproductive mode (Chapter II). On a broader spatial scale, I examine the relationship and importance of these factors to the occurrence of direct-developing amphibians in New World communities and investigate how these relationships vary across the distinct biomes of this region (Chapter III). Finally, I examine the distribution of species with this reproductive mode from the genus Ischnocnema in the Atlantic Forest. I evaluate the role of protected areas in ensuring the protection of these species in future scenarios of climate change (Chapter IV). In the first chapter, I point out the multiple hypotheses and potential selective forces that led to the evolution of direct development. The results of Chapter II corroborate to these hypotheses, where I test and demonstrate a greater influence of humidity, temperature seasonality, and functional diversity on the structure and occurrence of direct-developing anurans in local communities of the Atlantic Forest. In the third chapter, I demonstrate the importance of evolutionary history for the occurrence of direct development in tropical biomes of the New World, while for temperate biomes, I find a greater influence of abiotic factors (temperature and humidity). In the last chapter, I find that, despite being well represented in protected areas, many species of the genus Ischnocnema may experience significant reductions in their distribution areas. I thus demonstrate the importance of protected areas for the future of these species with an extremely specialized reproductive mode. These results provide important contributions to understanding the evolution of direct development in amphibians, as well as the potential positive impact on the conservation of the group.

Keywords: Atlantic Forest; Amphibians; climate changes; conservation; embryonic development; evolution; New World; protected areas

SUMÁRIO

INTRODUÇÃO GERAL

Os mecanismos associados à evolução biológica intrigam e fascinam os cientistas há tempos, no entanto, foi principalmente após a publicação de “A origem das Espécies” por Charles Darwin em 1859, que o estudo desses mecanismos abriu caminhos e gerou novas perspectivas. Com a intersecção destes interesses pelos aspectos evolutivos com os tradicionais estudos ecológicos, sobre os processos e padrões de distribuição da biodiversidade e das relações entre os organismos com o ambiente (físico e biótico), foi estabelecida a ecologia evolutiva (Pianka, 2011). E ecologia evolutiva busca compreender os processos ecológicos em um contexto evolutivo, a origem de novas linhagens e dos mecanismos e processos de especiação, e o surgimento e a evolução de novas estruturas, comportamentos e características, também conhecidas como inovações evolutivas (Mélo, 2019; Pigliucci, 2008). Diversos estudos vêm buscando compreender os mecanismos e os principais propulsores para o aparecimento dessas inovações nos mais diversos grupos taxonômicos.

Alta competição entre espécies, predação elevada e condições ambientais adversas são os candidatos-chave no contexto da evolução de novas características (Hoffmann e Herus, 2000; Langerhans, 2007; Losos e Mahler, 2010; Maccoll, 2011; Massol *et al.*, 2013). Esses mecanismos propiciaram o surgimento e a evolução de uma infinidade de novas inovações morfológicas, fisiológicas e comportamentais nos diferentes ramos da árvore da vida, como a produção de metabólitos secundários em plantas (Kariñho-Betancourt, 2017), os padrões de coloração das asas de borboletas (Moczek, 2008) e os chifres e galhadas dos cervídeos (Metz *et al.*, 2018). Outro exemplo de como as diferentes pressões seletivas guiaram a evolução de características de história de vida pode ser percebida através da alta diversidade reprodutiva apresentada pelos anfíbios.

Com mais de 70 modos reprodutivos descritos, os anfíbios abrangem uma gama de possibilidades reprodutivas, que variam desde a oviposição com desenvolvimento larval ocorrendo em ambientes aquáticos (o modo reprodutivo bifásico ancestral), até a reprodução e desenvolvimento acontecendo completamente em ambientes terrestres (Nunes-de-Almeida *et al.*, 2021). Nesses ambientes, espécies podem se empoleirar e ovipositar nas folhas de plantas, tanques de bromélias epífitas ou até mesmo se reproduzir na serapilheira das florestas (Haddad e Prado, 2005; Nunes-de-Almeida *et al.*, 2021). Além disso, níveis notáveis de especialização reprodutiva podem ser encontrados, como por exemplo, espécies de anfíbios marsupiais que carregam seus ovos e juvenis no dorso (por exemplo, espécies de *Fritziana*), espécies que chocam seus ovos no estômago ou sacos vocais (por exemplo, *Rheobatrachus silus* e *Rhinoderma darwini*), e espécies que tiveram o estágio larval suprimido (Haddad *et al.*, 2013; Jorquera *et al.*, 1974; Leong *et al.*, 1986). Nesse último caso, uma pequena parcela das espécies apresenta viviparidade, enquanto a grande maioria possui o modo reprodutivo conhecido como desenvolvimento direto, caracterizado pela oviposição (geralmente terrestre) com posterior eclosão em miniaturas dos adultos (Liedtke *et al.*, 2022; Nunes-de-Almeida *et al.*, 2021).

Aparecendo em diferentes linhagens da árvore evolutiva dos anfíbios, o desenvolvimento direto é observado em pelo menos 27% das espécies de anuros descritas (Furness e Capellini, 2022; Furness *et al.*, 2022; Liedtke *et al.*, 2022). Diferentemente do esperado, a evolução do desenvolvimento direto não seguiu passos sequenciais, sendo esse precedido pelos modos reprodutivos com oviposição terrestre e desenvolvimento aquático (Gomez-Mestre *et al.*, 2012; Liedtke *et al.*, 2022). Adicionalmente, o desenvolvimento direto foi antecedido tanto por ovos e girinos desprotegidos, quanto por larvas que se alimentam, conhecidas como exotróficas (Gomez-Mestre *et al.*, 2012). Dessa forma, esses aspectos podem indicar a provável atuação de diferentes promotores para a sua evolução. Nesse sentido, distintos fatores bióticos e abióticos já foram levantados como potenciais forças seletivas para o surgimento e a evolução do desenvolvimento direto nos anfíbios (Crump, 2015; Lutz, 1948; Magnusson e Hero, 1991; Wilbur e Collins, 1973).

Considerada possivelmente como o principal agente da diversificação reprodutiva dos anfíbios, a predação sobre os ovos e as larvas aquáticas pode ter atuado como pressão seletiva na evolução dos modos reprodutivos especializados ao reduzir a mortalidade das fases larvais em ambientes aquáticos (Crump, 2015; Gomez-Mestre e Warkentin, 2007; Haddad e Prado, 2005;

Magnusson e Hero, 1991). Essa afirmação ganha sustentação uma vez que um alto risco de predação dos girinos pode levar a mudanças nos locais de postura, de córregos e lagoas para poças pequenas e temporárias mais distantes (Buxton e Sperry, 2017; Duellman, 1992). Similarmente, a competição intensa em sítios reprodutivos também é classificada como uma das responsáveis pelo surgimento do desenvolvimento direto (Crump, 2015). Dentro de gêneros, por exemplo *Rhacophorus* e *Dendropsophus*, algumas espécies apresentam plasticidade reprodutiva, exibindo um modo reprodutivo mais usual com a possibilidade de um ou mais modos alternativos em resposta à densidade de predadores e competidores (Martins *et al.*, 1998; Nunes-de-Almeida *et al.*, 2021; Thibaudeau e Altig, 1999; Touchon e Warkentin, 2008, Touchon e Worley, 2015). Também, a evolução de modos reprodutivos terrestres com comportamento de amplexo e desovas escondidas em bromélias e câmaras subterrâneas é considerada uma resposta à competição entre machos e a poliandria (Zamudio *et al.*, 2018). No entanto, o ambiente físico também pode ter contribuído para a evolução do desenvolvimento direto em anfíbios.

A alta diversidade de modos reprodutivos também pode ser considerada mais uma resposta às condições ambientais da região em que as espécies evoluíram do que o resultado da história evolutiva compartilhada ente as famílias e espécies(Callery *et al.*, 2001; Denver *et al.*, 2002; Haddad e Prado, 2005). Por exemplo, espécies típicas de localidades montanhosas que utilizam principalmente os riachos como sítio reprodutivo podem acabar tendo seus ovos e larvas carreados pela correnteza, aumentando a mortalidade dos jovens (Goin e Goin, 1962). Dessa forma, algumas espécies apresentam adaptações em suas posturas para evitar a perda pela correnteza (Weygoldt, Carvalho e Silva, 1992). Incertezas ambientais associadas a certos sítios reprodutivos, como poças efêmeras que estão sujeitas a maiores riscos de dessecação, a baixa disponibilidade de recursos e oxigênio, podem levar a mudanças fisiológicas, resultando na antecipação da metamorfose e, consequentemente, contribuindo para a perda da fase larval e a evolução dessa característica (Callery *et al.*, 2001; Van Djik, 1971; Wassersug, 1986). Ainda, associações entre modos reprodutivos terrestres, incluindo o desenvolvimento direto, com ambientes íngremes e com pouca disponibilidade de água superficial já foram verificadas para anfíbios na África (Liedtke *et al*., 2017). Nesse contexto, as associações entre diferentes condições ambientais e tipos de habitats com as distintas estratégias reprodutivas também reforçam ainda mais a atuação de múltiplas pressões seletivas na evolução da reprodução terrestre (Lion *et al*., 2018; Müller *et al*., 2013).

A distribuição e a ocorrência dos anfíbios são fortemente influenciadas pelas condições climáticas e ambientais, sendo a maior parte desse grupo ainda dependente de ambientes aquáticos para a sua reprodução (Wells, 2007). No caso de anfíbios com reprodução terrestre e desenvolvimento direto, essa dependência pode ser suprida pela maior umidade dos ambientes florestais, tal qual encontrada nas florestas pluviais das Américas (Blaustein *et al*., 2010; Lion *et al*., 2018; Wells, 2007). Ainda, as relações entre as condições ambientais e a ocorrência de espécies de anfíbios pode ser dependente da região e escala analisada (Lion *et* al., 2018). O Novo Mundo é considerado um centro de diversificação de importantes linhagens de anfíbios de desenvolvimento direto, como é o caso do clado Terrarana (Hedges *et al*., 2008). Contendo mais de 1.200 espécies, esse grupo formado por cinco famílias (Brachycephalidae, Ceuthomantidae, Craugastoridae, Eleutherodactylidae e Strabomantidae) é o maior complexo de espécies de anuros reconhecido na filogenia dos anfíbios (Destnisky, 2023; Frost, 2023). A família Brachycephalidae por sua vez, é formada por pelo menos 79 espécies dos gêneros *Brachycephalus* e *Ischnocnema* (Frost, 2023). Ela está distribuída majoritariamente ao longo da Mata Atlântica, onde muitas destas espécies são endêmicas (Figueiredo *et al*., 2021). Portanto, esse bioma é considerado um importante reduto de espécies de anuros de desenvolvimento direto a nível global.

Considerada como um dos *hotspots* mundiais para a conservação da biodiversidade, a Mata Atlântica é um bioma altamente impactado pelas ações antrópicas e detém uma das maiores diversidades de espécies de anuros a nível global, muitas das quais são consideradas endêmicas e encontram-se ameaçadas de extinção (Figueiredo *et al*., 2021; Myers *et al*., 2000). Embora espécies com desenvolvimento direto sejam indiretamente favorecidas pela definição de áreas de conservação, uma vez que são fortemente relacionadas com as localidades mais conservadas (como as florestas de altitude), elas apresentam uma maior tendência ao declínio populacional e ao risco de extinção (Fontana *et al*., 2021; Loyola *et al*., 2008). Isso se deve às mudanças de história de vida associadas a esse tipo de reprodução, como menores ninhadas, ovos maiores e maior suscetibilidade a fungos patogênicos (Furness *et al*., 2022; Hero *et al*., 2005; Nowakowski *et al*., 2017, Pincheira-Donoso *et al*., 2021).

Com a crescente exploração e conversão das áreas florestais, estas espécies estão entre as primeiras a desaparecer após o desmatamento de seus habitats, sendo a dessecação pela evaporação da água um dos principais riscos à sobrevivência dos ovos (Haddad e Prado, 2005; Karl e Knight, 1998). Também, cenários futuros de mudanças climáticas podem resultar em contrações ou expansões nas distribuições de certas linhagens de anfíbios, chegando até a extinção de parte deste grupo na Mata Atlântica (Loyola *et al*., 2014; Vasconcelos *et al*., 2018). Por fim, o uso de informações a respeito da história de vida das espécies pode tornar as estratégias e planos de conservação mais eficazes (Loyola *et al*., 2008). Desta maneira, com as futuras perspectivas climáticas e ambientais, o destino de espécies com desenvolvimento direto ainda permanece incerto.

OBJETIVOS DA TESE

Nesta tese, através de uma perspectiva ecológica, procuro compreender como os modos reprodutivos de anuros se diversificaram e evoluíram, partindo de um ambiente até então aquático, alcançando o ambiente terrestre, e por fim chegando ao desenvolvimento direto. Neste contexto, investigo as potenciais forças seletivas que guiaram a evolução desse modo reprodutivo, e analiso o papel dos fatores abióticos e bióticos na evolução do desenvolvimento direto através de diferentes escalas e regiões. Além disso, também busco avaliar o grau de proteção das espécies de anuros com desenvolvimento direto do gênero *Ischnocnema* na Mata Atlântica, bem como as perspectivas futuras destas espécies frente às mudanças climáticas. Assim, por meio da minha tese, busco traçar uma linha cronológica sobre o conhecimento do desenvolvimento direto em anuros, abrangendo a compreensão do passado, a avaliação do presente e predição do futuro desse grupo de espécies com reprodução diferenciada.

ESTRUTURA DA TESE

A tese “*Desenvolvimento direto em anuros: Aspectos ecológicos e evolutivos*” está estruturada nos quatro seguintes capítulos:

Capítulo I – *Revisão do desenvolvimento direto em anuros: a evolução de uma estratégia reprodutiva*

Neste primeiro capítulo, através de uma revisão sistemática da literatura, identifico, esclareço e crio um panorama sobre as principais hipóteses relacionadas as forças seletivas que guiaram a evolução do desenvolvimento direto nos anfíbios. Artigo publicado na revista *Oecologia Australis* (doi: 10.4257/oeco.2022.2603.02).

Capítulo II – *Direct development in Atlantic Forest anurans: what can environmental and biotic influences explain about its evolution and occurrence?*

Neste capítulo, utilizando o panorama obtido no capítulo I e dados de comunidades locais, investigo as relações entre diversidade funcional, composição filogenética, clima, topografia e a proporção de anuros de desenvolvimento direto na Mata Atlântica, uma região estruturalmente complexa e detentora de uma das maiores diversidades de espécies do grupo. Através dos resultados faço considerações a respeito da evolução desse modo reprodutivo. Artigo publicado na revista *PLoS ONE* (doi: 10.1371/journal.pone.0291644).

Capítulo III – *From evolutionary history to environmental conditions: The determinants of direct development in New World anurans*

Aqui, seguindo uma abordagem semelhante à do capítulo anterior, amplio a escala e estendo meu foco para todo o Novo Mundo. Analiso como o ambiente biótico (composição filogenética e diversidade funcional) e abiótico (clima e topografia) estão relacionados com desenvolvimento direto em anuros do Novo Mundo. Também avalio como essa relação varia conforme os diferentes biomas dessa região continental. Assim, aqui busco testar se padrões evolutivos, como observado no capítulo anterior, podem agir de maneiras distintas. Artigo com previsão de submissão para a revista *Global Ecology and Biogeography*.

Capítulo IV – *Amphibian strongholds: protected areas and the future of direct-developing frogs of genus Ischnocnema in the Atlantic Forest under climate change*

Neste último capítulo, através da modelagem de distribuição de espécies, verifico a distribuição atual de espécies de anuros de desenvolvimento direto do gênero *Ischnocnema*, bem como as perspectivas futuras diante de diferentes cenários de mudanças climáticas. Por fim, também avalio o papel das áreas protegidas da Mata Atlântica em garantir a proteção dessas espécies. Artigo com previsão de submissão para a revista *Biological Conservation*.

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CAPÍTULO I

REVISÃO DO DESENVOLVIMENTO DIRETO EM ANUROS: A EVOLUÇÃO DE UMA ESTRATÉGIA REPRODUTIVA

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REVISÃO DO DESENVOLVIMENTO DIRETO EM ANUROS: A EVOLUÇÃO DE UMA ESTRATÉGIA REPRODUTIVA

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Running title: *Evolução do desenvolvimento direto em anuros*

Resumo: Anfíbios são conhecidos por apresentar a maior diversidade reprodutiva dentre os tetrápodes. Dentre os modos reprodutivos, um dos mais especializados é o desenvolvimento direto dos ovos terrestres, caracterizado pela ausência da fase larval (girino) e do processo de metamorfose. A evolução dessa estratégia reprodutiva vem sendo bastante discutida e ainda merece destaque, principalmente por ajudar a esclarecer os mecanismos envolvidos na independência de ambientes aquáticos para a reprodução do grupo, bem como para os vertebrados em geral. Neste trabalho, através de uma revisão sistemática, investigamos 15 artigos, buscando identificar e esclarecer as principais hipóteses e forças seletivas ecológicas que guiaram a evolução do desenvolvimento direto em anfíbios anuros. Nossos resultados, apontam especialmente os fatores bióticos (ex: predação e a competição), seguidos pelos fatores abióticos (ex: condições ambientais e climáticas) como os principais promotores da diversificação reprodutiva e evolução do desenvolvimento direto em anuros. Poucos trabalhos de fato testaram essas hipóteses, sendo esses geralmente realizados em escalas espaciais reduzidas, com poucas linhagens ou considerando os fatores isolados. Assim, destacamos a importância de futuros trabalhos que testem efetivamente o papel dos potenciais promotores ecológicos do surgimento e da evolução do desenvolvimento direto em anuros, principalmente levando em consideração diferentes regiões, escalas espaciais maiores e um maior número de clados dentro do grupo.

Palavras-chave: Anfíbios; Fatores seletivos; Modos reprodutivos; Reprodução

DIRECT DEVELOPMENT IN ANURANS: THE EVOLUTION OF A REPRODUCTIVE STRATEGY.

Abstract: Amphibians are known for having the greatest reproductive diversity among tetrapods. Among the reproductive modes, one of the most specialized is the direct development of terrestrial eggs, characterized by the absence of the larval phase (tadpole) and of metamorphosis. The evolution of this reproductive strategy has been widely discussed, and still deserves to be highlighted, mainly because it helps to clarify the mechanisms involved in the independence of the aquatic environments for the reproduction of the group, as well as for other vertebrates. In the present study, through a systematic review, we investigated 15 articles, seeking to identify and clarify the main ecological hypotheses and selective forces that guided the evolution of direct development in anuran amphibians. Our results, based in 15 studies, point especially to biotic factors (e.g. predation and competition), followed by abiotic factors (e.g. environmental and climatic conditions) as the main promoters of reproductive diversification and the evolution of direct development. Few studies have in fact evaluated these hypotheses, and these are generally carried out on reduced spatial scales, with few lineages or considering the factors in isolation. Therefore, we highlight the importance of future works that effectively test the role of potential ecological promoters of the arising and evolution of direct development in anurans, mainly considering different regions, larger spatial scales, and a greater number of clades within the group.

Keywords: Amphibians; Reproduction; Reproductive modes; Selective factors

INTRODUÇÃO

“Embora alguns sapos adotem o seu modo de desenvolvimento estereotipado (depositando milhares de ovos que se tornaram girinos livres nadantes), muitos outros evoluíram estratégias reprodutivas que beiram o improvável” (Duellman 1992, p.1). Uma das características dos anfíbios que talvez esteja entre as mais estudadas, complexas e interessantes são os modos reprodutivos. Os modos reprodutivos são considerados a reunião de determinados atributos reprodutivos, como o sítio e características das desovas e dos girinos, forma de nutrição e de desenvolvimento dos embriões, entre outros (Haddad & Prado 2005, Nunes-de-Almeida *et al.* 2021). Além disso, a taxa e a duração do desenvolvimento e estágio e tamanho das larvas também podem ser levados em consideração (Salthe & Duellman 1973). Os anfíbios se destacam como um grupo com uma ampla variedade de morfologias, relações ecológicas e a maior diversidade reprodutiva dentre os tetrápodes terrestres, características essas resultantes da história de vida complexa e primitiva do grupo (Duellman & Trueb 1986).

Os 71 modos reprodutivos até então descritos para anfíbios anuros, podem basicamente ser divididos em dois grandes grupos: (i) modos reprodutivos associados a espécies que ovipositam em ambientes aquáticos, que incluem o modo reprodutivo estereotipado considerado mais ancestral; e (ii) modos reprodutivos associados às espécies que ovipositam em ambientes terrestres, considerados modos reprodutivos derivados e portanto inovações evolutivas (Duellman &Trueb 1986, Haddad & Prado 2005, Gomez-Mestre *et al*. 2012, Nunes-de-Almeida *et al.* 2021). Diferentes gêneros apresentam diferentes estratégias reprodutivas. Ainda, espécies dentro de um mesmo gênero também podem apresentar plasticidade reprodutiva, apresentando um modo reprodutivo primitivo com a possibilidade de um ou mais modos alternativos em resposta às condições ambientais e à densidade de competidores (Martins *et al.* 1998, Thibaudeau & Altig 1999, Touchon & Warkentin 2008, Nunes-de-Almeida *et al.* 2021).

Assim como as demais características biológicas, as estratégias reprodutivas foram fixadas ao longo da história evolutiva das espécies, sendo correlacionadas com o nível de evolução ou adaptação (Angelini & Ghiara 1984). Os modos reprodutivos apresentaram radiação adaptativa em diversos ambientes, dessa forma a especialização reprodutiva evoluiu de forma independente ao longo das diferentes linhagens (Duellman & Trueb 1986, Meegaskumbura *et al*. 2015). Ainda, a alta diversidade reprodutiva dos anfíbios não é somente relacionada com as relações evolutivas entre espécies, mas também com as condições ambientais da região em que essas espécies evoluíram (Duellman & Trueb 1986, Callery *et al.* 2001, Denver *et al.* 2002, Haddad

& Prado 2005). Embora seja considerado primitivo e uma estratégia de história de vida de sucesso dentre os animais, o desenvolvimento bifásico tem sido substituído pelo desenvolvimento direto ao longo da história evolutiva de muitas espécies, sendo esse considerado uma das mudanças evolutivas mais extremas na história de vida dos anfíbios, bem como dos vertebrados (Duellman & Trueb 1986, Hanken *et al*. 1997, Callery *et al*. 2001).

Classificado como uma estratégia reprodutiva, o desenvolvimento direto dos ovos resulta em muitas transformações fundamentais tanto no desenvolvimento pré-eclosão, como em mudanças estruturais esqueléticas, musculares e glandulares, quanto na pós-eclosão (Hanken *et al*. 1997, Goldberg *et al.* 2020). A transformação mais extrema e característica é a perda da fase larval (girino), e consequentemente, a eclosão dos ovos por indivíduos que se assemelham a miniaturas do adulto. Espécies que se reproduzem através do desenvolvimento direto possuem menor número de ovos por ninhada e menos posturas por ano em comparação com as demais espécies; em contraponto seus ovos são maiores, com uma maior reserva nutricional (Angelini & Ghiara 1984, Callery *et al.* 2001). Além disso, a transição da oviposição aquática para a terrestre diminuiu o número de potenciais predadores dessas espécies, reduzindo assim significativamente a mortalidade nas fases larval e juvenil dos anfíbios, fases em que enfrentam uma maior gama de predadores (Duellman 1992). Essas mesmas características, associadas a uma distribuição reduzida e expansão limitada pelo clima apresentada por este grupo de espécies, também puderam permitir a continuação e perpetuação do modo reprodutivo mais ancestral na árvore dos anfíbios (Gomez-Mestre *et al.* 2012). Por outro lado, essas características, como as posturas reduzidas, distribuição restrita e o desenvolvimento direto podem ser relacionadas com o declínio populacional e o risco de extinção de espécies (Hero *et al.* 2005, Fontana *et al.* 2021). O desenvolvimento direto é encontrado ao longo de toda a árvore filogenética dos anuros, podendo ser observado em diversas espécies de pelo menos 22 famílias, sendo o modo reprodutivo exclusivo de determinadas famílias como: Eleutherodactylidae; Brachycephalidae; e Craugastoridae (Hedges *et al.* 2008, Oliveira *et al.* 2017, Frost 2021).

O surgimento do desenvolvimento direto não se deu de forma linear, mas sim através de uma sequência de padrões inesperados na sucessão de mudanças entre as estratégias reprodutivas, tendo evoluído de maneira frequente tanto de ovos terrestres quanto aquáticos, de larvas exotróficas (que se alimentam), ambos desprotegidos (Gomez-Mestre *et al.* 2012). Ainda, a sobrevivência e o desenvolvimento de ovos, bem como o crescimento das larvas de anfíbios é dependente das características tanto do ambiente físico, como biótico

(Alford 1999). Assim, o papel das principais pressões seletivas na evolução dos modos reprodutivos dos anfíbios torna-se uma questão importante a ser discutida. Dentre essas pressões podemos citar os fatores bióticos como a predação dos ovos e larvas, e a competição por sítios reprodutivos, bem como os fatores abióticos como a estrutura e complexidade ambiental (Magnusson & Hero 1991, Callery *et al*. 2001, Haddad & Prado 2005, Gomez-Mestre & Warkentin 2007).

Entender como ocorreu a diversificação dos modos reprodutivos dos anfíbios e a consequente evolução do desenvolvimento direto é de extrema importância. Além de fornecer novas ideias sobre a história evolutiva do grupo, também pode ajudar a elucidar uma das principais transições na evolução dos vertebrados que garantiu a saída do ambiente aquático, a independência da água para a reprodução e a conquista da terra. Desse modo, através de uma revisão da literatura publicada até 2020, buscamos apresentar e abordar as diferentes perspectivas relacionadas às pressões seletivas ecológicas na evolução do desenvolvimento direto em anfíbios anuros, procurando apresentar uma síntese do tema até o momento. Além disso, também procuramos apontar as lacunas existentes nos estudos ecológicos e evolutivos deste grupo, bem como sugerimos futuras direções a serem seguidas.

MATERIAL E MÉTODOS

Para entender quais os possíveis fatores relacionados ao surgimento e evolução do desenvolvimento direto em anuros, realizamos uma revisão sistemática através da base de dados "*Web of Science*" e "*Science Direct*" utilizando as seguintes palavras-chave e operadores para ampliar as buscas por possíveis variações gramaticais: [(*amphibia** OR *anura** OR *frog** OR *toad**) AND (*direct**) AND (*develop**) AND (*reproducti**) AND (*evoluti**)]. Não restringimos o ano de publicação. Todos os artigos tiveram suas informações básicas planilhadas (ano, título, autores e periódico). Após compilar os manuscritos iniciamos a filtragem seguindo três etapas: i) excluímos os artigos em que em seu título remetesse a outros tópicos de pesquisa, como por exemplo, artigos de descrição de espécies, análises morfológicas, fisiológicas e moleculares, entre outros; ii) realizamos a leitura dos resumos dos artigos restantes e excluímos todos aqueles que não tivessem uma menção direta ou indireta à evolução dos modos reprodutivos em anfíbios anuros; e iii) realizamos a leitura completa dos artigos selecionados nas duas primeiras etapas e excluímos aqueles que não tivessem nenhuma referência à evolução do desenvolvimento direto em anuros, bem como não mencionassem nenhum possível fator seletivo para o seu surgimento.

Com os artigos selecionados identificamos as forças seletivas potenciais para o surgimento e evolução do desenvolvimento direto em anuros e os agrupamos em duas categorias: i) fatores abióticos, que incluiu fatores relacionados à estrutura e a imprevisibilidade ambiental, e as condições climáticas; e ii) fatores bióticos, em que agrupamos as pressões referentes às interações e às pressões intrínsecas dos próprios indivíduos/espécies. Ainda, os artigos selecionados foram agrupados de acordo com a região biogeográfica e os grupos taxonômicos avaliados, a fim de reconhecer e indicar as lacunas de conhecimento sobre o tema.

RESULTADOS

Revisão sistemática

A busca inicial resultou em um total de 375 artigos publicados entre 1948 e 2020 (Tabela S1), no entanto, após a filtragem, apenas 15 manuscritos foram considerados na revisão por atenderam aos critérios pré-determinados. Através da análise dos artigos selecionados, publicados entre 1948 e 2017, encontramos 10 fatores que são discutidos como potenciais promotoras da diversificação reprodutiva e forças seletivas para o surgimento e evolução do desenvolvimento direto em anuros (Figura 1 e 2). Observamos que a maior parte dos manuscritos (N=10) aponta a predação como sendo o principal fator de seleção do desenvolvimento direto, seguido pela competição (N=9) e pela estrutura ambiental (N=6). Por outro lado, as três forças seletivas menos citadas correspondem também a fatores bióticos, sendo a seleção sexual, fatores genéticos e hormonais (Figura 2). Ainda, parte dos trabalhos (N=10) apenas citava os fatores na introdução ou discussão, baseado em outros estudos. Dentre os trabalhos avaliados, apenas cinco (Gomez-Mestre *et al.* 2012, Müller *et al.* 2013, Zamúdio *et al.* 2016, Liedtke *et al.* 2017, Portik *et al.* 2017) testaram efetivamente o papel destes fatores na evolução do desenvolvimento direto, sendo esses realizados em escala reduzida e/ou considerando linhagens específicas e fatores isolados. Apenas um dos trabalhos (Gomez-Mestre *et al.* 2012) foi realizado em ampla escala (global), no entanto considerou apenas os fatores climáticos como limitantes da evolução dos modos reprodutivos em anfíbios.

Figura 1. Esquema ilustrando os fatores apresentados como forças seletivas potenciais da origem e evolução do desenvolvimento direto em anuros. Caixas vermelhas correspondem as pressões seletivas bióticas, caixas azuis correspondem as pressões seletivas abióticas e a caixa verde corresponde aos fatores menos citados, mas também mencionados como potenciais forças seletivas. Baseado em 15 artigos publicados entre 1948 e 2017.

Figure 1. *Scheme illustrating the factors presented as potential selective forces of the origin and evolution of direct development in anurans. Red boxes correspond to biotic selective pressures, blue boxes correspond to abiotic selective pressures and the green box corresponds to factors less cited, but also mentioned as potential selective forces. Based on 15 articles published between 1948 and 2017.*

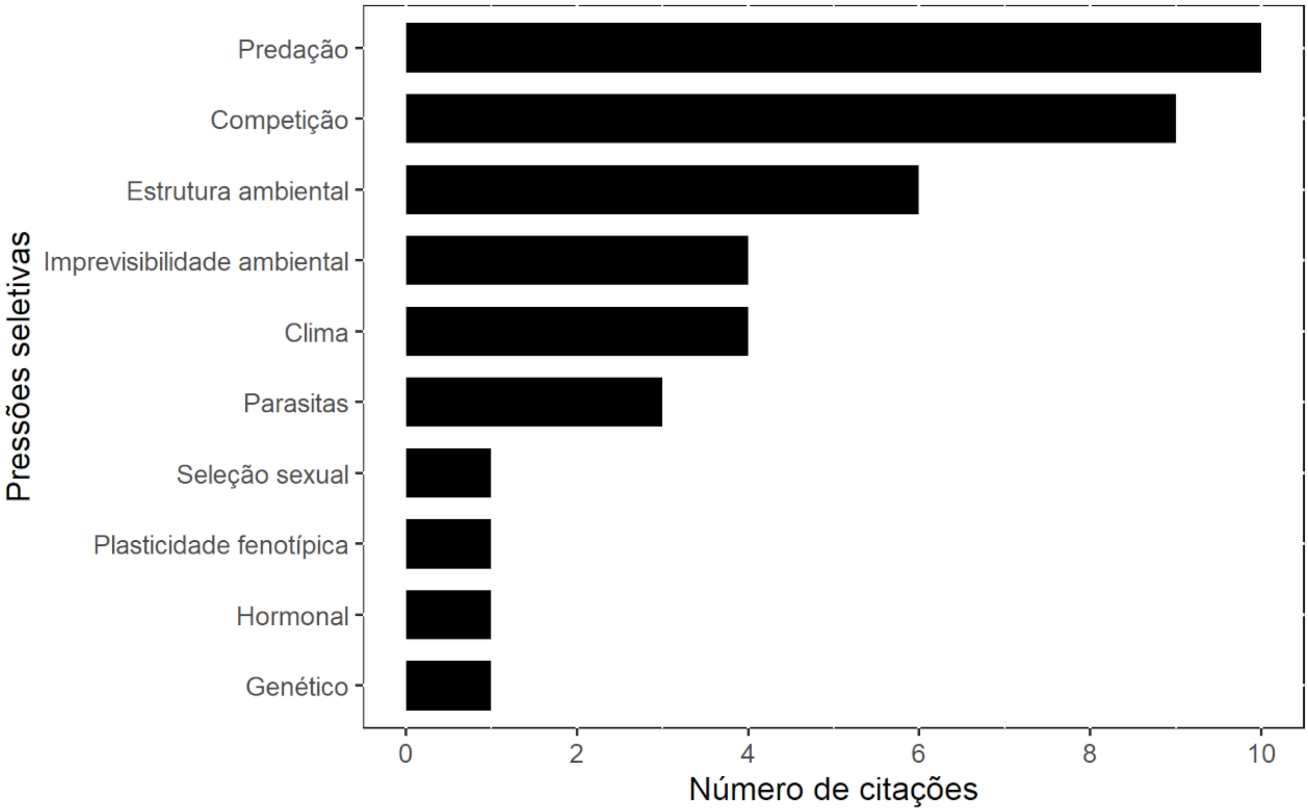

Figura 2. Número de citações de 15 artigos publicados entre 1948 e 2017 mencionando as potenciais forças seletivas da origem e evolução do desenvolvimento direto em anuros.

Figure 2. *Citations number of 15 articles published between 1948 and 2017 indicating the potential selective forces of the origin and evolution of direct development in anurans.*

DISCUSSÃO

Pressões seletivas bióticas na evolução do desenvolvimento direto em anuros

Predação

Os ovos e larvas aquáticas de anfíbios são predados por uma ampla diversidade de insetos aquáticos e vertebrados, incluindo os próprios anfíbios (Lutz 1948, Toledo *et al.* 2007). Citada primeiramente por Lutz (1948) como a principal responsável pela evolução ontogenética dos anfíbios, a predação de ovos e de larvas aquáticas desempenhou um importante papel no surgimento de diferentes características na história de vida dos anfíbios, principalmente no que diz respeito aos mecanismos antipredatórios (Chivers *et al.* 2001, McKeon & Summers 2013, Ferreira *et al.* 2019). Uma vez considerada como uma das principais causas de mortalidade na fase larval dos anfíbios, a vulnerabilidade à predação pode ser influenciada pelas características dos indivíduos, como o tamanho corporal, comportamento, coloração, seleção de micro-habitat e palatabilidade (Wilbur 1987, Alford 1999). Além disso, determinadas espécies podem apresentar plasticidade reprodutiva, alterando os locais de postura de riachos e lagoas com alto risco de predação dos ovos e larvas para lagoas e poças mais distantes, onde a predação tende a ser menor (Duellman 1992, Buxton & Sperry 2017). Dessa forma, a busca por ambientes com menores riscos de predação e, consequentemente, uma menor mortalidade da prole parece ter sido favorecida ao longo da evolução do grupo (Lutz 1948, Lynn 1961, del Pino & Escobar 1981). De fato, a predação é elencada como fator chave na estruturação de comunidades de girinos com diferentes graus de permanência (Heyer *et al.* 1975, Wilbur 1987, Buxton & Sperry 2017, Arribas *et al.* 2018), e pode ser fator chave para a reprodução fora dos ambientes aquáticos. No entanto, a troca do ambiente aquático pelo terrestre não isenta os ovos e larvas de predadores terrestres (Gomez-Mestre & Warkentin 2007, Wells 2007). Assim, a predação pode ser considerada como uma importante fonte de pressão seletiva do desenvolvimento direto.

Competição

Outro fator biótico citado pela maioria dos trabalhos como um dos principais responsáveis pelo surgimento e evolução do desenvolvimento direto em anfíbios foi a competição, tanto por sítios reprodutivos quanto por recursos alimentares. Além de adaptações morfológicas, como as alterações estruturais do embrião, algumas espécies ainda passaram por adaptações comportamentais que potencialmente diminuíram a mortalidade nas fases iniciais do seu ciclo de vida (Weygoldt & Carvalho-e-Silva 1992, Wells 2007). Da mesma forma como em locais com alto risco de predação, os anfíbios podem alterar seus locais de oviposição ou o próprio comportamento em resposta à alta densidade de competidores nos sítios reprodutivos (Martins *et al.* 1998, Buxton & Sperry 2017). Também, a presença de cuidado parental, como apresentada por diversas espécies pertencentes as famílias Dendrobatidae, Eleutherodactylidae, Microhylidae, entre outras, parece ser outra adaptação comportamental resultante da alta competição nos locais de oviposição (Weygoldt 1987, Brown *et al.* 2008, Vági *et al.* 2019). Gomez-Mestre *et al.* (2012) constataram que o cuidado parental além de ter evoluído conjuntamente com a reprodução terrestre, também está relacionado com o desenvolvimento direto. A força da competição entre girinos por recursos pode ser dependente do tipo de habitat de desenvolvimento das espécies; por exemplo, girinos de *Spea multiplicata*, espécie de poças sazonais, podem impedir que espécies majoritariamente de poças permanentes, como *Lithobates pipiens*, utilizem do mesmo ambiente, uma vez que suas taxas de desenvolvimento e crescimento tendem a ser maiores (Woodward 1982, 1983, Wilbur 1987).

Para os girinos que habitam poças a disputa por recursos alimentares é a principal fonte de competição intraespecífica principalmente para espécies que ocupam poças permanentes, onde a disponibilidade de recursos tende a ser limitada e mais escassa (Alford 1999). Também, a competição intraespecífica pode favorecer a diferenciação de fenótipos distintos no mesmo ambiente, como o surgimento de formas especializadas em diferentes recursos (Levis *et al.* 2020). Por outro lado, a competição interespecífica, além de poder promover alterações nas taxas de crescimento e desenvolvimento dos indivíduos (Griffiths *et al.* 1991, Laurila 2000), também é conhecida como uma das principais forças responsáveis pela diferenciação de nicho de espécies competidoras e, consequentemente, é uma das promotoras das inovações evolutivas das alternativas de história de vida (Lack 1947, Grant & Grant 2006). Inovações evolutivas podem variar desde a evolução de estruturas morfológicas, como a dentição da mandíbula inferior dos ceratofrídeos, o surgimento de morfotipos especializados em determinados recursos, como a forma carnívora da larva de *Spea bombifrons*, até a evolução das diferentes estratégias reprodutivas, como é o caso do desenvolvimento direto (Duellman & Trueb 1986, Farrar & Hey 1997, Fabrezi *et al.* 2016, Levis *et al.* 2020). Deste modo, a competição entre adultos em busca de sítios reprodutivos e entre girinos por condições e recursos disponíveis surge como um dos principais promotores do hábito de vida terrestre e evolução do desenvolvimento direto nos anfíbios.

Pressões seletivas abióticas na evolução do desenvolvimento direto em anuros

Estrutura ambiental e incertezas

Condições estruturais e físicas dos habitats, além de estarem relacionadas com a escolha de sítios de oviposição e a abundância de girinos, desempenharam um importante papel na revolução reprodutiva apresentada pelos anfíbios. Citada inicialmente por Wilbur & Collins (1973), a incerteza ambiental associada a determinados ambientes aquáticos resultou na seleção de diferentes estratégias reprodutivas, incluindo o desenvolvimento direto (Crump 1974, 2015). Por exemplo, uma vez que ambientes como riachos rápidos podem acabar carreando os ovos e larvas através da correnteza, aumentando a mortalidade dos jovens, estratégias de desenvolvimento direto em solos mais úmidos, nas proximidades desses ambientes podem ter sido favorecidas (Weygoldt & Carvalho-e-Silva 1992, Haddad & Prado 2005, Thomas *et al.* 2019). No entanto, a alta diversidade reprodutiva dos anfíbios também é um reflexo do extenso gradiente ambiental existente entre os sítios reprodutivos totalmente aquáticos e os totalmente terrestres. Dentre esses dois extremos, uma gama de espécies pode se reproduzir em poças permanentes ou extremamente sazonais, em cavidades ou câmaras com presença de água, fitotelmas, chegando até os solos úmidos das florestas (Haddad & Prado 2005).

Dentre as principais forças seletivas para diversificação e especialização reprodutiva dos anfíbios também podemos destacar outras características físicas como a topografia, e a ampla variedade de características e tipos de habitat e microhabitats (Brown & Brown 1992, Haddad & Prado 2005, de Lima *et al.* 2016). Em um dos poucos trabalhos em que o papel do ambiente sob a evolução reprodutiva dos anfíbios foi efetivamente testado, Müller *et al.* (2013) verificaram uma associação positiva entre a oviposição terrestre com os habitats florestais (independente da altitude) e entre o desenvolvimento larval terrestre e as florestas de altitude da África Oriental. Esses resultados indicaram que fatores específicos desse tipo de ambiente teriam uma forte influência na reprodução terrestre do grupo na região. Da mesma forma, Liedtke *et al.* (2017) verificaram que os modos reprodutivos terrestres de bufonídeos africanos, incluindo o desenvolvimento direto, evoluíram em ambientes de florestas íngremes onde a disponibilidade de água acumulada na superfície é mais baixa. Assim sendo, a troca do ambiente aquático pelo terrestre em busca do sucesso e da sobrevivência da prole também parece ter sido uma alternativa válida e eficiente tanto para a expansão geográfica quanto para a diversificação reprodutiva dos anfíbios.

Condições climáticas

Da mesma forma que as condições estruturais dos ambientes, o clima é um fator essencial para a distribuição, ocorrência e sobrevivência dos anfíbios. Gomez-Mestre *et al.* (2012) ao avaliarem o efeito do clima sob a evolução dos modos reprodutivos dos anfíbios a nível global, verificaram que as espécies de reprodução terrestre (incluindo espécies de desenvolvimento direto) estão associadas a ambientes mais quentes e úmidos (com temperaturas mais altas e maior precipitação). Por outro lado, o estudo de Liedtke *et al.* (2017), realizado em escala espacial menor, aponta que embora os anfíbios africanos de reprodução terrestre também sejam associados a locais úmidos, estes ambientes tendem a ser mais frios. Diferenças como essa podem ocorrer devido ao padrão de distribuição dos modos reprodutivos responder de diferentes maneiras de acordo com a escala ou região biogeográfica analisada, como apresentado por Lion *et al.* (2018). Os fatores climáticos, como os padrões de precipitação e de temperatura, também podem interferir e alterar o comportamento migratório, as estratégias e os ciclos reprodutivos dos anfíbios (Salthe & Duellman 1973, Todd & Winne 2006).

Ainda, as pressões ambientais climáticas além de levarem a alterações comportamentais, podem levar a alterações morfológicas e fisiológicas, como a redução do tamanho corporal das larvas, antecipação da metamorfose e o acúmulo de modificações no desenvolvimento larval, conduzindo dessa forma a evolução dos modos reprodutivos até o desenvolvimento direto (Duellman & Trueb 1986, Callery *et al.* 2001). Desse modo, além de fatores bióticos, como a predação e a competição, e dos fatores abióticos, como a estrutura ambiental, o clima também parece ter sido um importante propulsor da reprodução terrestre e principalmente do desenvolvimento direto em anfíbios.

Outras forças seletivas potenciais

Fatores menos estudados e, portanto, menos mencionados também podem ter contribuído na evolução dos modos reprodutivos dos anfíbios, principalmente no desenvolvimento direto. Na revisão sobre a evolução dos modos reprodutivos em anfíbios mais completa até então, Crump (2015) além de destacar o papel da predação, competição e da imprevisibilidade e estrutura ambiental na evolução dos modos reprodutivos, menciona outras possíveis forças seletivas, como a baixa concentração de oxigênio em poças tropicais (Van Djik 1971), a fuga do parasitismo (Todd 2007) e fatores genéticos (Altig & Crother 2006). Para Altig & Crother (2006), o surgimento do desenvolvimento direto pode ser resultado de alterações nos genes que regulam a cascata do desenvolvimento, assim a liberação ou restrição do desenvolvimento larval em conjunto com a evolução independente de um novo fenótipo de ovo, levaria ao surgimento desse modo reprodutivo alternativo. Essa hipótese também poderia explicar a evolução do desenvolvimento direto seguindo uma sequência inesperada, como proposta por Gomez-Mestre *et al.* (2012), embora seja pouco provável devido a distribuição do desenvolvimento direto em muitas linhagens distintas.

Wassersug (1986), por sua vez, desenvolveu uma teoria relacionando a evolução do desenvolvimento direto com a antecipação da metamorfose devido às condições ambientais e endocrinológicas. Segundo sua teoria, girinos aquáticos constantemente liberam hormônios inibidores da metamorfose (prostaglandinas) no meio, e ao se alimentarem, ingerem os hormônios que retardam o processo de metamorfose ao chegarem no trato digestivo. Assim, em ambientes com baixa densidade de recursos e, consequentemente, baixa ingestão de hormônios, a metamorfose seria antecipada. Já em espécies de desenvolvimento direto, a presença das reservas nutricionais no estômago dos embriões impediria o fluxo das prostaglandinas até o estômago das larvas, contribuindo com desenvolvimento ainda dentro do ovo (Wassersug 1986). Em uma nova abordagem, Zamúdio *et al.* (2016) introduziram a hipótese de a seleção sexual ter atuado como uma promotora da diversificação reprodutiva e da evolução da reprodução terrestre em hilídeos e leptodactilídeos, sendo confirmada por seus resultados. Ainda, associações entre mudanças dos sítios reprodutivos com as características ecomorfológicas das espécies também podem ter direcionado a evolução de modos reprodutivos aquáticos para os terrestres (Portik *et al.* 2017). Dessa forma, as várias forças seletivas podem atuar independentemente nas diferentes características dos modos reprodutivos (Zamúdio *et al.* 2016).

Considerando a Teoria de Conservadorismo de Nicho (Wiens & Graham 2005), onde há uma propensão das espécies de conservarem as características ecológicas ancestrais, certamente a evolução do desenvolvimento direto também enfrentou fatores limitantes como a própria história evolutiva do grupo. Campos *et al.* (2019), constataram a presença de alto sinal filogenético no tipo de desenvolvimento de anfíbios da Mata Atlântica. Nesse sentido, o conservadorismo de nicho reprodutivo pode ser um importante opositor à evolução do desenvolvimento direto, mantendo e perpetuando o desenvolvimento larval por milhões de anos em determinados clados, como nas famílias Hylidae e Phyllomedusidae (Wiens & Graham 2005, Campos *et al.* 2019). A retenção de características do nicho também pode impactar nos processos de expansão e na distribuição de espécies, restringindo as mesmas a ambientes mais estáveis, onde há maior ocorrência de modos reprodutivos especializados (Benício *et al.* 2021). Por fim, o desenvolvimento direto pode ter surgido e se difundido entre a árvore filogenética dos anfíbios através de evolução paralela das diferentes linhagens, sem seguir dessa forma um padrão sequencial com estágios intermediários de evolução dos modos reprodutivos dos anfíbios (Gomez-Mestre *et al.* 2012, Naumann *et al.* 2021). Assim, a evolução do desenvolvimento direto em anuros pode ter sido moldada tanto pela promoção por parte dos fatores bióticos e abióticos, como pela restrição por parte do componente filogenético (Nunes-de-Almeida *et al.* 2021).

Lacunas e futuras direções no conhecimento sobre a evolução do desenvolvimento *direto*

Quantificar o papel dos fatores bióticos na evolução do desenvolvimento direto em anfíbios ainda é desafiador, principalmente pela dificuldade de dimensionar os efeitos de interações como a predação e a competição para muitas comunidades ecológicas naturais. Da mesma forma, o efeito do ambiente também merece um maior destaque. Os poucos trabalhos que efetivamente avaliaram as forças seletivas foram desenvolvidos em escalas espaciais reduzidas e/ou para clados específicos. Müller *et al.* (2013) consideraram anfíbios da África Oriental; Zamúdio *et al.* (2016) avaliaram apenas duas famílias (Hylidae com ampla distribuição global, e Leptodactylidae com distribuição restrita as Américas); Lietdke *et al.* (2017) examinaram apenas uma família na África (Bufonidae); e Portik *et al.* (2017) apenas quatro famílias também na África (Arthroleptidae, Brevicipitidae, Hemisotidae e Hyperoliidae).

Outros aspectos a serem explorados nesse contexto são as possíveis influências de padrões geográficos e filogenéticos atuando sob estes resultados. Um exemplo é o quanto análises realizadas em grandes escalas espaciais, como a de Gomez-Mestre *et al.* (2012), poderiam apresentar resultados contrastantes em menores escalas. Nesse sentido, nenhum trabalho considerou todos os diferentes fatores aqui abordados. Além disso, podemos sugerir em outro ponto de vista, de que a diversidade de modos reprodutivos poderia até mesmo seguir um padrão da diversidade de espécies semelhante ao proposto por Dobzhansky (1950) para a diversidade de espécies. Neste caso, fatores bióticos teriam maior influência sob a evolução do desenvolvimento direto em anfíbios nas regiões tropicais, devido principalmente a maior diversidade de potenciais predadores e competidores nestes locais, enquanto nas regiões temperadas os fatores abióticos seriam os mais importantes em virtude da maior sazonalidade climática.

Destacamos a falta de estudos elencando a radiação ultravioleta (UV) e os contaminantes químicos, como os agroquímicos (herbicidas a base de glifosato) como forças seletivas potenciais na evolução do desenvolvimento direto, a qual também pode ser relacionada com mutações de DNA, erros genéticos, alterações de desenvolvimento e o declínio populacional dos anfíbios (Bernal *et al.* 2011, Alton & Franklin

2017, Londero *et al.* 2019). Assim, buscando garantir a sobrevivência e o sucesso da prole, a troca dos sítios reprodutivos aquáticos tradicionais (onde a incidência de raios UV e a concentração de agroquímicos tendem a ser maior) por sítios reprodutivos terrestres (mais protegidos da radiação e da contaminação química) pode ter auxiliado na evolução do desenvolvimento direto nos anuros. Nesse sentido, é importante que futuros trabalhos tentem englobar as várias potenciais forças seletivas em um viés macroecológico, ampliando as escalas espaciais analisadas, bem como as diferentes linhagens da árvore evolutiva do grupo.

CONCLUSÃO

Nossa revisão buscou identificar e esclarecer os papéis dos potenciais promotores ecológicos da evolução do desenvolvimento direto em anfíbios anuros. As diversas hipóteses levantadas nos trabalhos avaliados demonstraram que a atuação de fatores únicos e isolados talvez não seja a melhor hipótese para explicar o surgimento e a evolução do desenvolvimento direto dos ovos em anuros. Dessa forma, nossa revisão aponta que várias forças seletivas podem atuar independentemente nas diferentes características dos modos reprodutivos. Ainda, com a nossa revisão pudemos destacar o baixo número de trabalhos que efetivamente testaram os mecanismos por trás da evolução do desenvolvimento direto em anuros, sendo esses majoritariamente realizados em escalas espaciais reduzidas e com clados específicos. Também enfatizamos que pelo fato de a maior parte dos trabalhos apenas terem levantado e discutido hipóteses sobre a evolução do desenvolvimento direto, os fatores seletivos potenciais mais abordados podem não necessariamente ser aqueles que direcionaram a evolução desse modo reprodutivo. Por fim, salientamos a importância da realização de futuros trabalhos com essa temática, que podem ajudar a elucidar outros aspectos na evolução da reprodução terrestre dos anfíbios anuros, bem como dos vertebrados como um todo.

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Material Suplementar

Tabela S1. Lista dos 375 artigos encontrados na revisão sobre a evolução do desenvolvimento direto em anuros, descrevendo o ano, a autoria, o título do artigo, o título do periódico e se o documento foi selecionado ou não para a presente revisão.

Table S1. *List of 375 articles found in the review on the evolution of direct development in anurans, describing the year, the authorship, the article title, the journal title and if the article was selected or not for this review.*

Ano	Autoria	Título	Jornal	Selecionado
1948	Lutz, B.	Ontogenetic evolution in frogs	Evolution	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
1948	Jenkins, D. W.	Trombiculid mites affecting man .1. Bionomics with reference to epidemiology in the United-States	American Journal of Hygiene	Não
1952	Blair, C. B.	The effects of temperature treatments on Triturus eggs as expressed in larval tail-tip epithelium	Journal of Experimental Zoology	Não
1958	Madsen, H. F., & Bailey, J. B.	Biology and control of the leaf curl plum aphid in northern California	Journal of Economic Entomology	Não
1959	Brewin, B. I.	An account of larval budding in the compound ascidian, Hypsistozoa fasmeriana	Quarterly Journal of Microscopical Science	Não
1961	Lynn, W. G.	Types of amphibian metamorphosis	American Zoologist	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
1962	Brandom, W. F.	Karyoplasmic studies in haploid, androgenetic hybrids of California newts	Biological Bulletin	Não
1963	Crenshaw, J. W.	Direction of human evolution - a zoologists view	Human Biology	Não
1963	Nace, G. W., & Lavin, L. H.	Heterosynthesis and autosynthesis in the early stages of anuran development	American Zoologist	Não
1963	Macgregor, H. C.	Morphological variability and its physiological origin in oocyte nuclei of crested newt	Quarterly Journal of Microscopical Science	Não
1965	Mecham, J. S.	Genetic relationships and reproductive isolation in southeastern frogs of genera Pseudacris and Hyla	American Midland Naturalist	Não
1965	Littlejohn, M. J.	Premating isolation in the Hyla ewingi complex (Anura, Hylidae)	Evolution	Não
1973	Wilbur, H. M., & Collins, J. P.	Ecological aspects of amphibian metamorphosis	Science	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
1977	Picheral, B.	Fertilization of Pleurodeles .2. Penetration of spermatozoa and local reaction of egg	Journal of Ultrastructure Research	Não
1977	Johnson, G. M., & Klemm, D. J.	New species of leech, Batracobdella cryptobranchii n-sp (Annelida Hirudinea), parasitic on ozark hellbender	Transactions of the American Microscopical Society	Não

1977	Wilbur, H. M.	Propagule size, number, and dispersion pattern in ambystoma and asclepias	American Naturalist	Não
1977	Lamotte, M., & Lescure, J.	Ways of achieving independence from aquatic environment among Anura (Amphibia)	Terre Et La Vie-Revue D Ecologie Appliquee	Não
1978	Howard, R. D.	Evolution of mating strategies in bullfrogs, Rana catesbeiana	Evolution	Não
1978	Wake, M. H.	Reproductive biology of Eleutherodactylus jasperi (Amphibia, Anura, Leptodactylidae), with comments on evolution of live-bearing systems	Journal of Herpetology	Não
1979	Sage, R. D., & Selander, R. K.	Hybridization between species of the Rana pipiens complex in central Texas	Evolution	Não
1979	Scovassi, A. I., Wicker, R., & Bertazzoni, U.	Phylogenetic study on vertebrate mitochondrial-dna polymerase	European Journal of Biochemistry	Não
1980	Tilley, S. G.	Life histories and comparative demography of 2 salamander populations	Copeia	Não
1980	Wake, M. H.	The reproductive biology of Nectophrynoides malcolmi (Amphibia, Bufonidae), with comments on the evolution of reproductive modes in the genus Nectophrynoides	Copeia	Não
1981	Wachtel, S. S.	Conservatism of the h-y-h-w receptor	Human Genetics	Não
1981	del Pino, E. M., & Escobar, B.	Embryonic stages of Gastrotheca riobambae (Fowler) during maternal incubation and comparison of development with that of other egg-brooding hylid frogs	Journal of Morphology	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
1981	Clark, W. C.	Sperm transfer mechanisms - some correlates and consequences	New Zealand Journal of Zoology	Não
1981	Lyapkov, S. M., & Severtzov, A. S.	The mechanism of coexistence of 2 species of the far-east Anura	Zoologichesky Zhurnal	Não
1982	Berven, K. A.	The genetic basis of altitudinal variation in the wood frog Rana sylvatica .1. An experimental-analysis of life-history traits	Evolution	Não
1982	Wilkinson, J. K., & Sollnerwebb, B.	Transcription of Xenopus ribosomal-RNA genes by RNA polymerase-i invitro	Journal of Biological Chemistry	Não
1983	Frost, J. S., & Platz, J. E.	Comparative-assessment of modes of reproductive isolation among 4 species of leopard frogs (Rana pipiens complex)	Evolution	Não
1983	Baker, M. R., & Vaucher, C.	Parasitic helminths from Paraguay .4. Cosmocercoid nematodes from Phyllomedusa hypochondrialis (Daudin) (Amphibia, Hylidae)	Revue Suisse De Zoologie	Não
1984	Townsend, D. S., Stewart, M. M., & Pough, F. H.	Male parental care and its adaptive significance in a Neotropical frog	Animal Behaviour	Não
1984	Demski, L. S.	The evolution of neuroanatomical substrates of reproductive behavior: Sex steroid and LHRH-specific pathways including the terminal nerve	Integrative and Comparative Biology	Não
1985	Zweifel, R. G.	Australian frogs of the family Microhylidae	Bulletin of the American Museum of Natural History	Não
1985	Lazarus, L. H., Wilson, W. E., Gaudino, G., Irons, B. J., & Guglietta, A.	Evolutionary relationship between nonmammalian and mammalian peptides	Peptides	Não

1985	Tandy, M., Bogart, J. P., Largen, M. J., & Feener, D. J.	Variation and evolution in Bufo kerinyagae Keith, B. regularis Reuss and B. asmarae Tandy et al. (Anura Bufonidae)	Monitore Zoologico Italiano, Supplemento	Não
1985	Pierce, B. A. & Sikand, N.	Variation in acid tolerance of connecticut wood frogs - genetic and maternal effects	Canadian Journal of Zoology-Revue Canadienne De Zoologie	Não
1986	Severtsov, A. S.	Causes of evolutionary stability of populations in nature	Zhurnal Obshchei Biologii	Não
1986	Wassersug, R.	How does a tadpole know when to metamorphose - a theory linking environmental and hormonal cues	Journal of Theoretical Biology	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
1986	Townsend, D. S.	The costs of male parental care and its evolution in a Neotropical frog	Behavioral Ecology and Sociobiology	Não
1986	Lacey, E. P.	The genetic and environmental control of reproductive timing in a short-lived monocarpic species Daucus carota (Umbelliferae)	Journal of Ecology	Não
1986	Wake, M. H.	The morphology of Idiocranium russeli (Amphibia, Gymnophiona), with comments on miniaturization through heterochrony	Journal of Morphology	Não
1987	Travis, J., Emerson, S. B., & Blouin, M.	A quantitative-genetic analysis of larval life-history traits in Hyla crucifer	Evolution	Não
1987	Reznick, & Braun, B.	Fat cycling in the mosquitofish (Gambusia affinis) - fat storage as a reproductive adaptation	Oecologia	Não
1987	Elinson, R. P.	Fertilization and aqueous development of the Puerto-Rican terrestrial-breeding frog, Eleutherodactylus coqui	Journal of Morphology	Não
1987	Petranka, J. W., & Sih, A.	Habitat duration, length of larval period, and the evolution of a complex life cycle of a salamander, Ambystoma texanum	Evolution	Não
1988	Duellman, W. E., Maxson, L. R., & Jesiolowski, C. A.	Evolution of marsupial frogs (Hylidae, Hemiphractinae) - immunological evidence	Copeia	Não
1988	Newman, R. A.	Genetic-variation for larval anuran (Scaphiopus couchii) development time in an uncertain environment	Evolution	Não
1988	Giacoma, C., & Balletto, E.	Phylogeny of the salamandrid genus Triturus	Bollettino Di Zoologia	Não
1988	Andronikov, V. B.	The effect of continuous incubation of spermatozoa on their thermal-resistance and thermal selection	Tsitologiya	Não
1988	Woodward, B. D., Travis, J., & Mitchell, S.	The effects of the mating system on progeny performance in Hyla crucifer (Anura, Hylidae)	Evolution	Não
1989	Bruce, R. C.	Life-history of the salamander Desmognathus monticola, with a comparison of the larval periods of Desmognathus monticola and Desmognathus ochrophaeus	Herpetologica	Não

1989	Williamson, I., & Bull, C. M.	Life-history variation in a population of the Australian frog Ranidella signifera - egg size and early development	Copeia	Não
1990	Elinson, R. P., Delpino, E. M., Townsend, D. S, Cuesta, F. C., & Eichhorn, P.	A practical guide to the developmental biology of terrestrial-breeding frogs	Biological Bulletin	Não
1990	Long, J. A.	Heterochrony and the origin of tetrapods	Lethaia	Não
1990	Herzberg, F., Poting, A., & Wedlich, D.	Identification of ca2+-dependent cell-adhesion molecules in xenopus by the use of interspecies homology	Differentiation	Não
1990	Lamb, T., Novak, J. M., & Mahoney, D. L.	Morphological asymmetry and interspecific hybridization - a case-study using hylid frogs	Journal of Evolutionary Biology	Não
1990	Hausfater, G., Gerhardt, H. C., & Klump, G. M.	Parasites and mate choice in gray treefrogs, Hyla versicolor	American Zoologist	Não
1990	Semlitsch, R. D., Harris, R. N., & Wilbur, H. M.	Pedomorphosis in Ambystoma talpoideum - maintenance of population variation and alternative life-history pathways	Evolution	Não
1990	Mitchell, S. L.	The mating system genetically affects offspring performance in woodhouses toad (Bufo woodhousei)	Evolution	Não
1991	Koenig, W. D., Albano, S. S., & Dickinson, J. L.	A comparison of methods to partition selection acting via components of fitness - do larger male bullfrogs have greater hatching success	Journal of Evolutionary Biology	Não
1991	Bates, W. R., & Mallett, J. E.	Anural development of the ascidian Molgula pacifica (Huntsman)	Canadian Journal of Zoology-Revue Canadienne De Zoologie	Não
1992	Crespi, B. J.	Behavioral ecology of australian gall thrips (Insecta, Thysanoptera)	Journal of Natural History	Não
1992	Keddyhector, A. C., Wilczynski, W., & Ryan, M. J.	Call patterns and basilar papilla tuning in cricket frogs .2. Intrapopulation variation and allometry	Brain Behavior and Evolution	Não
1992	Ryan, M. J., & Keddyhector, A.	Directional patterns of female mate choice and the role of sensory biases	American Naturalist	Não
1992	Jeffery, W. R., & Swalla, B. J.	Factors necessary for restoring an evolutionary change in an anural ascidian embryo	Developmental Biology	Não
1993	Beachy, C. K.	Differences in variation in egg size for several species of salamanders (Amphibia, Caudata) that use different larval environments	Brimleyana	Não
1993	Vanwinkle, L. J.	Endogenous amino-acid-transport systems and expression of mammalian amino-acid-transport proteins in Xenopus oocytes	Biochimica Et Biophysica Acta	Não
1993	Maucuer, a., moreau, j., mechali, m., sobel, a.	Stathmin gene family - phylogenetic conservation and developmental regulation in Xenopus	Journal of Biological Chemistry	Não
1994	Procunier, W. S., Muro, A. I.	A midarm interchange as a potential reproductive isolating mechanism in the medically important Simulium neavei group (Diptera, Simuliidae)	Genome	Não

1994	Olsen, P. D., Cunningham, R. B., & Donnelly, C. F.	Avian egg morphometrics - allometric models of egg volume, clutch volume and shape	Australian Journal of Zoology	Não
1994	Collazo, A., & Marks, S. B.	Development of Gyrinophilus porphyriticus - identification of the ancestral developmental pattern in the salamander family Plethodontidae	Journal of Experimental Zoology	Não
1994	Semlitsch, R. D.	Evolutionary consequences of nonrandom mating - do large males increase offspring fitness in the anuran Bufo bufo	Behavioral Ecology and Sociobiology	Não
1994	Kearn, G. C.	Evolutionary expansion of the monogenea	International Journal for Parasitology	Não
1994	Scribner, K. T., & Avise, J. C.	Population cage experiments with a vertebrate - the temporal demography and cytonuclear genetics of hybridization in Gambusia fishes	Evolution	Não
1994	Stroumbakis, N. D., Li, Z. H., & Tolias, P. P.	RNA-stranded and single-stranded DNA-binding (SSB) proteins expressed during Drosophila melanogaster oogenesis - a homolog of bacterial and eukaryotic mitochondrial SSBS	Gene	Não
1994	Smith, T. G., Desser, S. S., & Martin, D. S.	The development of Hepatozoon sipedon sp-nov (Apicomplexa, Adeleina, Hepatozoidae) in its natural host, the northern water snake (Nerodia sipedon sipedon), in the culicine vectors Culex pipiens and C. territans, and in an intermediate host, the northern leopard frog (Rana pipiens)	Parasitology Research	Não
1995	Diesel, R., Baurle, G., & Vogel, P.	Cave breeding and froglet transport - a novel pattern of anuran brood care in the Jamaican frog, Eleutherodactylus cundalli	Copeia	Não
1995	Moury, J. D., & Hanken, J.	Early cranial neural crest migration in the direct-developing frog, Eleutherodactylus coqui	Acta Anatomica	Não
1995	Nurnberger, B., Barton, N., MacCallum, C., Gilchrist, J., & Appleby, M.	Natural selection on quantitative traits in the Bombina hybrid zone	Evolution	Não
1995	Moller, A. P., & Eriksson, M.	Pollinator preference for symmetrical flowers and sexual selection in plants	Oikos	Não
1995	Seymour, R. S., & Bradford, D. F.	Respiration of amphibian eggs	Physiological Zoology	Não
1996	Reynolds, J. D.	Animal breeding systems	Trends in Ecology & Evolution	Não
1996	Cloney, R. A., & Hansson, L. J.	Ascidian larvae: The role of test cells in preventing hydrophobicity	Acta Zoologica	Não
1996	Moore, R. D., Newton, B., & Sih, A.	Delayed hatching as a response of streamside salamander eggs to chemical cues from predatory sunfish	Oikos	Não
1996	Wake, D. B., & Hanken, J.	Direct development in the lungless salamanders: What are the consequences for developmental biology, evolution and phylogenesis?	International Journal of Developmental Biology	Não
1996	Wakahara, M.	Heterochrony and neotenic salamanders: Possible clues for understanding the animal development and evolution	Zoological Science	Não

1996	Titus, T. A., & Larson, A.	Molecular phylogenetics of desmognathine salamanders (Caudata: Plethodontidae): A reevaluation of evolution in ecology, life history, and morphology	Systematic Biology	Não
1996	Resetarits, W. J.	Oviposition site choice and life history evolution	American Zoologist	Não
1997	Kaplan, R. H., & King, E. G.	Egg size is a developmentally plastic trait: Evidence from long term studies in the frog Bombina orientalis	Herpetologica	Não
1997	Selvamurugan, N., Joost, O. H., Haas, E. S., Brown, J. W., Galvin, N. J., & Eliceiri, G. L.	Intracellular localization and unique conserved sequences of three small nucleolar RNAs	Nucleic Acids Research	Não
1997	Hanken, J., Jennings, D. H., Olsson, L.	Mechanistic basis of life-history evolution in anuran amphibians: Direct development	American Zoologist	Não
1997	Porter, A. H. Wenger, R., Geiger, H., Scholl, A., & Shapiro, A. M.	The Pontia daplidice edusa hybrid zone in northwestern Italy	Evolution	Não
1997	Tagawa, K., Jeffery, W. R., & Satoh, N.	The recently described ascidian species Molgula tectiformis is a direct developer	Zoological Science	Não
1998	Miaud, C., & Guyetant, R.	Elasticity and selection on life-history traits in a complex life cycle organism, the common Frog Rana temporaria (Amphibia : Anura)	Bulletin De La Societe Zoologique De France	Não
1998	Lieb, B., Carl, M., Hock, R., Gebauer, D., & Scheer, U.	Identification of a novel mRNA-associated protein in oocytes of Pleurodeles waltl and Xenopus laevis	Experimental Cell Research	Não
1998	Sappington, T. W., & Raikhel, A. S.	Molecular characteristics of insect vitellogenins and vitellogenin receptors	Insect Biochemistry and Molecular Biology	Não
1998	Castellano, S., Giacoma, C., Dujsebayeva, T., Odierna, G., & Balletto, E.	Morphometrical and acoustical comparison between diploid and tetraploid green toads	Biological Journal of the Linnean Society	Não
1998	Wake, M. H., & Dickie, R.	Oviduct structure and function and reproductive modes in amphibians	Journal of Experimental Zoology	Não
1998	Havin, L., Git, A., Elisha, Z., Oberman, F., Yaniv, K., Schwartz, S. P., Standard, N., &Yisraeli, J. K.	RNA-binding protein conserved in both microtubule- and microfilament-based RNA localization	Genes & Development	Não
1999	Broun, M., Sokol, S., R. & Bode, H.	Cngsc, a homologue of goosecoid, participates in the patterning of the head, and is expressed in the organizer region of Hydra	Development	Não
1999	Tournier, F., Bobinnec, Y., Debec, A., Santamaria, P., & Bornens, M.	Drosophila centrosomes are unable to trigger parthenogenetic development of Xenopus eggs	Biology of the Cell	Não
1999	Emerson, S. B., & Boyd, S. K.	Mating vocalizations of female frogs: Control and evolutionary mechanisms	Brain Behavior and Evolution	Não

1999	Merila, J., & Sheldon, B. C.	Testis size variation in the greenfinch Carduelis chloris: relevance for some recent models of sexual selection	Behavioral Ecology and Sociobiology	Não
1999	Wassarman, P. M.	The Parkes Lecture - Zona pellucida glycoprotein mZP3: a versatile player during mammalian fertilization	Journal of Reproduction and Fertility	Não
1999	Fang, H., Marikawa, Y., & Elinson, R. P.	Using your noggin to understand the evolution of the large egg of the direct developing frog Eleutherodactylus coqui	American Zoologist	Não
2000	Voss, S. R. & Shaffer, H. B.	Evolutionary genetics of metamorphic failure using wild-caught vs. laboratory axolotls (Ambystoma mexicanum)	Molecular Ecology	Não
2000	Zhou, L., Wang, Y., & Gui, J. F.	Genetic evidence for gonochoristic reproduction in gynogenetic silver crucian carp (Carassius auratus gibelio Bloch) as revealed by RAPD assays	Journal of Molecular Evolution	Não
2000	Hodin, J., & Riddiford, L. M.	Parallel alterations in the timing of ovarian Ecdysone Receptor and Ultraspiracle expression characterize the independent evolution of larval reproduction in two species of gall midges (Diptera: Cecidomyiidae)	Development Genes and Evolution	Não
2000	Mendelson, J. R., Da Silva, H. R., & Maglia, A. M.	Phylogenetic relationships among marsupial frog genera (Anura: Hylidae: Hemiphractinae) based on evidence from morphology and natural history	Zoological Journal of the Linnean Society	Não
2000	Marmayou, J., Dubois, A., Ohler, A., Pasquet, E., & Tillier, A.	Phylogenetic relationships in the Ranidae. Independent origin of direct development in the genera Philautus and Taylorana	Comptes Rendus De L Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
2000	Ehmcke, J., & Clemen, G.	Teeth and their sex-dependent dimorphic shape in three species of Costa Rican plethodontid salamanders (Amphibia: Urodela)	Annals of Anatomy-Anatomischer Anzeiger	Não
2001	Kotiaho, J. S.	Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence	Biological Reviews	Não
2001	Pahkala, M., Laurila, A., Bjorn, L. O., & Merila, J.	Effects of ultraviolet-B radiation and pH on early development of the moor frog Rana arvalis	Journal of Applied Ecology	Não
2001	Callery, E. M., Fang, H., & Elinson, R. P.	Frogs without polliwogs: Evolution of anuran direct development	Bioessays	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
2001	Parris, M. J.	Hybridization in leopard frogs (Rana pipiens complex): Variation in interspecific hybrid larval fitness components along a natural contact zone	Evolutionary Ecology Research	Não
2001	Hanken, J., Carl, T. F., K. Richardson, M., Olsson, L., Schlosser, G., Osabutey, C. K., & Klymkowsky, M. W.	Limb development in a nonmodel" vertebrate, the direct-developing frog Eleutherodactylus coqui"	Journal of Experimental Zoology	Não
2001	Beckham, Y. M., & Elinson, R. P.	Localization of mRNAs in Eleutherodactylus coqui oocytes and its implication for oocyte evolution	American Zoologist	Não
2002	Lampert, K. P., & Linsenmair, K. E.	Alternative life cycle strategies in the West African reed frog Hyperolius nitidulus: the answer to an unpredictable environment?	Oecologia	Não

2002	Knaut, H., Steinbeisser, H., Schwarz, H., & Nusslein-Volhard, C.	An evolutionary conserved region in the vasa 3 ' UTR targets RNA translation to the germ cells in the zebrafish	Current Biology	Não
2002	Olsson, L., Moury, J. D., Carl, T. F., Hastad, O., & Hanken, J.	Cranial neural crest-cell migration in the direct-developing frog, Eleutherodactylus coqui: molecular heterogeneity within and among migratory streams	Zoology	Não
2002	Elinson, R. P., & Beckham, Y.	Development in frogs with large eggs and the origin of amniotes	Zoology	Não
2002	Pappers, S. M., Van der Velde, G., Ouborg, N. J., & Van Groenendael, J. M.	Genetically based polymorphisms in morphology and life history associated with putative host races of the water lily leaf beetle, Galerucella nymphaeae	Evolution	Não
2002	Monnet, J. M., & Cherry, M. I.	Sexual size dimorphism in anurans	Proceedings of the Royal Society B-Biological Sciences	Não
2002	Bates, W. R.	The phylogenetic significance of maximum direct development in the ascidian, Molgula pacifica	Invertebrate Reproduction & Development	Não
2003	Voss, S. R., Prudic, K. L., Oliver, J. C., & Shaffer, H. B.	Candidate gene analysis of metamorphic timing in ambystomatid salamanders	Molecular Ecology	Não
2003	Gunzburger, M. S.	Evaluation of the hatching trigger and larval ecology of the salamander Amphiuma means	Herpetologica	Não
2003	Bolek, M. G., Janovy, J., & Irizarry-Rovira, A. R.	Observations on the life history and descriptions of coccidia (Apicomplexa) from the western chorus frog, Pseudacris triseriata triseriata, from eastern Nebraska	Journal of Parasitology	Não
2003	Lehtinen, R. M.	Parental care and reproduction in two species of mantidactylus (Anura: Mantellidae)	Journal of Herpetology	Não
2003	Haas, A.	Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura)	Cladistics	Não
2003	du Preez, L. H., Tinsley, R. C., & R. De Sa	Polystomatidae (Monogenea) of southern African anura: Eupolystoma vanasi n. sp parasitic in Schismaderma carens (Smith)	Systematic Parasitology	Não
2003	Wake, M. H.	Reproductive modes, ontogenies, and the evolution of body form	Animal Biology	Não
2003	Green, D. M.	The ecology of extinction: population fluctuation and decline in amphibians	Biological Conservation	Não
2003	Zhou, Y., Zhang, J., & King, M. L.	Xenopus autosomal recessive hypercholesterolemia protein couples lipoprotein receptors with the AP-2 complex in oocytes and embryos and is required for vitellogenesis	Journal of Biological Chemistry	Não
2003	McLachlan, E., White, T. W., Ugonabo, C. Olson, C., Nagy, J. I., & Valdimarsson, G.	Zebrafish Cx35: Cloning and characterization of a gap junction gene highly expressed in the retina	Journal of Neuroscience Research	Não
2004	Heyland, A., & Hodin, J.	Heterochronic developmental shift caused by thyroid hormone in larval sand dollars and its implications for phenotypic plasticity and the evolution of nonfeeding development	Evolution	Não

2004	Reyer, H. U., & Battic, I.	Identification of reproductive status in female frogs - a quantitative comparison of nine methods	Herpetologica	Não
2004	Pike, N.	Natural incidence of fruit flies with character states intermediate to those of the sibling species Bactrocera tryoni (Froggatt) and B neohumeralis (Hardy) (Diptera: Tephritidae)	Australian Journal of Entomology	Não
2004	Amano, T., Fu, L. Z., Sahu, S., Markey, M., & Shi, Y. B.	Substrate specificity of Xenopus matrix metalloproteinase stromelysin-3	International Journal of Molecular Medicine	Não
2004	Heyland, A., Reitzel, A. M., & Hodin, J.	Thyroid hormones determine developmental mode in sand dollars (Echinodermata: Echinoidea)	Evolution & Development	Não
2004	Bates, W. R.	Ultraviolet irradiation of eggs and blastomere isolation experiments suggest that gastrulation in the direct developing ascidian, Molgula pacifica, requires localized cytoplasmic determinants in the egg and cell signaling beginning at the two-cell stage	Evolution & Development	Não
2005	Gonzales, B. Yang, H., Henning, D., & Valdez, B. C.	Cloning and functional characterization of the Xenopus orthologue of the Treacher Collins syndrome (TCOF1) gene product	Gene	Não
2005	Cockrem, J. F.	Conservation and behavioral neuroendocrinology	Hormones and Behavior	Não
2005	Buckley, C. R., Michael, S. F., & Irschick, D. J.	Early hatching decreases jumping performance in a direct-developing frog, Eleutherodactylus coqui	Functional Ecology	Não
2005	Hero, J. M., Williams, S. E., & Magnusson, W. E.	Ecological traits of declining amphibians in upland areas of eastern Australia	Journal of Zoology	Não
2005	Grether, G. F.	Environmental change, phenotypic plasticity, and genetic compensation	American Naturalist	Não
2005	Bates, W. R.	Environmental factors affecting reproduction and development in ascidians and other protochordates	Canadian Journal of Zoology	Não
2005	Evans, M. E. K., & Dennehy, J. J.	Germ banking: Bet-hedging and varlable release from egg and seed dormancy	Quarterly Review of Biology	Não
2005	Schmeller, D. S., O'Hara, R., and Kokko, H.	Male adaptive stupidity: male mating pattern in hybridogenetic frogs	Evolutionary Ecology Research	Não
2005	Goberdhan, D. C. I., Meredith, D., Boyd, C. A. R., & Wilson, C.	PAT-related amino acid transporters regulate growth via a novel mechanism that does not require bulk transport of amino acids	Development	Não
2005	Kokubum, M. N. D., & Giaretta, A. A.	Reproductive ecology and behaviour of a species of Adenomera (Anura, Leptodactylinae) with endotrophic tadpoles: Systematic implications	Journal of Natural History	Não
2005	Nath, K., Boorech, J. L., Beckham, Y. M., Burns, M. M., & Elinson, R. P.	Status of RNAs, localized in Xenopus laevis oocytes, in the frogs Rana pipiens and Eleutherodactylus coqui	Journal of Experimental Zoology Part B-Molecular and Developmental Evolution	Não
2005	Hasegawa, H.	Two new genera of the x (Nematoda: Oxyuroidea) found in rhacophorid frogs of the Ryukyu Archipelago, Japan	Journal of Parasitology	Não
2006	Bentsen, C. L., Hunt, J., Jennions, M. D., & Brooks, R.	Complex multivariate sexual selection on male acoustic signaling in a wild population of Teleogryllus commodus	American Naturalist	Não

2006	Uller, T., Sagvik, J., & Olsson, M.	Crosses between frog populations reveal genetic divergence in larval life history at short geographical distance	Biological Journal of the Linnean Society	Não
2006	Burley, L. A., Moyer, A. T., & Petranka, J. W.	Density of an intraguild predator mediates feeding group size, intraguild egg predation, and intra- and interspecific competition	Oecologia	Não
2006	Cobellis, G., Cacciola, G., Scarpa, D., Meccariello, R., Chianese, R., Franzoni, M. F., Mackie, K., Pierantoni, R., & Fasano, S.	Endocannabinoid system in frog and rodent testis: Type-1 cannabinoid receptor and fatty acid amide hydrolase activity in male germ cells	Biology of Reproduction	Não
2006	Annalisa, V., Baj, G., Leone, E., & Tongiorgi, E.	Evolutionary conserved mechanisms of RNA trafficking in neurons and the regulation of spine morphology	Caryologia	Não
2006	Hayakawa, S.	No cancer in cancers: Evolutionary trade-off between successful viviparity and tumor escape from the adaptive immune system	Medical Hypotheses	Não
2006	Kupfer, A., Muller, H., Antoniazzi, M. M., Jared, C., Greven, H., Nussbaum, R. A., & Wilkinson, M.	Parental investment by skin feeding in a caecilian amphibian	Nature	Não
2007	Pfennig, D. W., & Rice, A. M.	An experimental test of character displacement's role in promoting postmating isolation between conspecific populations in contrasting competitive environments	Evolution	Não
2007	Randrianiaina, R.-D., Glaw, F., Thomas, M., Glos, J., Raminosoa, N., Vences, M.	Descriptions of the tadpoles of two species of Gephyromantis, with a discussion of the phylogenetic origin of direct development in mantellid frogs	Zootaxa	Não
2007	Heinicke, M. P., Duellman, W. E., & Hedges, S. B.	Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal	Proceedings of the National Academy of Sciences of the United States of America	Não
2007	Ireland, D. H., Wirsing, A. J., & Murray, D. L.	Phenotypically plastic responses of green frog embryos to conflicting predation risk	Oecologia	Não
2007	Hoskin, C. J., & McCallum, H.	Phylogeography of the parasitic fly Batrachomyia in the Wet Tropics of north-east Australia, and susceptibility of host frog lineages in a mosaic contact zone	Biological Journal of the Linnean Society	Não
2007	Summers, K., McKeon, C. S., Heying, H., Hall, J., & Patrick, W.	Social and environmental influences on egg size evolution in frogs	Journal of Zoology	Não
2007	Keyghobadi, N.	The genetic implications of habitat fragmentation for animals	Canadian Journal of Zoology	Não
2008	Smirnov, S. V.	Direct development in the salamanders, its origin and evolution	Zhurnal Obshchei Biologii	Não
2008	Grosjean, S., Delorme, M., Dubois, A., & Ohler, A.	Evolution of reproduction in the Rhacophoridae (Amphibia, Anura)	Journal of Zoological Systematics and Evolutionary Research	Não

2008	Takahashi, M. K., & Parris, M. J.	Life cycle polyphenism as a factor affecting ecological divergence within Notophthalmus viridescens	Oecologia	Não
2008	De Block, M., McPeek, M. A., & Stoks, R.	Life-history evolution when Lestes damselflies invaded vernal ponds	Evolution	Não
2008	Cooper, N., Bielby, J., Thomas, G. H., & Purvis, A.	Macroecology and extinction risk correlates of frogs	Global Ecology and Biogeography	Não
2008	Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G., & Porter, W. P.	Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates	Ecography	Não
2008	Shook, D. R., & Keller, R.	Morphogenic machines evolve more rapidly than the signals that pattern them: Lessons from amphibians	Journal of Experimental Zoology Part B-Molecular and Developmental Evolution	Não
2008	Jirku, M., Valigurova, A., Koudela, B., Krizek, J., Modry, D., & Slapeta, J.	New species of Cryptosporidium Tyzzer, 1907 (Apicomplexa) from amphibian host: morphology, biology and phylogeny	Folia Parasitologica	Não
2008	Wilkinson, M., Kupfer, A. Marques-Porto, R., Jeffkins, H., Antoniazzi, M. M., & Jared, C.	One hundred million years of skin feeding? Extended parental care in a Neotropical caecilian (Amphibia: Gymnophiona)	Biology Letters	Não
2008	Flores, M. V. C., Lam, E. Y. N., Crosier, K. E., & Crosier, P. S.	Osteogenic transcription factor Runx2 is a maternal determinant of dorsoventral patterning in zebrafish	Nature Cell Biology	Não
2008	Goudet, G., Mugnier, S., Callebaut, I., & Monget, P.	Phylogenetic analysis and identification of pseudogenes reveal a progressive loss of zona pellucida genes during evolution of vertebrates	Biology of Reproduction	Não
2008	Carlile, M., Nalbant, P., Preston-Fayers, K., McHaffie, G. S., & Werner, A.	Processing of naturally occurring sense/antisense transcripts of the vertebrate Slc34a gene into short RNAs	Physiological Genomics	Não
2008	Ivanovic, A., Sotiropoulos, K., Furtula, M., Dzukic, G., & Kalezic, M. L.	Sexual size and shape evolution in European newts (Amphibia: Caudata: Salamandridae) on the Balkan Peninsula	Journal of Zoological Systematics and Evolutionary Research	Não
2008	Kazanskaya, O., Ohkawara, B., Heroult, M., Wu, W., Maltry, N., Augustin, H. G., & Niehrs, C.	The Wnt signaling regulator R-spondin 3 promotes angioblast and vascular development	Development	Não
2009	Arntzen, J. W., Jehle, R., Bardakci, F., Burke, T., & Wallis, G. P.	Asymmetric viability of reciprocal-cross hybrids between crested and marbled newts (Triturus cristatus and T marmoratus)	Evolution	Não
2009	Evsikov, A. V., & Evsikova C. M. de	Evolutionary origin and phylogenetic analysis of the novel oocyte-specific eukaryotic translation initiation factor 4E in Tetrapoda	Development Genes and Evolution	Não
2009	Li, J.-t., Che, J., Murphy, R. W., Zhao, H., Zhao, E.-m., Rao, D.-q., & Zhang, Y.-p.	New insights to the molecular phylogenetics and generic assessment in the Rhacophoridae (Amphibia: Anura) based on five nuclear and three mitochondrial genes, with comments on the evolution of reproduction	Molecular Phylogenetics and Evolution	Não
2009	Badets, M., & Verneau, O.	Origin and evolution of alternative developmental strategies in amphibious	Organisms Diversity & Evolution	Não

		sarcopterygian parasites (Platyhelminthes, Monogenea, Polystomatidae)		
2009	Anderson, A. L., & Brown, W. D.	Plasticity of hatching in green frogs (Rana clamitans) to both egg and tadpole predators	Herpetologica	Não
2009	Nakamura, M.	Sex determination in amphibians	Seminars in Cell & Developmental Biology	Não
2009	Bogdanovic, A. M., Ivanovic, A., Tomanovic, Z., Zikic, V., Stary, P., & Kavallieratos, N. G.	Sexual dimorphism in Ephedrus persicae (Hymenoptera: Braconidae: Aphidiinae): intraspecific variation in size and shape	Canadian Entomologist	Não
2009	Kupfer, A.	Sexual size dimorphism in caecilian amphibians: analysis, review and directions for future research	Zoology	Não
2009	Perez, O. D., Lai, N. B., Buckley, D., del Pino, E. M., & Wake, M. H.	The Morphology of Prehatching Embryos of Caecilia orientalis (Amphibia: Gymnophiona: Caeciliidae)	Journal of Morphology	Não
2009	Gahete, M. D., Duran-Prado, M., Luque, R. M., Martinez-Fuentes, A. J., Quintero, A., Gutierrez-Pascual, E., Cordoba-Chacon, J., Malagon, M. M., Gracia-Navarro, F., & Castano, J. P.	Understanding the Multifactorial Control of Growth Hormone Release by Somatotropes Lessons from Comparative Endocrinology	Trends in Comparative Endocrinology and Neurobiology	Não
2009	Dziminski, M. A., Vercoe, P. E., & Roberts, J. D.	Variable offspring provisioning and fitness: a direct test in the field	Functional Ecology	Não
2009	Exbrayat, J.-M., & Raquet, M.	Vertebrate Evolution: The Strange Case of Gymnophionan Amphibians	Evolutionary Biology: Concept, Modeling, and Application	Não
2010	Hasumi, M.	Age, Body Size, and Sexual Dimorphism in Size and Shape in Salamandrella keyserlingii (Caudata: Hynobiidae)	Evolutionary Biology	Não
2010	Badets, M., Morrison, C., & Verneau, O.	Alternative parasite development in transmission strategies: how time flies!	Journal of Evolutionary Biology	Não
2010	Greenlees, M. J., Phillips, B. L., & Shine, R.	An invasive species imposes selection on life-history traits of a native frog	Biological Journal of the Linnean Society	Não
2010	Bagheri-Fam, S., Sinclair, A. H., Koopman, P., & Harley, V. R.	Conserved regulatory modules in the Sox9 testis-specific enhancer predict roles for SOX, TCF/LEF, Forkhead, DMRT, and GATA proteins in vertebrate sex determination	International Journal of Biochemistry & Cell Biology	Não
2010	Presgraves, D. C.	Darwin and the Origin of Interspecific Genetic Incompatibilities	American Naturalist	Não
2010	Nadachowska, K.	Divergence with gene flow - the amphibian perspective	Herpetological Journal	Não
2010	Zikic, V., Tomanovic, Z., Kavallieratos, N. G., Stary, P., & Ivanovic, A.	Does allometry account for shape variability in Ephedrus persicae Froggatt (Hymenoptera: Braconidae: Aphidiinae) parasitic wasps?	Organisms Diversity & Evolution	Não

2010	Ficetola, G. F., Scali, S., Denoel, M., Montinaro, G., Vukov, T. D., Zuffi, M. A. L., & Padoa-Schioppa, E.	Ecogeographical variation of body size in the newt Triturus carnifex: comparing the hypotheses using an information-theoretic approach	Global Ecology and Biogeography	Não
2010	Badets, M., Mitta, G., Galinier, R., & Verneau, O.	Expression patterns of Abd-A/Lox4 in a monogenean parasite with alternative developmental paths	Molecular and Biochemical Parasitology	Não
2010	Tsutsui, K., Bentley, G. E., Bedecarrats, G., Osugi, T., Ubuka, T., & Kriegsfeld, L. J.	Gonadotropin-inhibitory hormone (GnIH) and its control of central and peripheral reproductive function	Frontiers in Neuroendocrinology	Não
2010	Yoshimoto, S., Ikeda, N., Izutsu, Y., Shiba, T., Takamatsu, N., & Ito, M.	Opposite roles of DMRT1 and its W-linked paralogue, DM-W, in sexual dimorphism of Xenopus laevis: implications of a ZZ/ZW-type sex-determining system	Development	Não
2010	Bi, K., & Bogart, J. P.	Probing the meiotic mechanism of intergenomic exchanges by genomic in situ hybridization on lampbrush chromosomes of unisexual Ambystoma (Amphibia: Caudata)	Chromosome Research	Não
2010	Holt, W. V., & Lloyd, R. E.	Sperm storage in the vertebrate female reproductive tract: How does it work so well?	Theriogenology	Não
2010	Nokhbatolfoghahai, M., Mitchell, N. J., & Downie, J. R.	Surface ciliation and tail structure in direct-developing frog embryos: a comparison between Myobatrachus gouldii and Pristimantis (= Eleutherodactylus) urichi	Herpetological Journal	Não
2011	Brychtova, V., Vojtesek, B., & Hrstka, R.	Anterior gradient 2: A novel player in tumor cell biology	Cancer Letters	Não
2011	Gompert, Z.; & Buerkle, C. A.	Bayesian estimation of genomic clines	Molecular Ecology	Não
2011	Narayan, E. J., Hero, J. M., Christi, K. S., & Morley, C. G.	Early developmental biology of Platymantis vitiana including supportive evidence of structural specialization unique to the ceratobatrachidae	Journal of Zoology	Não
2011	Barry, M. J.	Effects of copper, zinc and dragonfly kairomone on growth rate and induced morphology of Bufo arabicus tadpoles	Ecotoxicology and Environmental Safety	Não
2011	Kerney, R.	Embryonic Staging Table for a Direct-Developing Salamander, Plethodon cinereus (Plethodontidae)	Anatomical Record-Advances in Integrative Anatomy and Evolutionary Biology	Não
2011	Warkentin, K. M.	Environmentally Cued Hatching across Taxa: Embryos Respond to Risk and Opportunity	Integrative and Comparative Biology	Não
2011	Elinson, R. P., Sabo, M. C., Fisher, C., Yamaguchi, T., Orii, H., & Nath, K.	Germ plasm in Eleutherodactylus coqui, a direct developing frog with large eggs	Evodevo	Não
2011	Touchon, J. C., Urbina, J., & Warkentin, K. M.	Habitat-specific constraints on induced hatching in a treefrog with reproductive mode plasticity	Behavioral Ecology	Não
2011	Whittington, I. D., & Kearn, G. C.	Hatching Strategies in Monogenean (Platyhelminth) Parasites that Facilitate Host Infection	Integrative and Comparative Biology	Não

2011	May, S., Zeisset, I., & Beebee, T. J. C.	Larval fitness and immunogenetic diversity in chytrid-infected and uninfected natterjack toad (Bufo calamita) populations	Conservation Genetics	Não
2011	Lai, F., Zhou, Y., Luo, X., Fox, J., & King, M. L.	Nanos1 functions as a translational repressor in the Xenopus germline	Mechanisms of Development	Não
2011	Julaton, V. T. A., & Pera, R. A. R.	NANOS3 function in human germ cell development	Human Molecular Genetics	Não
2011	Pedersen, C. A.	Oxytocin regulation of maternal behavior: From rodents to humans	Oxytocin, Vasopressin, and Related Peptides in the Regulation of Behavior	Não
2011	Hoskin, C. J., Tonione, M., Higgie, M., MacKenzie, J. B., Williams, S. E., VanDerWal, J., & Moritz, C.	Persistence in Peripheral Refugia Promotes Phenotypic Divergence and Speciation in a Rainforest Frog	American Naturalist	Não
2011	Pereira, R. J., Monahan, W. B., & Wake, D. B.	Predictors for reproductive isolation in a ring species complex following genetic and ecological divergence	Bmc Evolutionary Biology	Não
2011	Takahashi, M. K., Takahashi, Y. Y., & Parris, M. J.	Rapid Change in Life-Cycle Polyphenism across a Subspecies Boundary of the Eastern Newt, Notophthalmus viridescens	Journal of Herpetology	Não
2011	Miller, D. A., Clark, W. R., Arnold, S. J., Bronikowski, A. M.	Stochastic population dynamics in populations of western terrestrial garter snakes with divergent life histories	Ecology	Não
2011	Laudet, V.	The Origins and Evolution of Vertebrate Metamorphosis	Current Biology	Não
2012	Chen, W., Wu, Q. G., Su, Z. X., & Lu, X.	Age, body size and clutch size of Rana kunyuensis, a subtropical frog native to China	Herpetological Journal	Não
2012	Oromi, N., Sanuy, D., Sinsch, U.	Altitudinal variation of demographic life-history traits does not mimic latitudinal variation in natterjack toads (Bufo calamita)	Zoology	Não
2012	Kaefer, I. L., Tsuji-Nishikido, B. M., & Lima, A. P.	Beyond the river: underlying determinants of population acoustic signal variability in Amazonian direct-developing Allobates (Anura: Dendrobatoidea)	Acta Ethologica	Não
2012	Pfennig, D. W., Pfennig, K. S.	Development and evolution of character displacement	Year in Evolutionary Biology	Não
2012	Baugh, A. T., Hoke, K. L., & Ryan, M. J.	Development of communication behaviour: Receiver ontogeny in Tungara frogs and a prospectus for a behavioural evolutionary development	Scientific World Journal	Não
2012	Santiago-Alarcon, D., Palinauskas, V., & Schaefer, H. M.	Diptera vectors of avian Haemosporidian parasites: untangling parasite life cycles and their taxonomy	Biological Reviews	Não
2012	Goldberg, J., Vera Candioti, F., & Sebastian Akmentins, M.	Direct-developing frogs: ontogeny of Oreobates barituensis (Anura: Terrarana) and the development of a novel trait	Amphibia-Reptilia	Não
2012	Santos, J. C.	Fast molecular evolution associated with high active metabolic rates in poison frogs	Molecular Biology and Evolution	Não
2012	Cha, S.-W., McAdams, M., Kormish, J., Wylie, C., & Kofron, M.	Foxi2 Is an Animally Localized Maternal mRNA in Xenopus, and an Activator of the Zygotic Ectoderm Activator Foxi1e	Plos One	Não

2012	Xiang, M. A., Linser, P. J., Price, D. A., & Harvey, W. R.	Localization of two Na+- or K+-H+ antiporters, AgNHA1 and AgNHA2, in Anopheles gambiae larval Malpighian tubules and the functional expression of AgNHA2 in yeast	Journal of Insect Physiology	Não
2012	Hertwig, S. T., Lilje, K. E., Min, P. Y., Haas, A., Das, I.	Molecular evidence for direct development in the Rhacophorid frog, Philautus acutus (Rhacophoridae, Anura) from Borneo	Raffles Bulletin of Zoology	Não
2012	Smirina, E. M., & Roitberg, E. S.	On investigations of the reptilian growth in the directions suggested by Am Sergeev	Zoologichesky Zhurnal	Não
2012	Gomez-Mestre, I., Pyron, R. A., & Wiens, J. J.	Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs	Evolution	Sim. Testam os fatores climáticos em escala global como limitantes da evolução dos modos reprodutivos em anfíbios, incluíndo o desenvolvimento direto
2012	Hertwig, S. T., Das, I., Schweizer, M., Brown, R., & Haas, A.	Phylogenetic relationships of the Rhacophorus everetti-group and implications for the evolution of reproductive modes in Philautus (Amphibia: Anura: Rhacophoridae)	Zoologica Scripta	Não
2012	Hjernquist, M. B., Soderman, F., Jonsson, K. I., Herczeg, G., Laurila, A., & Merila, J.	Seasonality determines patterns of growth and age structure over a geographic gradient in an ectothermic vertebrate	Oecologia	Não
2012	Angelopoulou, R., Lavranos, G., & Manolakou, P.	Sex determination strategies in 2012: towards a common regulatory model?	Reproductive Biology and Endocrinology	Não
2012	Hangartner, S., Laurila, A., Raesaenen, K.	The quantitative genetic basis of adaptive divergence in the moor frog (Rana arvalis) and its implications for gene flow	Journal of Evolutionary Biology	Não
2012	Mueller, C. A. Augustine, S., Kooijman, S. A. L. M., Kearney, M. R., & Seymour, R. S.	The trade-off between maturation and growth during accelerated development in frogs	Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology	Não
2012	Nokelainen, O., Hegna, R. H., Reudler, J. H., Lindstedt, C., & Mappes, J.	Trade-off between warning signal efficacy and mating success in the wood tiger moth	Proceedings of the Royal Society B-Biological Sciences	Não
2013	Cajade, R., Marangoni, F., & Gangenova, E.	Age, body size and growth pattern of Argenteohyla siemersi pederseni (Anura: Hylidae) in northeastern Argentina	Journal of Natural History	Não
2013	Badets, M., Du Preez, L., & Verneau, O.	Alternative development in Polystoma gallieni (Platyhelminthes, Monogenea) and life cycle evolution	Experimental Parasitology	Não
2013	Llusia, D., Marquez, R. Beltran, J. F., Benitez, M., & do Amaral, J. P.	Calling behaviour under climate change: geographical and seasonal variation of calling temperatures in ectotherms	Global Change Biology	Não
2013	Fernandez-Mazuecos, M., Luis Blanco-Pastor, J., Gomez, J. M., & Vargas, P.	Corolla morphology influences diversification rates in bifid toadflaxes (Linaria sect. Versicolores)	Annals of Botany	Não
2013	Nascimento, L. P., Siqueira, D. M., & dos Santos-Costa, M. C.	Diet, Reproduction, and Sexual Dimorphism in the Vine Snake, Chironius fuscus (Serpentes: Colubridae), from Brazilian Amazonia	South American Journal of Herpetology	Não

2013	Hertwig, S. T., Schweizer, M., Das, I., & Haas, A.	Diversification in a biodiversity hotspot - The evolution of Southeast Asian rhacophorid tree frogs on Borneo (Amphibia: Anura: Rhacophoridae)	Molecular Phylogenetics and Evolution	Não
2013	Kumaran, N., Balagawi, S., Schutze, M. K., & Clarke, A. R.	Evolution of lure response in tephritid fruit flies: phytochemicals as drivers of sexual selection	Animal Behaviour	Não
2013	Herrmann, H. W., & Branch, W. R.	Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist	Journal of Arid Environments	Não
2013	Müller, H., Liedtke, H. C., Menegon, M., Beck, J., Ballesteros-Mejia, L., Nagel, P., & Loader, S. P.	Forests as promoters of terrestrial life-history strategies in East African amphibians	Biology Letters	Sim. Avaliaram a relação entre o ambiente (tipos de habitat) e a reprodução terrestre (incluíndo o desenvolvimento direto) em anfíbios do leste africano
2013	Crespi, E. J., Williams, T. D., Jessop, T. S., & Delehanty, B.	Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals?	Functional Ecology	Não
2013	Reinhardt, T., Steinfartz, S., Paetzold, A., Weitere, M.	Linking the evolution of habitat choice to ecosystem functioning: direct and indirect effects of pond-reproducing fire salamanders on aquatic-terrestrial subsidies	Oecologia	Não
2013	Taboada, C., Grant, T., Lynch, J. D., & Faivovich, J.	New morphological synapomorphies for the New World direct-developing frogs (Amphibia: Anura: Terrarana)	Herpetologica	Não
2013	Zhang, L., & Lu, X.	Ontogenetic mechanisms underlying sexual size dimorphism in Urodele amphibians: An across-species approach	Current Zoology	Não
2013	Bruce, R. C.	Size-mediated tradeoffs in life-history traits in dusky salamanders	Copeia	Não
2013	Poo, S., & Bickford, D. P.	The adaptive significance of egg attendance in a South-East Asian tree frog	Ethology	Não
2014	Judge, K. A., Ting, J. J., Gwynne, D. T.	Condition dependence of female choosiness in a field cricket	Journal of Evolutionary Biology	Não
2014	Leon-Olea, M., Martyniuk, C. J., Orlando, E. F., Ottinger, M. A., Rosenfeld, C. S., Wolstenholme, J. T., & Trudeau, V. L.	Current concepts in neuroendocrine disruption	General and Comparative Endocrinology	Não
2014	Delia, J. R. J., Ramirez-Bautista, A., & Summers, K.	Glassfrog embryos hatch early after parental desertion	Proceedings of the Royal Society B-Biological Sciences	Não
2014	Murata, K., Conte, F. S., McInnis, E., Fong, T. H., & Cherr, G. N.	Identification of the origin and localization of chorion (egg envelope) proteins in an ancient fish, the white sturgeon, Acipenser transmontanus	Biology of Reproduction	Não
2014	San Mauro, D., Gower, D. J., Mueller, H., Loader, S. P., Zardoya, R., Nussbaum, R. A., Wilkinson, M.	Life-history evolution and mitogenomic phylogeny of caecilian amphibians	Molecular Phylogenetics and Evolution	Não
2014	While, G. M., & Uller, T.	Quo vadis amphibia? Global warming and breeding phenology in frogs, toads and salamanders	Ecography	Não

2014	Dufresne, F., Stift, M., Vergilino, R., Mable, B. K.	Recent progress and challenges in population genetics of polyploid organisms: an overview of current state-of-the-art molecular and statistical tools	Molecular Ecology	Não
2014	Aran, R. P., Steffen, M. A., Martin, S. D., Lopez, O. I., & Bonett, R. M.	Reduced effects of thyroid hormone on gene expression and metamorphosis in a paedomorphic plethodontid salamander	Journal of Experimental Zoology Part B-Molecular and Developmental Evolution	Não
2014	Elinson, R. P., & Stewart, J. R.	The corn snake yolk sac becomes a solid tissue filled with blood vessels and yolk-rich endodermal cells	Biology Letters	Não
2014	Simoes, P. I., Stow, A., Hoedl, W., Amezquita, A., Farias, I. P., & Lima, A. P.	The value of including intraspecific measures of biodiversity in environmental impact surveys is highlighted by the Amazonian brilliant-thighed frog (Allobates femoralis)	Tropical Conservation Science	Não
2014	Klug, H., & Bonsall, M. B.	What are the benefits of parental care? The importance of parental effects on developmental rate	Ecology and Evolution	Não
2015	Hutter, C. R., Lambert, S. M., Cobb, K. A., Andriampenomanana, Z. F., & Vences, M.	A new species of bright-eyed treefrog (Mantellidae) from Madagascar, with comments on call evolution and patterns of syntopy in the Boophis ankaratra complex	Zootaxa	Não
2015	Pereira, E. B., Collevatti, R. G., Kukubum, M. N. C., Miranda, N. E. O., & Maciel, N. M.	Ancestral reconstruction of reproductive traits shows no tendency toward terrestriality in leptodactyline frogs	BMC Evolutionary Biology	Não
2015	Raquet, M. A., Measey, G. J., & Exbrayat, J. M.	Annual variation of ovarian structures of Boulengerula taitana (Loveridge 1935), a Kenyan caecilian	African Journal of Herpetology	Não
2015	Crump, M. L.	Anuran Reproductive Modes: Evolving Perspectives	Journal of Herpetology	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
2015	Seshadri, K. S., Gururaja, K. V., & Bickford, D. P.	Breeding in bamboo: a novel anuran reproductive strategy discovered in Rhacophorid frogs of the Western Ghats, India	Biological Journal of the Linnean Society	Não
2015	Medina, D., Garner, T. W. J., Carrascal, L. M., & Bosch, J.	Delayed metamorphosis of amphibian larvae facilitates Batrachochytrium dendrobatidis transmission and persistence	Diseases of Aquatic Organisms	Não
2015	De Lisle, S. P., & Rowe, L.	Ecological character displacement between the sexes	American Naturalist	Não
2015	Wellborn, G. A., & Langerhans, R. B.	Ecological opportunity and the adaptive diversification of lineages	Ecology and Evolution	Não
2015	Liu, T., Cheng, J., Wang, C., Niu, J., Wang, B., Zhai, J., Shafi, M., Zhang, Q., Qi, J., & He, Y.	Genetic characteristics and evolution of Pitx2 in sinistral tongue sole, Cynoglossus semilaevis and dextral stone flounder, Kareius bicoloratus	Pakistan Journal of Zoology	Não
2015	VanCompernolle, S., Smith, P. B., Bowie, J. H., Tyler, M. J., Unutmaz, D., & Rollins-Smith, L. A.	Inhibition of HIV infection by caerin 1 antimicrobial peptides	Peptides	Não
2015	Mangold, A., Trenkwalder, K., Ringler, M., Hoedl, W., & Ringler, E.	Low reproductive skew despite high male-biased operational sex ratio in a glass frog with paternal care	BMC Evolutionary Biology	Não

2015	Meegaskumbura, M., Senevirathne, G., Biju, S. D., Garg, S., Meegaskumbura, S., Pethiyagoda, R., Hanken, J., & Schneider, C. J.	Patterns of reproductive-mode evolution in Old World tree frogs (Anura, Rhacophoridae)	Zoologica Scripta	Não
2015	Castroviejo-Fisher, S., Padial, J. M., De La Riva, I., Pombal Jr, J. P., Da Silva, H. R., Rojas-Runjaic, F. J. M., Medina-Mendez, E., & Frost, D. R.	Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development	Zootaxa	Não
2015	Pfennig, K. S., Pfennig, D. W., Porter, C., & Martin, R. A.	Sexual selection's impacts on ecological specialization: an experimental test	Proceedings of the Royal Society B-Biological Sciences	Não
2015	Qi, Y., Zhang, W., Huang, L., Luo, Z., Zhao, M., & Wu, H.	Significant male biased sexual size dimorphism in Leptobrachium leishanensis	Asian Herpetological Research	Não
2015	Yu, T. L., & Guo, Y. S.	Testes asymmetry of Bufo gargarizans in relation to body condition and age	Acta Herpetologica	Não
2016	Bonett, R. M.	An integrative endocrine model for the evolution of developmental timing and life history of Plethodontids and other salamanders	Copeia	Não
2016	Kikuta, S., Endo, H., Tomita, N., Takada, T., Morita, C., Asaoka, K., & Sato, R.	Characterization of a ligand-gated cation channel based on an inositol receptor in the silkworm, Bombyx mori	Insect Biochemistry and Molecular Biology	Não
2016	Plard, F., Gaillard, J.-M., Coulson, T., & Tuljapurkar, S.	Des differences, pourquoi? Transmission, maintenance and effects of phenotypic variance	Journal of Animal Ecology	Não
2016	de Lima, A. V. P., Reis, A. H., Amado, N. G., Cassiano-Lima, D., Borges-Nojosa, D. M., Oria, R. B., & Abreu, J. G.	Developmental aspects of the direct-developing frog Adelophryne maranguapensis	Genesis	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
2016	Lee, W.-S., Mangel, M., & Peres-Neto, P.	Environmental integration: patterns of correlation between environmental factors, early life decisions, and their long-term consequences	Evolutionary Ecology Research	Não
2016	Yoshioka, M., Meeks, C., & Summers, K.	Evidence for begging as an honest signal of offspring need in the biparental mimic poison frog	Animal Behaviour	Não
2016	Miura, I., Ohtani, H., Ogata, M., & Ezaz, T.	Evolutionary changes in sensitivity to hormonally induced gonadal sex reversal in a frog species	Sexual Development	Não
2016	McNeil, G. V., Friesen, C. N., Gray, S. M., Aldredge, A., & Chapman, L. J.	Male colour variation in a eurytopic African cichlid: the role of diet and hypoxia	Biological Journal of the Linnean Society	Não
2016	Moore, M. P., & Whiteman, H. H.	Natal philopatry varies with larval condition in salamanders	Behavioral Ecology and Sociobiology	Não
2016	Agnese, M., Valiante, S., Rosati, L., Andreuccetti, P., & Prisco, M.	Pituitary adenylate cyclase-activating peptide (PACAP) and PAC(1) receptor in the testis of cartilaginous fish Torpedo marmorata: A molecular and phylogenetic study	Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology	Não

2016	Zamúdio, K. R., Bell, R. C., Nali, R. C., Haddad, C. F. B., & Prado, C. P. A.	Polyandry, Predation, and the Evolution of Frog Reproductive Modes	American Naturalist	Sim. Testaram a seleção sexual como promotora da diversificação reprodutiva e da evolução da reprodução terrestre nas famílias Hylidae e Leptodactylidae
2016	Warne, R. W., & Catenazzi, A.	Pouch brooding marsupial frogs transfer nutrients to developing embryos	Biology Letters	Não
2016	Botto, V., & Castellano, S.	Signal reliability and multivariate sexual selection in a lek-breeding amphibian	Behavioral Ecology	Não
2016	Kupfer, A., Maxwell, E., Reinhard, S., & Kuehnel, S.	The evolution of parental investment in caecilian amphibians: a comparative approach	Biological Journal of the Linnean Society	Não
2016	Portik, D. M., & Blackburn, D. C.	The evolution of reproductive diversity in Afrobatrachia: A phylogenetic comparative analysis of an extensive radiation of African frogs	Evolution	Sim. Avaliaram a evolução do desenvolvimento direto em quatro famílias de anfíbios africanos, avaliaram associações entre características ecomorfológicas e a diversidade reprodutiva, e entre modos reprodutivos terrestres e o habitat de reprodução das espécies
2017	Vivante, A., Mann, N., Yonath, H., Weiss, A.-C., Getwan, M., Kaminski, M. M., Bohnenpoll, T., Teyssier, C., Chen, J., Shril, S., van der Vem, A. T., Ityel, H., Schmidt, J. M., Widmeier, E., Bauer, S. B., Sanna-Cherchi, S., Gharavi, A. G., Lu, W., Magen, D., Shukrun, R., Lifton, R. P., Tasic, V., Stanescu, H. C., Cavailles, V., Kleta, R., Anikster, Y., Dekel, B., Kispert, A., Lienkamp, S. S., & Hildebrandt, F.	A Dominant Mutation in Nuclear Receptor Interacting Protein 1 Causes Urinary Tract Malformations via Dysregulation of Retinoic Acid Signaling	Journal of the American Society of Nephrology	Não
2017	Plouhinec, J.-L., Medina-Ruiz, S., Borday, C., Bernard, E., Vert, J.-P., Eisen, M. B., Harland, R. M., & Monsoro-Burq, A. H.	A molecular atlas of the developing ectoderm defines neural, neural crest, placode, and nonneural progenitor identity in vertebrates	Plos Biology	Não
2017	Vargas, A. O., Krabichler, Q., & Guerrero-Bosagna, C.	An epigenetic perspective on the midwife toad experiments of Paul Kammerer (1880-1926)	Journal of Experimental Zoology Part B-Molecular and Developmental Evolution	Não
2017	Nelson, D. V., Klinck, H., Carbaugh-Rutland, A., Mathis, C. L., Morzillo, A. T., & Garcia, T. S.	Calling at the highway: The spatiotemporal constraint of road noise on Pacific chorus frog communication	Ecology and Evolution	Não
2017	Senevirathne, G., Kerney, R., & Meegaskumbura, M.	Comparative postembryonic skeletal ontogeny in two sister lineages of old-world tree frogs (Rhacophoridae: Taruga, Polypedates)	PLoS ONE	Não
2017	Spencer, R. J., Van Dyke, J. U., & Thompson M. B.	Critically evaluating best management practices for preventing freshwater turtle extinctions	Conservation Biology	Não

2017	Schweiger, S., Naumann, B., Larson, J. G., Moeckel, L., & Mueller, H.	Direct development in African squeaker frogs (Anura: Arthroleptidae: Arthroleptis) reveals a mosaic of derived and plesiomorphic characters	Organisms Diversity & Evolution	Não
2017	Liles, L. A., Cecala, K. K., Ennen, J. R., & Davenport, J. M.	Elevated temperatures alter competitive outcomes and body condition in southern Appalachian salamanders	Animal Conservation	Não
2017	Castillo, D. M.	Factors contributing to the accumulation of reproductive isolation: A mixed model approach	Ecology and Evolution	Não
2017	Fetters, T. L., & McGlothlin, J. W.	Life histories and invasions: accelerated laying rate and incubation time in an invasive lizard, Anolis sagrei	Biological Journal of the Linnean Society	Não
2017	Korsos, G., Cenkvari, E., Gaspardy, A., & Fekete S.	Peculiar laboratory animals, experimental models	Magyar Allatorvosok Lapja	Não
2017	Lofeu, L., Brandt, R., & Kohlsdorf, T.	Phenotypic integration mediated by hormones: associations among digit ratios, body size and testosterone during tadpole development	BMC Evolutionary Biology	Não
2017	Holmes, I. A., Grundler, M. R., & Rabosky, A. R. D.	Predator perspective drives geographic variation in frequency-dependent polymorphism	American Naturalist	Não
2017	Gordon, N. M., Ralph, M. Z., & Stratman, K. D.	Rapid character displacement of different call parameters in closely related treefrogs (Hyla cinerea and H. gratiosa)	Behavioral Ecology and Sociobiology	Não
2017	O. Jimenez-Robles; J. M. Guayasamin; S. R. Ron; I. De la Riva	Reproductive traits associated with species turnover of amphibians in Amazonia and its Andean slopes	Ecology and Evolution	Sim. Não testam nenhuma hipótese, apenas apontam possíveis fatores que estariam relacionados a evolução do desenvolvimento direto em anfíbios
2017	Mauricio Ortega-Andrade, H., Rojas-Soto, O. R., Espinosa de los Monteros, A., Valencia, J. H., Read, M., & Ron, S. R.	Revalidation of Pristimantis brevicrus (Anura, Craugastoridae) with taxonomic comments on a widespread Amazonian direct-developing frog	Herpetological Journal	Não
2017	O'Brien, D. M., Katsuki, M., & Emlen, D. J.	Selection on an extreme weapon in the frog-legged leaf beetle (Sagra femorata)	Evolution	Não
2017	Gomez, J., & Linan-Cembrano, G.	SpotEgg: an image-processing tool for automatized analysis of colouration and spottiness	Journal of Avian Biology	Não
2017	Dugas, M. B., Strickler, S. A., & Stynoski, J. L.	Tadpole begging reveals high quality	Journal of Evolutionary Biology	Não
2017	Liedtke, H. C., Mueller, H., Hafner, J., Penner, J., Gower, D. J., Mazuch, T., Roedel, M.-O., & Loader, S. P.	Terrestrial reproduction as an adaptation to steep terrain in African toads	Proceedings of the Royal Society B-Biological Sciences	Sim. Avaliaram como a evolução da reprodução terrestre (incluíndo o desenvolvimento direto) em bufonídeos africanos é relacionada com as características abióticas do habitat destas espécies
2017	Onorati, M., & Vignoli, L.	The darker the night, the brighter the stars: consequences of nocturnal brightness on amphibian reproduction	Biological Journal of the Linnean Society	Não
2017	Santos, M. T. T., Pezzuti, T. L., Barata, I. M., Fortes Leite, F. S., & Garcia, P. C. A.	The tadpole of the microendemic, bromeligenous Crossodactylodes itambe (Anura, Leptodactylidae) from the endangered 'Campo Rupestre' of southeastern Brazil, with additional comments on natural history	South American Journal of Herpetology	Não
2017	Wang, X., Liu, S., & Liu, Z.	Underwater sonar image detection: A combination of nonlocal spatial information and quantum-inspired shuffled frog leaping algorithm	PLoS ONE	Não

2018	Zhong, M., Yu, X., & Liao, W.	A review for life-history traits variation in frogs especially for anurans in China	Asian Herpetological Research	Não
2018	Bohenek, J. R., & Resetarits, W. J. Jr.	Are direct density cues, not resource competition, driving life history trajectories in a polyphenic salamander?	Evolutionary Ecology	Não
2018	Hardy, S. P., Hardy, D. R., & Gil, K. C.	Avian nesting and roosting on glaciers at high elevation, Cordillera Vilcanota, Peru	Wilson Journal of Ornithology	Não
2018	Nicolaus, M., & Edelaar, P.	Comparing the consequences of natural selection, adaptive phenotypic plasticity, and matching habitat choice for phenotype-environment matching, population genetic structure, and reproductive isolation in meta-populations	Ecology and Evolution	Não
2018	Ibragimova, D. V., & Lyapkov, S. M.	Demographic and morphometric characteristics of the moor frog (Rana arvalis) from a transformed habitat in the Khanty-Mansy autonomous region - Yugra	Zoologichesky Zhurnal	Não
2018	Cabezas-Cartes, F., Boretto, J. M., & Ibarguengoytia, N. R.	Effects of climate and latitude on age at maturity and longevity of lizards studied by skeletochronology	Integrative and Comparative Biology	Não
2018	Cullen, E., Fernandez-Mazuecos, M., & Glover, B. J.	Evolution of nectar spur length in a Glade of Linaria reflects changes in cell division rather than in cell expansion	Annals of Botany	Não
2018	Seshadri, K. S., & Bickford, D. P.	Faithful fathers and crooked cannibals: the adaptive significance of parental care in the bush frog Raorchestes chalazodes, Western Ghats, India	Behavioral Ecology and Sociobiology	Não
2018	Amat, F., & Meiri, S.	Geographical, climatic and biological constraints on age at sexual maturity in amphibians	Biological Journal of the Linnean Society	Não
2018	De Lisle, S. P., Paiva, S., & Rowe, L.	Habitat partitioning during character displacement between the sexes	Biology Letters	Não
2018	Palka, M., Tomczak, A., Grabowska, K., Machowska, M., Piekarowicz, K., Rzepecka, D., & Rzepecki, R.	Laminopathies: what can humans learn from fruit flies	Cellular & Molecular Biology Letters	Não
2018	Liedtke, H. C., Gower, D. J., Wilkinson, M., & Gomez-Mestre, I.	Macroevolutionary shift in the size of amphibian genomes and the role of life history and climate	Nature Ecology & Evolution	Não
2018	Ruuskanen, S., & Hsu, B.-Y.	Maternal Thyroid Hormones: An Unexplored Mechanism Underlying Maternal Effects in an Ecological Framework	Physiological and Biochemical Zoology	Não
2018	Taucce, P. P. G., Canedo, C., Parreiras, J. S., Drummond, L. O., Nogueira-Costa, P., & Haddad, C. F. B.	Molecular phylogeny of Ischnocnema (Anura: Brachycephalidae) with the redefinition of its series and the description of two new species	Molecular Phylogenetics and Evolution	Não
2018	Dornburg, A., Warren, D. L., Zapfe, K. L., Morris, R., Iglesias, T. L., Lamb, A., Hogue, G., Lukas, L., & Wong, R.	Testing ontogenetic patterns of sexual size dimorphism against expectations of the expensive tissue hypothesis, an intraspecific example using oyster toadfish (Opsanus tau)	Ecology and Evolution	Não
2018	Pennell, M. W., Mank, J. E., & Peichel, C. L.	Transitions in sex determination and sex chromosomes across vertebrate species	Molecular Ecology	Não

2018	De la Riva, I., Chaparro, J. C., Castroviejo-Fisher, S., & Padial, J. M.	Underestimated anuran radiations in the high Andes: five new species and a new genus of Holoadeninae, and their phylogenetic relationships (Anura: Craugastoridae)	Zoological Journal of the Linnean Society	Não
2019	Cummins, D., Kennington, W. J., Rudin-Bitterli, T., & Mitchell, N. J.	A genome-wide search for local adaptation in a terrestrial-breeding frog reveals vulnerability to climate change	Global Change Biology	Não
2019	Peace, A., O'Regan, S. M., Spatz, J. A., Reilly, P. L., Hill, R. D., Carter, E. D., Wilkes, R. P., Waltzek, T. B., Miller, D. L., & Gray, M. J.	A highly invasive chimeirc ranavirus can decimate tadpole populations rapidly through multiple transmission pathways	Ecological Modelling	Não
2019	Jiang, K., Wang, K., Wang, Y.-F., Li, C., & Che, J.	A new species of the endemic Himalayan genus Liurana (Anura, Ceratobatrachidae) from southeastern Tibet, China, with comments on the distribution, reproductive biology, and conservation of the genus	Zoological Research	Não
2019	Mai, C. L., & Liao, W. B.	Brain size evolution in anurans: a review	Animal Biology	Não
2019	Gould, J.	Build me up to break me down: frothed spawn in the sandpaper frog, Lechriodus fletcheri, is formed by female parents and later broken down by their offspring	Australian Journal of Zoology	Não
2019	Smiseth, P. T.	Coordination, cooperation, and conflict between caring parents in burying beetles	Frontiers in Ecology and Evolution	Não
2019	Sou, S. K., Sow, K. K., & Nandi, A. P.	Description of a new species of Rhabdias Stiles and Hassall, 1905 (Nematoda, Rhabdiasidae) in Duttaphrynus melanostictus (Schneider, 1899) from West Bengal, India	Acta Parasitologica	Não
2019	Ortega-Recalde, O., Hore, T. A.	DNA methylation in the vertebrate germline: balancing memory and erasure	DNA Methylation	Não
2019	Zumbado-Ulate, H., Nelson, K. N., Garcia-Rodriguez, A., Chaves, G., Arias, E., Bolanos, F., Whitfield, S. M., & Searle, C. L.	Endemic infection of Batrachochytrium dendrobatidis in Costa Rica: Implications for amphibian conservation at regional and species level	Diversity-Basel	Não
2019	Laslo, M., Denver, R. J., & Hanken, J.	Evolutionary conservation of thyroid hormone receptor and deiodinase expression dynamics in ovo in a direct-developing frog, Eleutherodactylus coqui	Frontiers in Endocrinology	Não
2019	Paluh, D. J., Coloma, L. A., & Blackburn, D. C.	Evolutionary Lability in Life History, Morphology, and Performance in Andean Marsupial Frogs	Integrative and Comparative Biology	Não
2019	Cai, Y. L., Mai, C. L., & Liao, W. B.	Frogs with denser group-spawning mature later and live longer	Scientific Reports	Não
2019	Oromi, N., Valbuena-Urena, E., Soler-Membrives, A., Amat, F., Camarasa, S., Carranza, S., Sanuy, D., & Denoel, M.	Genetic structure of lake and stream populations in a Pyrenean amphibian (Calotriton asper) reveals evolutionary significant units associated with paedomorphosis	Journal of Zoological Systematics and Evolutionary Research	Não
2019	Pujol-Buxo, E., Riano, G. M., & Llorente, G. A.	Mild segregation in the breeding preferences of an invasive anuran (Discoglossus pictus) and its main native competitor (Epidalea calamita) in ephemeral ponds	Amphibia-Reptilia	Não

2019	Bardua, C., Wilkinson, M., Gower, D. J., Sherratt, E., & Goswami, A.	Morphological evolution and modularity of the caecilian skull	BMC Evolutionary Biology	Não
2019	Chuliver, M., & Scanferla, A.	Morphology and postnatal ontogeny of the dentition of Chthonerpeton indistinctum (Gymnophiona: Typhlonectidae)	Amphibia-Reptilia	Não
2019	Morsy, K., Al-Kahtani, M., Shati, A., El-Kott, A., Abdel-Gaber, R., & Fol, M.	New host and locality record of Parapharyngodon japonicus (Nematoda: Oxyuroidea) from the Egyptian changeable lizard Agama mutabilis (Agamidae): A light and scanning electron microscopy	Helminthologia	Não
2019	Sauer, M., & Kleine-Vehn, J.	PIN-FORMED and PIN-LIKES auxin transport facilitators	Development	Não
2019	Nousch, M.; Yeroslaviz, A., & Eckmann, C. R.	Stage-specific combinations of opposing poly(A) modifying enzymes guide gene expression during early oogenesis	Nucleic Acids Research	Não
2019	Ledbetter, N. M., & Bonett, R. M.	Terrestriality constrains salamander limb diversification: Implications for the evolution of pentadactyly	Journal of Evolutionary Biology	Não
2019	Mohanty, N. P., & Measey, J.	The global pet trade in amphibians: species traits, taxonomic bias, and future directions	Biodiversity and Conservation	Não
2019	von May, R., Catenazzi, A., Santa-Cruz, R., Gutierrez, A. S., Moritz, C., & Rabosky, D. L.	Thermal physiological traits in tropical lowland amphibians: Vulnerability to climate warming and cooling	PLoS ONE	Não
2019	Seidl, F., Levis, N. A., Jones, C. D., Monroy-Eklund, A., Ehrenreich, I. M., & Pfennig, K. S.	Variation in hybrid gene expression: Implications for the evolution of genetic incompatibilities in interbreeding species	Molecular Ecology	Não
2020	Rojo-Bartolome, I., Santana de Souza, J. E., Diaz de Cerio, O., Cancio, I.	Duplication and subfunctionalisation of the general transcription factor IIIA (gtf3a) gene in teleost genomes, with ovarian specific transcription of gtf3ab	Plos One	Não
2020	Goldberg, J., Taucce, P. P. G., Ines Quinzio, S., Haddad, C. F. B., & Vera Candioti, F.	Increasing our knowledge on direct-developing frogs: The ontogeny of *Ischnocnema henselii* (Anura: Brachycephalidae)	Zoologischer Anzeiger	Não
2020	Dufresnes, C., Pribille, M., Alard, B., Goncalves, H., Amat, F., Crochet, P.-A., Dubey, S., Perrin, N., Fumagalli, L., Vences, M., & Martinez-Solano I.	Integrating hybrid zone analyses in species delimitation: lessons from two anuran radiations of the Western Mediterranean	Heredity	Não
2020	Fusinatto, L. A., Diniz, B. L. T., de Siqueira, A. S., Van Sluys, M., Sequeira, F., & Duarte Rocha, C. F.	Living in a tiny world: reproductive biology and population ecology of the Neotropical miniature frog Euparkerella aff. brasiliensis (Terraranae, Strabomantidae)	Amphibia-Reptilia	Não
2020	Trudeau, V. L., & Somoza, G. M.	Multimodal hypothalamo-hypophysial communication in the vertebrates	General and Comparative Endocrinology	Não
2020	Rowinski, P. K., Laurila, A., Gotthard, K., Sowersby, W., Lind, M. I., Richter-Boix, A., Eckerstrom-Liedholm, S., & Bogen, B.	Parental effects influence life history traits and covary with an environmental cline in common frog populations	Oecologia	Não

2020	Suriadna, N. M., Mykytynets, G. I., Pupins, M., & Gasso, V. Y.	Population systems of Eurasian water frogs (Pelophylax) in the south of Ukraine	Biosystems Diversity	Não
2020	Dobolyi, A., Olah, S., Keller, D., Kumari, R., Fazekas, E. A., Csikos, V., Renner, E., & Cservenak, M.	Secretion and function of pituitary prolactin in evolutionary perspective	Frontiers in Neuroscience	Não
2020	Lukas, P., & Olsson, L.	Sequence of chondrocranial development in the oriental fire bellied toad Bombina orientalis	Journal of Morphology	Não
2020	Savinykh, N. P., & Shabalkina, S. V.	Shoot-formation model as a basis for adaptations of flowering plants	Contemporary Problems of Ecology	Não
2020	Longo, A. V., Rodriguez-Gomez, C. A., Zegarra, J. P., Monzon, O., Claudio-Hernandez, H. J., Joglar, R. L., Zamúdio, K. R., Burrowes, P. A., & Lopez-Torres, A. L	Tick parasitism as a cost of sexual selection and male parental care in a Neotropical frog	Ecosphere	Não

CAPÍTULO II

DIRECT DEVELOPMENT IN ATLANTIC FOREST ANURANS: WHAT CAN ENVIRONMENTAL AND BIOTIC INFLUENCES EXPLAIN ABOUT ITS EVOLUTION AND OCCURRENCE?

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Direct development in Atlantic Forest anurans: what can environmental and biotic influences explain about its evolution and occurrence?

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Abstract

Different environmental and biological factors can originate and support different alternative life histories in different taxonomic groups. Likewise, these factors are important for the processes that assemble and structure communities. Amphibians, besides being highly susceptible to environmental conditions, have various reproductive strategies, such as the direct development of individuals. Several hypotheses have been raised about possible selective pressures related to the emergence of direct development in anurans, as well as the relationship between environmental characteristics and the occurrence of these species. Such investigations, however, have mainly focused on specific clades and/or regions. Here, we use structural equation modelling to investigate the relationships between different abiotic (temperature, precipitation, humidity, and terrain slope) and biotic (phylogenetic composition and functional diversity) factors and the proportion of species with direct development in 766 anuran communities of the Atlantic Forest, a biome with a vast diversity of anuran species and high environmental complexity. Anuran communities with higher proportions of direct developing species were found to be mainly influenced by low potential evapotranspiration, low temperature seasonality, and high functional diversity. Phylogenetic composition and terrain slope were also found to be important in determining the occurrence of these species in Atlantic Forest communities. These results show the importance of these factors in the structuring of these communities and provide important contributions to the knowledge of direct development in anurans.

Introduction

As the result of a long and complex evolutionary history, the great diversity of amphibian species represents numerous morphological and behavioral varieties, an abundance of ecological relationships, and the greatest diversity of reproductive modes among tetrapods [1]. Seventy-four reproductive modes are currently described for amphibians, 56 of which are exclusive to anurans

[2]. These anuran modes represent collections of reproductive traits, such as oviposition site, spawning and larval characteristics, and type of development [2, 3]. Deviating from the ancestral reproductive mode of a biphasic life cycle with a larval phase in the form of a tadpole, is direct development [1, 4]. Direct development in anurans is characterized by the absence of a free-living larval stage, with the hatching of miniatures of adult forms. The morphological and physiological modifications resulting from the alteration of biphasic development to a single-phase life cycle impose specific requirements and tolerances on these species, especially in terms of humidity [5, 6].

Direct developing anurans are mostly associated with climatically stable environments, such as forests with higher levels of humidity and structural complexity [7–9]. In the same way that the evolutionary diversification of reproductive modes is related to distinct factors, the emergence and evolution of direct development in anurans has diverse evolutionary hypotheses, as discussed by Fontana et al. 2022 [10]. The most discussed of these hypotheses proposes direct development as an alternative trait resulting from evolutionary processes linked to the action of biotic factors, such as predation of aquatic eggs and larvae and/or competition for reproductive sites [3, 11, 12]. Also, the hidden amplexus of certain terrestrial breeders (some species of the families Hylidae and Leptodactylidae) may exemplify how sexual selection (competition among males for reproductive females and polyandry avoidance) molded the evolution of reproductive modes in anurans [13]. Alternatively, the abiotic environment has also been presented as a potential selective force in the evolution of direct development. Climatic conditions, such as seasonality, precipitation, and temperature, play important roles in determining the distribution of these species [4, 9]. Furthermore, environmental structure, such as topography, may have also been an important selective factor, since more structurally complex locales can enhance the loss and mortality of aquatic eggs and larvae through water flow [9, 14].

Continuously distributed along the Brazilian coast and penetrating inland regions, the Atlantic Forest has enormous environmental heterogeneity, with different forest formations, microclimatic conditions, and variations in relief [15, 16]. Due to these characteristics, the Atlantic

Forest supplies a myriad of different habitats and microhabitats that harbor an enormous diversity of plants and animals with a high rate of endemism, earning it recognition as a global biodiversity hotspot [17, 18]. Among Atlantic Forest animals, the great diversity of anurans stands out, with this tropical forest sheltering almost 10% of known anuran species, placing it among the regions with the greatest diversity of this group [19, 20].

The evolutionary and ecological relationships, different life histories, and great diversity of morphologies and reproductive modes of anurans are reflected not only in their high taxonomic diversity but also in their high phylogenetic and functional diversities in the Atlantic Forest [21, 22]. Phylogenetic diversity (PD) is a biodiversity metric used to explore the evolutionary history of species, based on branch lengths of a phylogenetic tree [23]. Functional diversity (FD), on the other hand, not only reflects the variability of species traits in communities but can also be used as a metric to investigate complementarity in resource use, or niche differentiation, and to understand how these traits influence the functioning of communities and ecosystems [24]. Since these metrics reflect ecological and evolutionary patterns that occur in communities, they can be used to infer processes related to the response of species to biotic interactions, ecosystem functioning, and patterns related to community structure [23, 25–27]. Therefore, the use of these metrics can reveal the influence of distinct factors on community assemblages, such as past competition and predation among species (in communities that present phylogenetic and/or functional overdispersion), as well as the influence of environmental filters (in communities displaying phylogenetic and/or functional clustering) [28, 29]. Since biotic interactions, such as competition among species and predation, are difficult to measure in natural communities, the use of PD and FD metrics as proxies for local coexistence mechanisms and these interactions is perhaps a valid alternative.

Understanding how biotic and abiotic factors are related to direct development in anurans is crucial, since these relationships can help to discover the conditions that are favorable or unfavorable for the occurrence of reproductive modes in distinct environments. Furthermore, based on these relationships, new insights can be gained into the evolution of terrestrial reproductive modes, such as direct development. Thus, here we employ structural equation modelling (SEM) to evaluate the relationships among environmental characteristics (climate and topography), biotic characteristics (phylogenetic composition and functional diversity), and the proportion of direct developing anuran species in communities of the Atlantic Forest. (Fig 1).

As mentioned above, the evolution of anuran direct development can be a result of driving forces due to the actuation of abiotic factors. Thus, we expected to find higher proportions of direct developing anuran species in communities that are climatically stable and with elevated levels of humidity and rough terrain. If ecological mechanisms (e.g., competition, predation, parasitism) are also forces related to the divergence and evolution of traits, and if these mechanisms are linked to the main hypotheses regarding the evolution of direct development in anurans, we would expect that communities that experienced high levels of these interactions in the past would currently have higher levels of functional diversity and higher proportions of direct developing anuran species. In this context, communities that historically experienced high competition and predation rates must have undergone functional divergence, with species occupying new niches. As a result, these communities should currently exhibit greater functional diversity and greater proportions of direct developing anuran species.

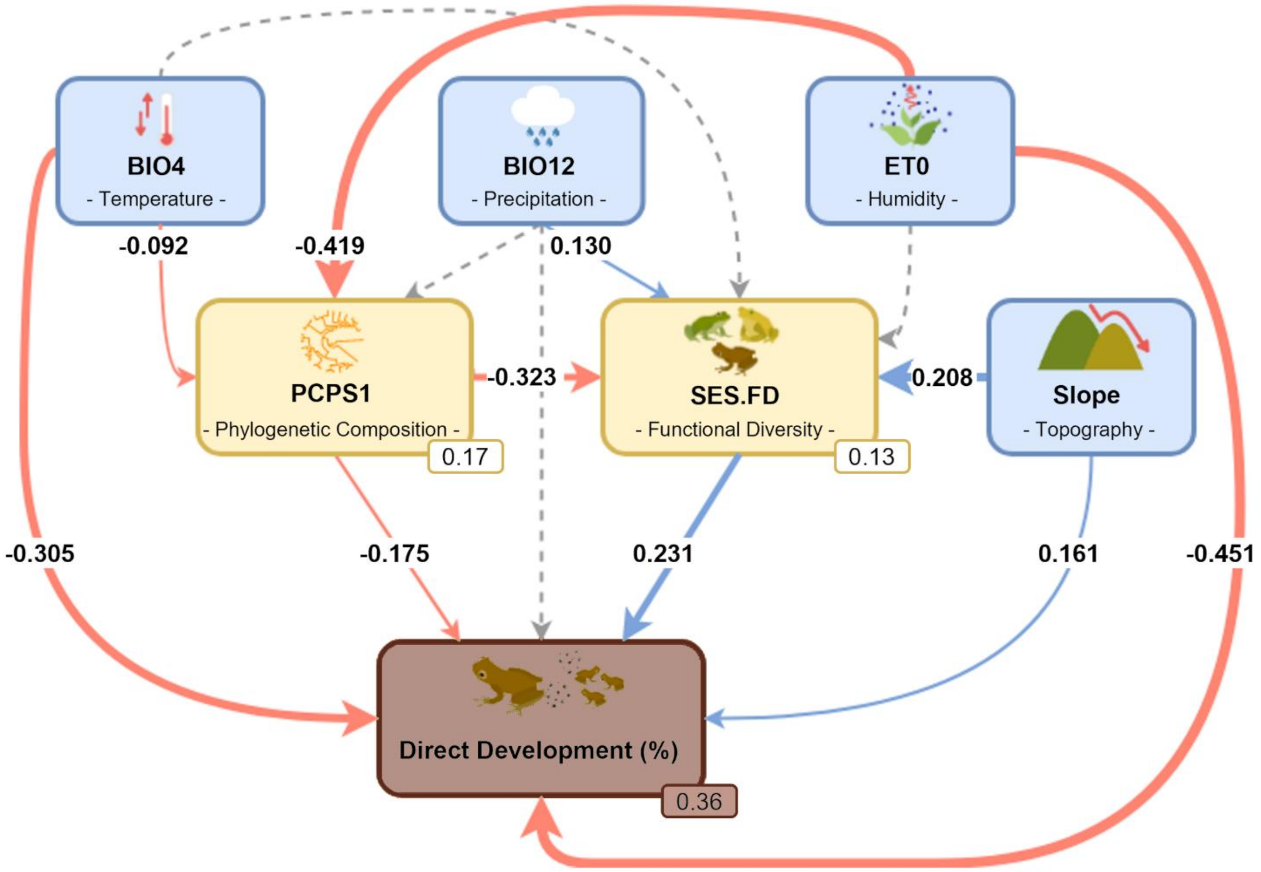

Fig 1. Investigated relationships of abiotic and biotic factors with direct developing anurans in the Atlantic Forest. Piecewise SEM model showing the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct developing species (brown box) in anuran communities of the Atlantic Forest. Significant relationships are presented in blue (positive relationship) and red (negative relationships) arrows. Values on arrows correspond to standardized coefficients. R^2 values for endogenous variables are presented in the small boxes. The thickness of arrows is proportional to the magnitude of the standardized coefficients. BIO4 – temperature seasonality; bio12 – annual precipitation; ET0 – potential evapotranspiration; PCPS1 – first PCPS eigenvector; SES.FD – standardized effect size of functional diversity; and %DD – proportion of direct developing species in the anuran communities.

Material and methods

Data collection

Direct developing species in Atlantic Forest anuran communities

To evaluate the influences of biotic and abiotic variables on the proportion of direct developing species in Atlantic Forest anuran communities, we first created a subset of anuran communities using the database of Atlantic Forest amphibian communities of Vancine et al. 2018 [30] (S1 File). We chose to use this data set because: i) it compiles occurrence data for species that co-occur at the same place and time (study sites) distributed along the entire extension of the Atlantic Forest, thus reflecting real local communities of the region; ii) it comprises a large number of study sites (1,163), species (528) and specimen records (17,169); and iii) the data were already accurately compiled and revised. We initially prepared the data by removing all localities with missing or inaccurate geographic coordinates and those with a record of only a single anuran species. Then we calculated the observed proportion of direct developing species in each of the communities. However, as species occurrence and distribution can influence the average values of traits within communities [31], we controlled the effect of species composition on the proportion of direct developing species in the communities using null models, as proposed by Pillar and Duarte 2010 [32] and Peres-Neto et al. 2017 [33]. For this, we created a matrix containing the development type for each species present in the communities (**D matrix**). We then calculated the observed proportion of direct developing species in each community. Next, we generated a set of 999 null proportions through **D matrix** randomization and calculated the mean and standard deviation of these proportions. Finally, based on the standardized effect size metrics, we used the observed proportions and the means and standard deviations of the null proportions to calculate the proportion of direct developing species free from the composition effect for each of the communities. In total, our analyzed database comprised a comprehensive collection of 766 communities distributed along the extension of the Atlantic Forest (Fig 2).

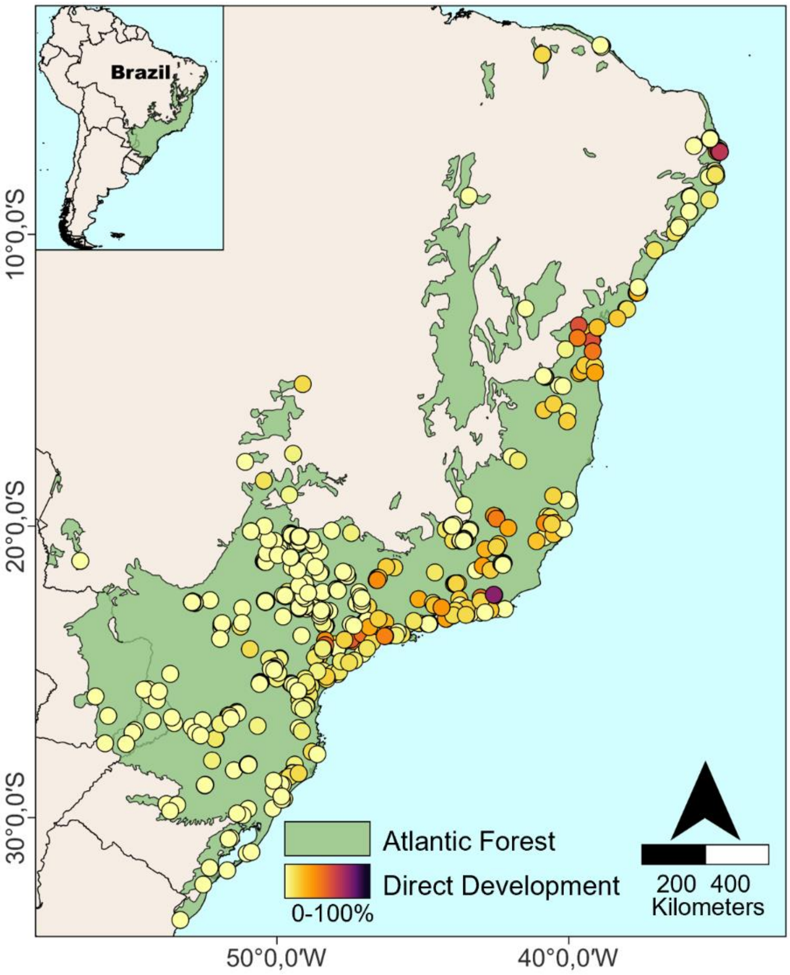

Fig 2. Distribution of the 766 analyzed Atlantic Forest anuran communities. The color gradient represents the observed proportion of direct developing anurans in the evaluated communities (points). Base layer sources: South America shape file retrieved from the Database of Global Administrative Areas (GADM) under an open license (CC-BY): https://gadm.org/license.html; Atlantic Forest limits reprinted from Muylaert et al. 2018 [34] under a CC BY license, with permission from Muylaert (GNU General Public License, https://github.com/LEEClab/ATLANTIC-limits/blob/master/LICENSE); communities (points) distributions were mapped based on records retrieved from Vancine et al. 2018 [30]. Modified with permission from Vancine et al. 2018 [30].

Bioclimatic and topographic variables

To investigate the relationship among biotic and abiotic factors and the proportion of direct-developing anuran species in Atlantic Forest communities, we gathered bioclimatic and topographic data for each of the previously selected communities, utilizing their geographic coordinates. We downloaded the 19 bioclimatic variables from WorldClim 2.1 (https://www.worldclim.org/data/worldclim21.html) [35, 36] and potential evapotranspiration (ET0) from Global Aridity Index and Potential Evapotranspiration Climate Database (https://csidotinfo.wordpress.com/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v3/) [37]. We considered terrain slope as the topographic variable, which represents the gradient of change in terrain elevation and is related to water accumulation and the direction and velocity of water flow [38]. Thus, slope reflects important aspects of terrain topography that can favor or hinder oviposition and survival of anuran offspring in the environment, such as waterbody availability and water flow velocity. This measure was downloaded from the EarthEnv database (www.earthenv.org) [38]. After downloading the data, we cropped all the rasters to match the extent of the Atlantic Forest boundaries [34], to obtain the bioclimatic and topographic values for each selected community. All rasters were downloaded at a resolution of 30 arc-seg (approximately 1km at the equator).

To reduce the number of abiotic variables in our final model, we initially fitted two linear models using the proportion of direct development species in each community as the response variable and abiotic variables (temperature and precipitation) as predictors. We then selected models based on the Akaike information criterion (AIC) [39]. The AIC ranks a given set of distinct candidate models based on their respective goodness-of-fit to data and the associated model complexity, reflecting the amount of information loss. Consequently, models with lower AIC values are deemed the most appropriate, representing an optimized balance between accurate data fitting and model simplicity [39]. We used stats and MuMIn packages of the R environment [40, 41] to perform the fitting and selection of models. After model selection, and due to the importance of these variables to the occurrence and distribution of anurans [42–45] (S2 File), we opted to use the following variables in our model: temperature seasonality (BIO4) – representing temperature;

annual precipitation (BIO12) – representing precipitation; potential evapotranspiration – representing humidity; and terrain slope – representing topography.

Phylogenetic composition

To consider the evolutionary history of the assemblages and to determine its role in the occurrence of direct developing species in Atlantic Forest anuran communities, we opted to incorporate phylogenetic composition in our final model. To do this, we created a phylogenetic tree of our species pool (subtree) using as a base the consensus phylogenetic hypothesis proposed by Jetz and Pyron 2018 [46]. We used the geiger package [47] to prune and check the correspondence between the species pool of our data set and the consensus phylogenetic hypothesis and identified the absence of eight species, also referred to as phylogenetically uncertain taxa (PUTs), namely: *Chiasmocleis lacrimae; Eleutherodactylus bilineatus; Boana cambui, Phrynomedusa dryade; Phyllomedusa rustica; Proceratophrys mantiqueira; Scinax melanodactylus;* and *Trachycephalus typhonius.* We included these PUTs in the subtree by using information from the literature to define the most derived consensus clade (MDCC), which represents the most basal node containing the closest living relative [for more details see 48]. We added the PUTs to our subtree (S1 Appendix) using PAM v0.9 software [48]. We then used a principal coordinates of phylogenetic structure (PCPS) analysis, a method based on a principal coordinates analysis (PCoA) of a matrix containing phylogeny-weighted species composition (**P** matrix), which produces a series of eigenvectors that describe orthogonal gradients of phylogenetic structure [49, 50]. Whereas the first PCPS eigenvector (with higher eigenvalues) captures deeper relationships in the phylogeny (basal nodes of the phylogenetic tree), subsequent PCPS eigenvectors describe the relationships between more recent lineages (terminal nodes) [51]. We used the PCPS package [52] in the R environment to obtain phylogenetic composition [47].

Functional diversity

To calculate FD, we initially compiled information about reproductive and morphological traits using data sets, articles and books to create a database containing the following seven functional traits: i) oviposition type (two categories: aquatic or terrestrial); ii) development type (two categories: larval or direct); iii) juvenile habitat (three categories: terrestrial, aquatic, or semiterrestrial – the last for those that inhabit and occupy both environments); iv) oviposition site (seven categories: eggs directly into water or submersed substrate; eggs in bubble nests on still water; eggs in foam nests; eggs embedded in back of aquatic female; eggs on ground, rocks or in burrows; arboreal eggs attached on plants; or eggs carried by terrestrial adults); v) body length; vi) head width; and vii) tibia length (S3 File). We used mean values for morphological traits whenever they were accessible in the literature, but in cases where only maximum values were available, those were considered. We chose these traits because they can be related to resource use complementarity, reproductive niche differentiation, and habitat use [53, 54], and thus are able to indicate possible effects of species co-occurrence and interspecific competition.

Despite the effort, we were not able to collect information about head width for 139 species and tibia length for 146 species. Therefore, for species with missing data, we inferred these traits through a maximum likelihood approach using the phylogenetic tree and the Rphylopars package [55]. This approach of trait inference assumes that the traits are correlated with each other, and with phylogenetic relationships among species [55, 56]. We also evaluated possible differences in the analyses that excluded traits associated with direct development, since the use of these traits could indicate a circular relationship with the proportion of direct developing species in communities. After finding no differences, we decided to retain these traits in our analysis. After creating the trait matrix, we performed a phylogenetic eigenvector regression (PVR) using the daee package [57] to control the effects of phylogenetic autocorrelation on functional traits. PVR is based on calculating a phylogenetic distance matrix followed by performing a PCoA, which produces a series of orthogonal eigenvectors that are independent of phylogenetic structure [58].

Finally, to reduce the effect of species number on functional diversity in the Atlantic Forest amphibian communities and to allow comparisons of communities with different richness values, we calculated the standardized effect size of functional diversity (SES.FD) [59]. These metrics are based on null model analyses and allow the removal of possible biases related to species richness when considering both observed values and values generated by null models and can also reveal phylogenetic or functional patterns of community structure [59]. In this case, while communities structured by biotic factors, such as competition and predation, will present functional overdispersion (identified by positive values of SES.FD), communities strongly influenced by abiotic factors, such as environmental filters, will present functional clustering (identified by negative values of SES.FD) [60–62].

To calculate SES.FD we generated a distance matrix based on the first 283 phylogenetic eigenvectors (which contained 95% of data variation) previously obtained from the PVR analysis, which were later transformed into a dendrogram using the stats package [41]. Then, based on the dendrogram, we calculated the observed functional diversity of Petchey and Gaston 2002 [25, 63], a metric that is derived from the phylogenetic diversity of Faith [23] and is based on the sum of branch lengths of a functional dendrogram. To calculate SES.FD we used as the null model the permutation of the species on the terminal nodes of the dendrogram (taxa.labels), 999 randomizations and the picante package [64].

Data analyses

To evaluate the relationships among biotic and abiotic variables and the proportion of direct developing species in Atlantic Forest anuran communities, as proposed in Fig 1, we used SEM by piecewise [65]. The use of SEM models enables us to investigate and confirm direct and indirect causal relationships, proposed from a conceptual model, which is generated a priori based on specific knowledge of the studied system, while piecewise allows us to incorporate random effects and autocorrelation structures in the models [65, 66]. We used the first PCPS eigenvector (PCPS 1) and the standardized effect size of functional diversity (SES.FD) as indicative of biotic factors. We chose these metrics because they allow us to investigate the effect of evolutionary history and aspects related to species co-occurrence. For the abiotic factors, we used temperature seasonality (BIO4) (as an indicator of temperature), annual precipitation (BIO12) (as an indicator of precipitation), potential evapotranspiration (ET0) (as an indicator of air humidity), and slope (as an indicator of topography).

Prior to fitting the SEM model, we tested and verified the absence of spatial autocorrelation in the data. To do this, we constructed generalized least squares models (GLS) containing the abiotic and biotic variables, and the proportion of direct developing species (S4 File) with exponential autocorrelation structure using the geographic coordinates of each community (latitude and longitude) using the nlme package [67]. Finally, we used these GLS models to generate our final SEM model through the piecewiseSEM package [65]. We considered SEM model validity through statistical significance ($p > 0.05$). All variables were previously standardized, and the analyses were performed in R [41].

Results

Our full dataset comprised 464 species of 19 families distributed among 766 anuran communities along the full extension of the Atlantic Forest, with species richness ranging from 2 to 49 species per community (mean = 13.48, SD = 9.17). Just over 10% (49) of the recorded species had a reproductive mode with direct development, and they were concentrated in a few lineages (Fig 3A, see more detailed in S2 Appendix). About 31% (237) of the evaluated communities contained species with direct development, with the others being exclusively composed of species with larval development. The proportion of direct-developing anurans in the communities ranged from 0 to 100% (mean = 4.32%, SD = 9.23), with a maximum richness of 10 species with direct development within a community. Communities with higher proportions of direct developing species were found spatially clustered in the southern Atlantic Forest and penetrating some areas in the northern Atlantic Forest (Fig 2).

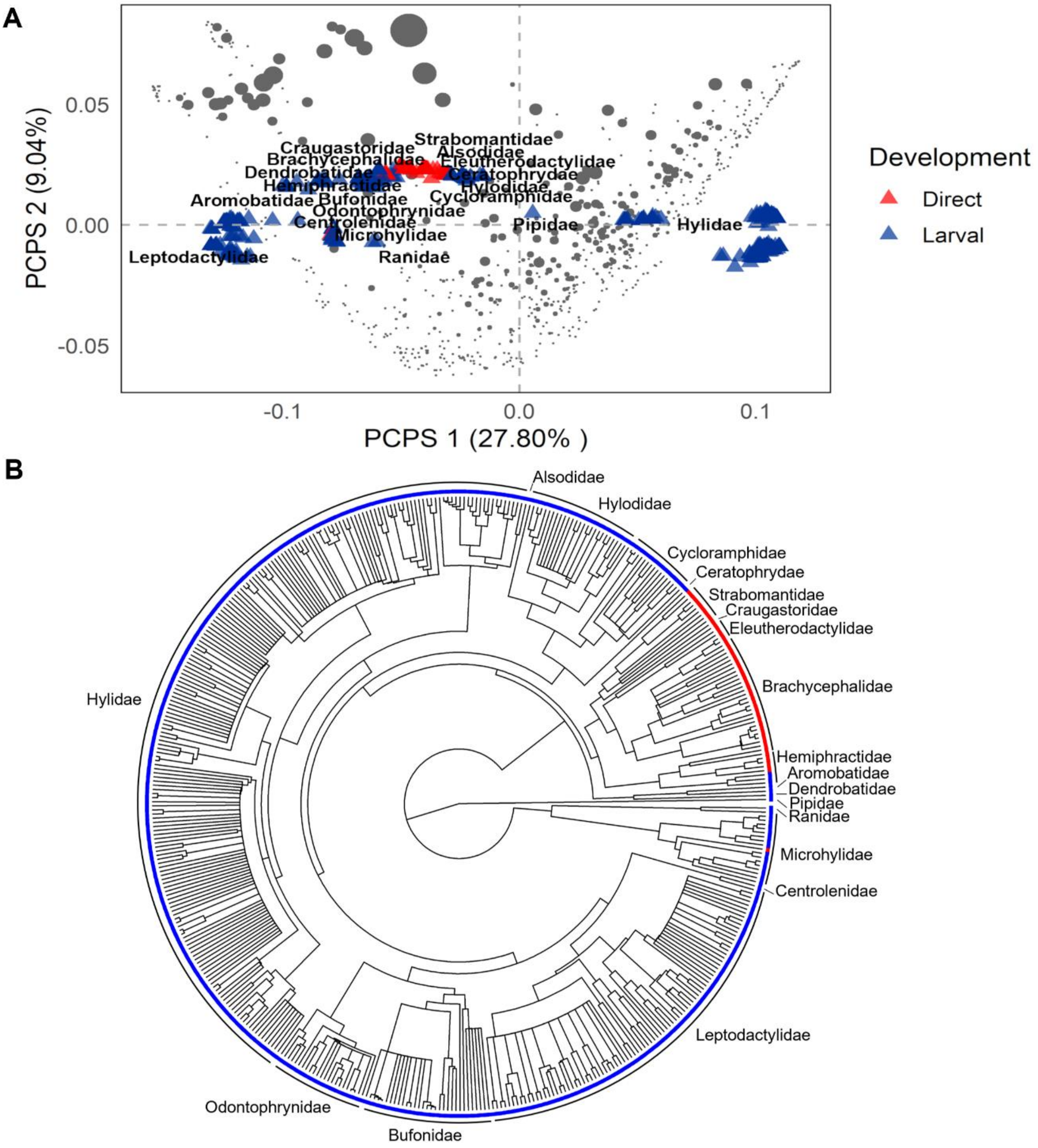

Fig 3. Direct development and Atlantic Forest anurans (A) Phylogenetic distribution of direct development in 464 Atlantic Forest anurans. Families outlined in blue comprise species with biphasic development, while families highlighted in red encompass species with direct development. Species relationships were based on the consensus phylogenetic tree of Jetz and Pyron 2018 [46]. For a more detailed version with species names, see S2 Appendix. (B) Scatter plot of PCPS eigenvectors 1 and 2 generated for anurans occurring in Atlantic Forest communities. Gray circle size indicates the proportion of direct developing species in the communities, while red and blue triangles represent direct development larval development, respectively.

Together the first two PCPS eigenvectors captured 36.84% of the total variation in the phylogenetic composition data. Eigenvector 1 split communities that were formed by hylids with lower proportions of direct developing anurans from those formed by aquatic and terrestrial species (other lineages) with higher proportions of direct developing species. In turn, PCPS 2 was positively related to communities formed by terrestrial species with higher proportions of direct developing species and negatively related to communities formed by species with aquatic reproductive modes (Leptodactylidae, Microhylidae and Ranidae, Fig 3B).

Our model, which correlates the selected climatic and topographic variables, phylogenetic composition, and functional diversity with the proportion of direct-developing species in Atlantic Forest anuran communities, explained 36% of the variation in the data (Fischer's $C_2 = 2.635$, $p = 0.268$, Fig 4, and S5 File). Potential evapotranspiration was the principal factor explaining the proportion of direct developing species, being negatively related ($r = -0.451$), followed by temperature seasonality with a negative effect ($r = -0.305$) and functional diversity with a positive effect ($r = 0.231$). Only annual precipitation had no direct effect on the proportion of direct developing anurans; however, it had a small effect on functional diversity. Also, climate and topography together explained 17% of the variation in phylogenetic composition and 13% of the variation in functional diversity (SES.FD) (Fig 4, and S5 File).

The communities with the highest proportions of direct developing anurans were distributed in regions with low to moderate temperature seasonality, low potential evapotranspiration and steeply sloping topography (see Fig S1 in S3 Appendix). Although we could not find any significant pattern of functional structural in the vast majority of the studied communities, southern Atlantic Forest communities showed negative values of SES.FD, indicating functionally similar species (functional clustering; see Fig S2 in S3 Appendix). Conversely, a few communities in the northern Atlantic Forest presented positive values of SES.FD, which suggests that these communities are composed of functionally distinct species (functional overdispersion) (Fig S2 in S3 Appendix).

Discussion

Direct development in Atlantic Forest anuran communities

Atlantic Forest anuran communities are composed of a variety of species with distinct evolutionary histories, physiological requirements, and reproductive strategies. The analyzed species pool included about 65% of the 719 anuran species currently known for the Atlantic Forest [20]. Our results showed that most of the communities are composed of species with larval development, which is considered ancestral and phylogenetically predominant among amphibians [1, 4, 68]. Ten-percent of the anuran species considered in the present study have direct development as a reproductive strategy, whereas estimates at the global level indicate about 25% [69]. At least a third of the described species in the Neotropical region have direct development, with Central American forests being the main refuge of these species, followed by the Atlantic Forest [4, 70, 71]. Although direct development is widespread throughout the phylogeny of amphibians and has evolved multiple times in different lineages [4], in the Atlantic Forest this reproductive strategy is concentrated in certain families and genera, such as the clade Terrarana and some species of the family Hemiphractidae [19, 72].

The clade Terrarana is a species complex, formed by four families of direct developing anurans (Brachycephalidae, Craugastoridae, Eleutherodactylidae, and Strabomantidae), distributed throughout the New World (North, Central, and South America and West Indies) [72]. It emerged in South America during the Cenozoic and has since dispersed and radiated to the other regions [72, 73]. In addition to terrarans and some hemiphractids, the phylogenetic tree of anurans of the Atlantic Forest reveals the presence of another clade with a single species representing direct development (*Myersiella microps*). The finding that almost all direct developers of the Atlantic Forest belong to only one clade supports the idea that South America served as a center of origin for this group of species. It also supports the idea that past environmental conditions of the coastal portion of the Atlantic Forest restricted the dispersal and occurrence of certain lineages to a suitable ecological niche [7, 73, 74], such as the case for Brachycephalidae. The family Brachycephalidae, represented by the genera *Brachycephalus* and *Ischnocnema,* is the most represented lineage of direct developers in the Atlantic Forest. It is associated with montane forests, with a distribution restricted mainly to southern and southeastern portions of the Atlantic Forest [72,75, 76]. However, the present results indicated that the proportion of direct developers in the communities is not just a mere reflection of the center of origin of these few clades in the Atlantic Forest, but is also a result of selective forces, such those due to biotic and abiotic factors.

Biotic factors and direct development in Atlantic Forest anuran communities

The effect of biotic factors on the evolution of direct development has never been effectively evaluated at the community scale, only by species-specific experiments. In this way, when functional diversity was used as a proxy of co-occurrence mechanisms, the model showed a significant positive relationship between this metric and the proportion of direct developing species in Atlantic Forest anuran communities. Thus, our results indicated that communities with higher functional diversity (and, therefore, increased likelihood of all kinds of biotic interactions such as competition and predation) were formed by a higher proportion of direct developing species, suggesting that direct development evolved as an alternative to minimize and/or avoid biotic pressures, as the main evolutionary hypotheses proposed [10, 11, 77]. Furthermore, a scenario can be envisioned in which even without these interactions, the evolution of alternative reproductive modes by pure neutral mechanisms can be favored by enhanced functional diversity of other functional traits. In this context, when species arrive in new environments, those with more specialized reproductive modes that deviate from the classical aquatic reproductive modes, such as direct developers, will be able to occupy new niches [1, 68, 78], avoiding the inhibitions imposed by priority effects.

Patterns of phylogenetic and/or functional structure of communities can be identified at different scales, reflecting the action of distinct processes in their formation [79]. Paz et al. 2022 [62] found some communities in extreme environments of the Atlantic Forest to be functionally clustered , suggesting that environmental filters played a significant role in assembling them [28, 60, 62]. Communities that are strongly influenced by environmental conditions can be molded and structured by the selection of traits related to high competitive capacity of species [80]. The structural model developed here aimed to provide the best alternative to assessing how distinct factors influenced community structure. However, functional clustering or overdispersion patterns were not detected in the majority of the studied anuran communities. Consequently, our results, at the community scale, indicated that stochastic processes were probably more critical for community assembly [28, 81]. Nevertheless, it is important to point out that only a few traits that could be assessed were explored. Therefore, the perceived absence of a significant pattern of functional structure in most communities may in fact be a consequence of stochastic processes, as mentioned above, but also a result of other aspects not explored here since results can vary according to the selected functional traits [82]. Some examples of other traits are those related to movement, reproduction, and habitat use/selection, such as migration and dispersion movements, sexual dimorphism and number of eggs or offspring, and habitat preference, respectively [53].

Abiotic factors and direct development in Atlantic Forest anuran communities

As expected, we verified that the proportion of direct developing species in Atlantic Forest anuran communities is related to both biotic factors, namely phylogenetic composition and functional diversity, and abiotic factors, namely climate and topography. The different responses of amphibians to climatic conditions are known to be mediated by their reproductive modes [83]. Reproductive specialization can be considered not only a result of the phylogenetic relationships among families but also as a response to the environmental conditions of the region in which the species evolved [1, 3, 8]. In this sense, Lourenço-de-Moraes et al. 2020 [84], showed that the high richness and endemism rates of amphibians in the Atlantic Forest can be explained by climatic conditions, such as annual mean temperature and annual precipitation. Similarly, environmental factors, such as climate and environmental structure, can also define and delimit the occurrence and proportion of amphibians with terrestrial reproduction in communities [4 8, 9].

Historically, the climatic seasonality of the coastal region of the Atlantic Forest delimited and restricted the occurrence of species with specialized reproductive modes to this portion that is climatically more stable [7]. Amphibians from the tropics tend to possess a narrower amplitude in the temperature dimension of their niche due to low-temperature seasonality in the region [43]. In this context, the negative relationship found between the proportion of direct developing species in Atlantic Forest anuran communities and temperature seasonality reinforces the idea that climatic conditions must have influenced the evolution of direct development [4]. It is also important to highlight that montane environments in the coastal region have not only provided suitable conditions for the occurrence of species with distinct life histories, but also currently condense the largest forest remnants of the Atlantic Forest [7, 85]. Therefore, the montane forests function as important refuges for the conservation of amphibian functional diversity, since species with specialized reproductive modes, such as direct development, are highly susceptible to environmental changes [21, 86–88].

Although terrestrial direct developers show high independence from water bodies, they remain dependent on humidity in the environment [77]. In the same way that climatic oscillations restricted the expansion of the distributions of species with specialized reproductive modes, the high humidity level of the Atlantic Forest favored the high phylogenetic and reproductive diversity found in the region [7, 42]. The importance of annual precipitation to the richness, occurrence, and distribution of anurans has already been demonstrated by several studies undertaken in different regions [89–92]. Ochoa-Ochoa et al. 2019 [92] found that amphibian functional diversity is influenced by climate, with humid mountain regions being the most diverse due to high annual precipitation and low precipitation seasonality. Here, we did not find a direct effect of annual precipitation on the proportion of direct developing species in the studied Atlantic Forest anuran communities, although we observed a negative relationship between this proportion and potential evapotranspiration. Nonetheless, these results do not necessarily reject the importance of these variables to these anurans, since we verified an indirect effect of annual precipitation on the occurrence of direct developing species mediated by functional diversity. Similarly, when considering spatial autocorrelation, Gimenez and Vasconcelos 2022 [93] also did not find a correlation between the diversity of terrestrial reproductive modes (non-aquatic eggs) and annual precipitation and evapotranspiration in the Atlantic Forest but verified that these reproductive modes are related to the presence of ombrophilous forests (evergreen). Thus, the water and humidity requirements of anurans, especially terrestrial breeders (including direct developers), might be supplied by specific conditions of humid microhabitats that are only perceived at finer, and not larger, spatial scales. Another factor that is also considered to promote reproductive diversification and specialization is the complex topography of the Atlantic Forest [3]. High altitude regions are known to possess higher topographic heterogeneity, which directly influences biodiversity [94, 95]. Among the different topographic measures, slope is related to the direction and velocity of water flow, as well as water accumulation, which exercises distinct pressures on organisms [38]. In environments with high slopes, the velocity of water flow tends to be more accentuated, which may affect the different organisms that occupy these environments and increase the mortality of non-adapted species [96]. In this sense, some studies have mentioned terrain topography as a potential driving force in the evolution of terrestrial reproduction and direct development. Liedtke et al. 2017 [9] verified a strong relationship between high slope environments and the occurrence of terrestrial breeders (including those with direct development), whereas Portik et al. 2016 [97] did not detect co-evolutionary relationships between terrestrial oviposition sites and lotic environments. Whereas our results do not effectively confirm this hypothesis, they do suggest it, since we observed a higher proportion of direct developing anurans in localities with greater slopes.

Contributions, perspectives and future directions of knowledge of anuran direct development

Despite the important relationships observed among the climatic conditions, topography, biotic factors, and the proportion of direct development species in the studied Atlantic Forest anuran communities, a significant part of our data remained unexplained. In this context, other factors that we did not evaluate here could also be related to the structuring of these communities, such as micro-environmental and biogeographical factors. As noted by Lion et al. 2019 [45], environmental variables can act in diverse ways on the occurrence and proportion of terrestrial-breeding amphibians in communities depending on the biogeographic region that is considered. Since Lutz 1948 [11] spotlighted the probable factors related to the evolution of direct development in amphibians, several other authors have been investigating and testing these hypotheses but focusing on species-specific experiments, and/or factors independently. Here, we are proposing an integrated way to explore the relationships among distinct factors (biotic and abiotic) and direct development in anurans. We recognize that our model does not encompass other different factors and sources of variation. Nevertheless, it does indeed provide a meaningful framework for understanding the important mechanisms influencing real biological communities. Thus, future analyses comparing the relationships among abiotic and biotic factors and direct development in anurans performed at different scales and in other regions, and thus encompassing distinct species pools, more clades and greater climatic and environmental variability, will be able to show distinct patterns among these relationships and help to amplify knowledge about this specialized reproductive mode.

Direct developers have particular life history and ecological traits, such as an association with high-altitude environments, restricted distributions, and smaller clutches with larger eggs, traits that can be associated with extinction risk [5, 71, 98–101]. As verified here, the occurrence of direct developing species of Atlantic Forest anuran communities was mostly associated with temperature seasonality and potential evapotranspiration, hence, future climatic changes can impoverish these communities, especially by the loss of this group of species. Additionally, the use of information about life-history traits, such as the developmental mode of anurans, can be useful to indicate priority areas for conservation efforts [102]. In this sense, we also highlight the importance of conservation plans and actions specific to these species, as well as to high-altitude forests, which are true refuges for direct developing anurans, to ensure the maintenance and conservation of different anuran evolutionary and life histories. Moreover, the observed relationships among abiotic and biotic variables and the proportion of direct developing anurans can also help to reinforce the hypothesis that multiple selective forces guided the evolution of this reproductive mode. Finally, we emphasize the importance of our results as one of the few studies that effectively aimed to relate anuran direct development with distinct factors on a wide spatial scale, independently of specific lineages and families, and involving many evaluated communities.

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Supporting information

S1 File. Atlantic Forest anuran communities. Subset of 766 Atlantic Forest anuran communities based on Vancine et al. 2018 [30] data.[1]

S2 File. Model selection used for temperature and precipitation variable selection.

S3 File. Dataset of life-history traits of Atlantic Forest anurans.

S4 File. References of dataset of life-history traits of Atlantic Forest anurans.

S5 File. Data of Atlantic Forest anuran communities. Biotic and abiotic factors, and the proportion of direct development species of 766 Atlantic Forest anuran communities. *Standardized data.[1]

S6 File. Result of piecewiseSEM model. Direct and indirect effects of predictor variables on proportion of direct developing species of Atlantic Forest anuran communities.

S1 Appendix. Phylogenetic tree of the Atlantic Forest anurans.[1]

S2 Appendix. Phylogenetic distribution of the development mode of 464 Atlantic Forest anurans.[1]

S3 Appendix. Distribution of Atlantic Forest anuran communities and environmental variables.

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[1] Arquivos disponíveis na página do artigo publicado: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0291644

S2 File – Model selection used for temperature and precipitation variable selection.

Model selection: Temperature variables

Components	GL	logLik	AICc	delta	weight
1,2,4,6,7	7	-1006.10	2026.35	0	0.15
1,2,4,6,7,9	8	-1005.42	2027.04	0.69	0.11
2,3,4,5,6,7	8	-1005.46	2027.11	0.77	0.10
1,2,4,6,7,8	8	-1005.50	2027.20	0.85	0.10
1,2,3,4,6,7	8	-1005.61	2027.40	1.06	0.09
1,2,4,5,6,7	8	-1005.62	2027.43	1.08	0.09
2,3,4,6,7	7	-1006.64	2027.43	1.08	0.09
2,3,4,6,7,8	8	-1005.78	2027.76	1.41	0.08
1,2,3,4,6,7,8	9	-1004.93	2028.10	1.75	0.06
1,2,3,4,5,6,7	9	-1004.93	2028.11	1.76	0.06
1,2,3,4,6,7,9	9	-1004.94	2028.13	1.78	0.06

Term codes

BIO1	BIO10	BIO11	BIO2	BIO3	BIO4	BIO7	BIO8	BIO9
1	2	3	4	5	6	7	8	9

Model-averaged coefficients

(full average)

	Estimate	S.E	Adj. Error	z value	Pr(>|z|)
Intercept	1.76E-15	3.26E-02	3.26E-02	0.000	1.000
BIO1	**-1.05E+00**	**8.87E-01**	**8.87E-01**	**1.181**	**0.237**
BIO10	**1.76E+00**	**8.95E-01**	**8.96E-01**	**1.968**	**0.049**
BIO2	**-1.07E+00**	**3.38E-01**	**3.38E-01**	**3.167**	**0.001**
BIO4	**-2.04E+00**	**7.17E-01**	**7.17E-01**	**2.841**	**0.004**
BIO7	**1.30E+00**	**3.97E-01**	**3.97E-01**	**3.282**	**0.001**
BIO9	2.20E-02	6.69E-02	6.69E-02	0.329	0.742
BIO11	-1.47E+00	1.86E+00	1.86E+00	0.791	0.429
BIO3	6.79E-02	1.60E-01	1.60E-01	0.424	0.671
BIO8	-1.72E-02	4.31E-02	4.31E-02	0.400	0.689

(conditional average)

	Estimate	S.E	Adj. Error	z value	Pr(>|z|)
Intercept	1.77E-15	3.26E-02	3.26E-02	0	1
BIO1	**-1.43E+00**	**7.24E-01**	**7.25E-01**	**1.978**	**0.047**
BIO10	**1.76E+00**	**8.95E-01**	**8.96E-01**	**1.968**	**0.049**
BIO2	**-1.07E+00**	**3.38E-01**	**3.38E-01**	**3.167**	**0.001**
BIO4	**-2.04E+00**	**7.17E-01**	**7.17E-01**	**2.841**	**0.004**
BIO7	**1.30E+00**	**3.97E-01**	**3.97E-01**	**3.282**	**0.001**
BIO9	1.28E-01	1.11E-01	1.12E-01	1.150	0.250
BIO11	-2.68E+00	1.75E+00	1.75E+00	1.529	0.126
BIO3	2.64E-01	2.18E-01	2.18E-01	1.209	0.226
BIO8	-7.21E-02	6.17E-02	6.18E-02	1.167	0.243

Model selection: Precipitation variables

Components	GL	logLik	AICc	delta	weight
1,2,3,4,6,7,8	9	-1028.07	2074.37	0	0.30
1,2,3,4,6,7	8	-1029.11	2074.42	0.05	0.30
2,3,4,6,7	7	-1030.29	2074.72	0.35	0.25
2,3,4,5,6,7	8	-1029.82	2075.83	1.46	0.15

Term codes

BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
1	2	3	4	5	6	7	8

Model-averaged coefficients

(full average)

	Estimate	S.E	Adj. Error	z value	Pr(>|z|)
Intercept	-1.46E-15	3.36E-02	3.37E-02	0	1
BIO12	**1.79E-01**	**2.01E-01**	**2.06E-01**	**0.891**	**0.372**
BIO13	**4.38E-01**	**1.79E-01**	**1.79E-01**	**2.440**	**0.014**
BIO14	**1.37E+00**	**3.16E-01**	**3.17E-01**	**4.326**	**1.52E-05**
BIO15	**-9.59E-01**	**2.09E-01**	**2.09E-01**	**4.575**	**4.80E-06**
BIO17	**-2.26E+00**	**3.43E-01**	**3.43E-01**	**6.570**	**<2E-16**
BIO18	**-1.88E-01**	**7.44E-02**	**7.45E-02**	**2.533**	**0.011**
BIO19	**-1.10E-01**	**7.65E-02**	**7.66E-02**	**1.438**	**0.150**
BIO16	2.28E-01	2.37E-01	2.37E-01	0.960	0.337

(conditional average)

	Estimate	S.E	Adj. Error	z value	Pr(>|z|)
Intercept	-1.46E-15	3.36E-02	3.37E-02	0	1
BIO12	**2.99E-01**	**1.78E-01**	**1.78E-01**	**1.682**	**0.092**
BIO13	**4.38E-01**	**1.76E-01**	**1.80E-01**	**2.440**	**0.014**
BIO14	**1.37E+00**	**3.16E-01**	**3.17E-01**	**4.326**	**1.52E-05**
BIO15	**-9.59E-01**	**2.09E-01**	**2.09E-01**	**4.575**	**4.80E-06**
BIO17	**-2.25E+00**	**3.43E-01**	**3.43E-01**	**6.570**	**<2E.16**
BIO18	**-1.88E-01**	**7.44E-02**	**7.45E-02**	**2.533**	**0.011**
BIO19	**-1.10E-01**	**7.65E-02**	**7.66E-02**	**1.438**	**0.150**
BIO16	2.28E-01	2.37E-01	2.37E-01	0.960	0.337

S3 File - Dataset of life-history traits of Atlantic Forest anurans. OT – oviposition type (0 – aquatic; 1 – terrestrial); Dev – development type (0 – aquatic; 1 – terrestrial); Aquatic - juvenile habitat aquatic; Terrestrial - juvenile habitat terrestrial; Semiterrestrial - juvenile habitat semiterrestrial; S1 – eggs directly into water or submersed substrate; S2 – eggs in bubble nests on still water; S3 – eggs in foam nests; S4 – eggs embedded in back of aquatic female; S5 – eggs on ground, rocks or in burrows; S6 – arboreal eggs attached on plants; S7 – eggs carried by terrestrial adults; BL – body length; HW - head width; TL – tibia length; Obs – observation; Ref – reference.

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Adelophryne baturitensis	1	1	0	1	0	0	0	0	0	1	0	0	16.3	5.27	5.03	Head width inferred	1,2,3,27
Adelophryne pachydactyla	1	1	0	1	0	0	0	0	0	1	0	0	11.1	4.19	4.88	Head width inferred	1,2,3,27
Adenomera ajurauna	1	0	0	1	0	0	0	1	0	0	0	0	19	7.09	8.15		1,2,3,5
Adenomera andreae	1	0	0	1	0	0	0	1	0	0	0	0	28	9.91	12.82		1,2,3,29
Adenomera araucaria	1	0	0	1	0	0	0	1	0	0	0	0	18.5	6.02	8.17		1,2,3,28
Adenomera bokermanni	1	0	0	1	0	0	0	1	0	0	0	0	23	7.82	10.12		1,2,3,29
Adenomera diptyx	1	0	0	1	0	0	0	1	0	0	0	0	24	8.2	10.94	Tibia length inferred	1,2,3
Adenomera engelsi	1	0	0	1	0	0	0	1	0	0	0	0	22	7.37	10.66		1,2,3,6
Adenomera hylaedactyla	1	0	0	1	0	0	0	1	0	0	0	0	30	10.29	13.38		1,2,3,29
Adenomera marmorata	1	0	0	1	0	0	0	1	0	0	0	0	25	8.4	11.05		1,2,3,29
Adenomera nana	1	0	0	1	0	0	0	1	0	0	0	0	18	5.91	8.7		1,2,3,117
Adenomera thomei	1	0	0	1	0	0	0	1	0	0	0	0	23.5	6.07	7.84		1,2,3,30
Allobates goianus	1	0	1	0	0	0	0	0	0	1	0	0	15.83	5.17	7.66	Head width and tibia length inferred	1,2,3
Allobates olfersioides	1	0	1	0	0	0	0	0	0	1	0	0	16.9	5.1	7.5		1,2,3,31
Ameerega picta	1	0	1	0	0	0	0	0	0	1	0	0	24.4	6.55	10.62	Tibia length inferred	1,2,3
Aplastodiscus albofrenatus	0	0	1	0	0	1	0	0	0	0	0	0	41.6	12.97	19.26		1,2,3,4
Aplastodiscus albosignatus	0	0	1	0	0	1	0	0	0	0	0	0	52	13.28	21.58		1,2,3,4
Aplastodiscus arildae	0	0	1	0	0	1	0	0	0	0	0	0	41.6	12.6	18.7		1,2,3,4
Aplastodiscus cavicola	0	0	1	0	0	1	0	0	0	0	0	0	37.3	11.6	17.3		1,2,3,4
Aplastodiscus cochranae	0	0	1	0	0	1	0	0	0	0	0	0	50.3	16.65	20.69		1,2,3,4
Aplastodiscus ehrhardti	0	0	1	0	0	1	0	0	0	0	0	0	39.1	10.38	17.27		1,2,3,4
Aplastodiscus eugenioi	0	0	1	0	0	1	0	0	0	0	0	0	39	13	19.8		1,2,3,4
Aplastodiscus flumineus	0	0	1	0	0	1	0	0	0	0	0	0	50.4	14.3	23.6		1,2,3,4
Aplastodiscus ibirapitanga	0	0	1	0	0	1	0	0	0	0	0	0	43.4	13.3	19.3		1,2,3,32
Aplastodiscus leucopygius	0	0	1	0	0	1	0	0	0	0	0	0	45.1	13.4	20.02	Head width and tibia length inferred	1,2,3
Aplastodiscus perviridis	0	0	1	0	0	1	0	0	0	0	0	0	46.1	14.97	18.88		1,2,3,4
Aplastodiscus sibilatus	0	0	1	0	0	1	0	0	0	0	0	0	33.6	10.4	15.9		1,2,3,4

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Aplastodiscus weygoldti	0	0	1	0	0	1	0	0	0	0	0	0	41.7	13.7	20.8		1,2,3,4
Arcovomer passarellii	0	0	1	0	0	1	0	0	0	0	0	0	25.6	6.38	9.51	Head width and tibia length inferred	1,2,3
Bahius bilineatus	1	1	0	1	0	0	0	0	0	1	0	0	25	9.08	12.2	Head width and tibia length inferred	1,2,3
Barycholos ternetzi	1	1	0	1	0	0	0	0	0	1	0	0	28.5	11.03	12.85	Head width and tibia length inferred	1,2,3
Boana albomarginata	0	0	1	0	0	1	0	0	0	0	0	0	62	21	30		1,2,3,4
Boana albopunctata	0	0	1	0	0	1	0	0	0	0	0	0	75	17.4	31.9		1,2,3,4
Boana atlantica	0	0	1	0	0	1	0	0	0	0	0	0	43.5	13.83	18.3		1,2,3,4
Boana bandeirantes	0	0	1	0	0	1	0	0	0	0	0	0	29.13	10.06	17.13		1,2,3,33
Boana bischoffi	0	0	1	0	0	1	0	0	0	0	0	0	69	19.24	30.9		1,2,3,4
Boana caingua	0	0	1	0	0	1	0	0	0	0	0	0	38	8.32	17.45		1,2,3,4
Boana caipora	0	0	1	0	0	1	0	0	0	0	0	0	44.3	11.8	17.3		1,2,3,4
Boana cambui	0	0	1	0	0	1	0	0	0	0	0	0	30.6	10.5	15.9		1,2,3,15
Boana crepitans	0	0	1	0	0	1	0	0	0	0	0	0	75	23	36		1,2,3,4
Boana curupi	0	0	1	0	0	1	0	0	0	0	0	0	41.95	13.65	21.35		1,2,3,34
Boana ericae	0	0	1	0	0	1	0	0	0	0	0	0	31.8	10.8	16.9		1,2,3,36
Boana exastis	0	0	1	0	0	1	0	0	0	0	0	0	99	30.2	50.1		1,2,3,4
Boana faber	0	0	1	0	0	1	0	0	0	0	0	0	104	40.48	58.13		1,2,3,4
Boana fasciata	0	0	1	0	0	1	0	0	0	0	0	0	35.4	11.39	20.07		1,2,3,37
Boana freicanecae	0	0	1	0	0	1	0	0	0	0	0	0	40	15.3	21.7		1,2,3,38
Boana guentheri	0	0	1	0	0	1	0	0	0	0	0	0	47	10.4	16.74		1,2,3,4
Boana jaguariaivensis	0	0	1	0	0	1	0	0	0	0	0	0	26.6	7.8	13.1		1,2,3,39
Boana joaquini	0	0	1	0	0	1	0	0	0	0	0	0	56.4	16.69	27.33		1,2,3,4
Boana latistriata	0	0	1	0	0	1	0	0	0	0	0	0	51.6	13.7	22		1,2,3,4
Boana leptolineata	0	0	1	0	0	1	0	0	0	0	0	0	39	8.6	15.2		1,2,3,4
Boana lundii	0	0	1	0	0	1	0	0	0	0	0	0	52.34	17.07	29.26	Tibia length inferred	1,2,3
Boana marginata	0	0	1	0	0	1	0	0	0	0	0	0	51.1	15.6	24.3		1,2,3,4
Boana multifasciata	0	0	1	0	0	1	0	0	0	0	0	0	50.2	15.7	29.2		1,2,3,40
Boana paranaiba	0	0	1	0	0	1	0	0	0	0	0	0	48.95	16.65	29.1		1,2,3,40
Boana pardalis	0	0	1	0	0	1	0	0	0	0	0	0	75	23.36	35.06		1,2,3,4
Boana poaju	0	0	1	0	0	1	0	0	0	0	0	0	45.6	12.3	19.5		1,2,3,4
Boana polytaenia	0	0	1	0	0	1	0	0	0	0	0	0	41.5	11.81	19.05		1,2,3,4
Boana pombali	0	0	1	0	0	1	0	0	0	0	0	0	65.7	19.2	30.2		1,2,3,4

Species	OT	Dev	Aquatic	Terrestrial	Semiterrestrial	S1	S2	S3	S4	S5	S6	S7	BL	HW	TL	Obs	Ref
Boana prasina	0	0	1	0	0	1	0	0	0	0	0	0	55	13.86	22.8		1,2,3,4
Boana pulchella	0	0	1	0	0	1	0	0	0	0	0	0	50	14.01	22.97		1,2,3,4
Boana punctata	0	0	1	0	0	1	0	0	0	0	0	0	41.7	12.5	18.9		1,2,3,4
Boana raniceps	0	0	1	0	0	1	0	0	0	0	0	0	82	22	40		1,2,3,4
Boana semiguttata	0	0	1	0	0	1	0	0	0	0	0	0	48	14.3	22.7		1,2,3,4
Boana semilineata	0	0	1	0	0	1	0	0	0	0	0	0	52	24.43	34.8		1,2,3,4
Boana stellae	0	0	1	0	0	1	0	0	0	0	0	0	56	15.17	24.64		1,2,3,4
Boana stenocephala	0	0	1	0	0	1	0	0	0	0	0	0	39	7.7	14		1,2,3,4
Bokermannohyla alvarengai	0	0	1	0	0	1	0	0	0	0	0	0	140.9	44.68	57.03	Head width and tibia length inferred	1,2,3
Bokermannohyla astartea	0	0	1	0	0	1	0	0	0	0	0	0	45	15.88	25.58		1,2,3,4
Bokermannohyla capra	0	0	1	0	0	1	0	0	0	0	0	0	64.1	19.63	28.2		1,2,3,41
Bokermannohyla caramaschii	0	0	1	0	0	1	0	0	0	0	0	0	70	22.47	32.56		1,2,3,4
Bokermannohyla carvalhoi	0	0	1	0	0	1	0	0	0	0	0	0	67	23	33		1,2,3,4
Bokermannohyla circumdata	0	0	1	0	0	1	0	0	0	0	0	0	71	21.6	30		1,2,3,4
Bokermannohyla hylax	0	0	1	0	0	1	0	0	0	0	0	0	64	20.4	29.8		1,2,3,4
Bokermannohyla ibitipoca	0	0	1	0	0	1	0	0	0	0	0	0	42.7	14.1	20		1,2,3,4
Bokermannohyla izecksohni	0	0	1	0	0	1	0	0	0	0	0	0	50.8	16.3	24.6		1,2,3,4
Bokermannohyla luctuosa	0	0	1	0	0	1	0	0	0	0	0	0	61.9	18.6	27.3		1,2,3,4
Bokermannohyla martinsi	0	0	1	0	0	1	0	0	0	0	0	0	64	21	28.66		1,2,3,4
Bokermannohyla nanuzae	0	0	1	0	0	1	0	0	0	0	0	0	44	20.5	20.5		1,2,3,4
Bokermannohyla oxente	0	0	1	0	0	1	0	0	0	0	0	0	47.15	15.1	21.6		1,2,3,4
Bokermannohyla saxicola	0	0	1	0	0	1	0	0	0	0	0	0	55	18.17	25.54	Head width and tibia length inferred	1,2,3
Brachycephalus alipioi	1	1	0	1	0	0	0	0	0	1	0	0	16.2	5.6	5.4		1,2,3,42
Brachycephalus didactylus	1	1	0	1	0	0	0	0	0	1	0	0	10.7	4.19	5.29	Head width and tibia length inferred	1,2,3
Brachycephalus ephippium	1	1	0	1	0	0	0	0	0	1	0	0	19.7	6.54	6.75	Head width and tibia length inferred	1,2,3
Brachycephalus garbeana	1	1	0	1	0	0	0	0	0	1	0	0	18.6	6.43	6.03		1,2,3,118
Brachycephalus hermogenesi	1	1	0	1	0	0	0	0	0	1	0	0	15	3.2	4.3		1,2,3, 43
Brachycephalus nodoterga	1	1	0	1	0	0	0	0	0	1	0	0	13.4	5.1	4.5		1,2,3,44
Brachycephalus pitanga	1	1	0	1	0	0	0	0	0	1	0	0	14	4.9	4.7		1,2,3,45
Ceratophrys aurita	0	0	1	0	0	1	0	0	0	0	0	0	149	48.45	58.37	Head width and tibia length inferred	1,2,3
Chiasmocleis alagoana	0	0	1	0	0	1	0	0	0	0	0	0	27.8	6.57	9.62		1,2,3,46
Chiasmocleis albopunctata	0	0	1	0	0	1	0	0	0	0	0	0	30.4	7	9		1,2,3,131

Species	OT	Dev	Aquatic	Terrestrial	Semiterrestrial	S1	S2	S3	S4	S5	S6	S7	BL	HW	TL	Obs	Ref
Chiasmocleis capixaba	0	0	1	0	0	1	0	0	0	0	0	0	20.2	5.37	6.7		1,2,3,47
Chiasmocleis crucis	0	0	1	0	0	1	0	0	0	0	0	0	20.2	6.1	8.6		1,2,3,48
Chiasmocleis lacrimae	0	0	1	0	0	1	0	0	0	0	0	0	24.4	6.52	8.31	Head width and tibia length inferred	1,2,3
Chiasmocleis leucosticta	0	0	1	0	0	0	1	0	0	0	0	0	23.6	6.22	9.42		1,2,3,47
Chiasmocleis mantiqueira	0	0	1	0	0	1	0	0	0	0	0	0	22.8	5.92	8.8		1,2,3,12
Chiasmocleis schubarti	0	0	1	0	0	1	0	0	0	0	0	0	34.5	7.57	10.77		1,2,3,47
Corythomantis greeningi	0	0	1	0	0	1	0	0	0	0	0	0	86.5	24.48	33.08	Head width and tibia length inferred	1,2,3
Crossodactylodes izecksohni	0	0	1	0	0	1	0	0	0	0	0	0	15	5.76	8.16	Head width and tibia length inferred	1,2,3
Crossodactylus caramaschii	0	0	1	0	0	1	0	0	0	0	0	0	27.2	8	13.05		1,2,3,49
Crossodactylus cyclospinus	0	0	1	0	0	1	0	0	0	0	0	0	24.5	8.23	12.96		1,2,3,50
Crossodactylus dantei	0	0	1	0	0	1	0	0	0	0	0	0	30	10.12	15.07	Head width and tibia length inferred	1,2,3
Crossodactylus dispar	0	0	1	0	0	1	0	0	0	0	0	0	33.8	12.1	17.08	Head width and tibia length inferred	1,2,3
Crossodactylus gaudichaudii	0	0	1	0	0	1	0	0	0	0	0	0	35.1	11.7	16.94	Head width and tibia length inferred	1,2,3
Crossodactylus schmidti	0	0	1	0	0	1	0	0	0	0	0	0	33.3	10.55	15.81	Head width and tibia length inferred	1,2,3
Crossodactylus trachystomus	0	0	1	0	0	1	0	0	0	0	0	0	25.8	8.7	13.47	Head width and tibia length inferred	1,2,3
Cycloramphus acangatan	1	0	0	1	0	0	0	0	0	1	0	0	48.1	17.72	13.42		1,2,3,51
Cycloramphus asper	1	0	0	0	1	0	0	0	0	1	0	0	46	19.32	20.7		1,2,3,52
Cycloramphus bolitoglossus	1	0	0	1	0	0	0	0	0	1	0	0	39.8	17.14	18.58	Head width and tibia length inferred	1,2,3
Cycloramphus boraceiensis	1	0	0	0	1	0	0	0	0	1	0	0	50.2	21.1	23.09		1,2,3,52
Cycloramphus carvalhoi	1	0	0	1	0	0	0	0	0	1	0	0	37	16.9	17.69	Head width and tibia length inferred	1,2,3
Cycloramphus eleutherodactylus	1	0	0	1	0	0	0	0	0	1	0	0	58.3	25.65	27.69		1,2,3,52
Cycloramphus fuliginosus	1	0	0	0	1	0	0	0	0	1	0	0	64.3	27.64	28.29		1,2,3,52
Cycloramphus izecksohni	1	0	0	0	1	0	0	0	0	1	0	0	34.9	14.5	17.3		1,2,3,53
Cycloramphus lithomimeticus	1	0	0	0	1	0	0	0	0	1	0	0	29.5	11.1	13.76		1,2,3,54
Cycloramphus lutzorum	1	0	0	0	1	0	0	0	0	1	0	0	58	24.65	26.97		1,2,3,52
Cycloramphus migueli	1	0	0	1	0	0	0	0	0	1	0	0	42.1	19.2	14		1,2,3,23
Cycloramphus mirandaribeiroi	1	0	0	0	1	0	0	0	0	1	0	0	68.6	29.84	33.95		1,2,3,52
Cycloramphus parvulus	1	0	0	1	0	0	0	0	0	1	0	0	29.6	14.62	14.98	Head width and tibia length inferred	1,2,3
Dendrophryniscus berthalutzae	0	0	1	0	0	1	0	0	0	0	0	0	24	9.88	10.23	Head width inferred	1,2,3
Dendrophryniscus brevipollicatus	0	0	1	0	0	1	0	0	0	0	0	0	25	10.09	10.25	Head width inferred	1,2,3,44
Dendrophryniscus carvalhoi	0	0	1	0	0	1	0	0	0	0	0	0	19	8.44	8.74	Head width inferred	1,2,3
Dendrophryniscus leucomystax	0	0	1	0	0	1	0	0	0	0	0	0	23	9.55	9.79	Head width and tibia length inferred	1,2,3

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Dendrophryniscus proboscideus	0	0	1	0	0	1	0	0	0	0	0	0	41	15.08	16.3	Head width and tibia length inferred	1,2,3
Dendropsophus anceps	0	0	1	0	0	1	0	0	0	0	0	0	42	14	22		1,2,3,4
Dendropsophus araguaya	0	0	1	0	0	1	0	0	0	0	0	0	20.5	6	9.6		1,2,3,35
Dendropsophus berthalutzae	1	0	1	0	0	0	0	0	0	0	1	0	24	7	9.79		1,2,3,4
Dendropsophus bipunctatus	0	0	1	0	0	1	0	0	0	0	0	0	30	23.43	8.5		1,2,3,4
Dendropsophus branneri	0	0	1	0	0	1	0	0	0	0	0	0	25	6.06	10		1,2,3,4
Dendropsophus cerradensis	0	0	1	0	0	1	0	0	0	0	0	0	19.3	6	9.3		1,2,3,35
Dendropsophus cruzi	0	0	1	0	0	1	0	0	0	0	0	0	25	6.07	10.7		1,2,3,55
Dendropsophus decipiens	1	0	1	0	0	0	0	0	0	0	1	0	21	7	10		1,2,3,4
Dendropsophus elegans	0	0	1	0	0	1	0	0	0	0	0	0	35.7	9.8	16.7		1,2,3,4
Dendropsophus elianeae	0	0	1	0	0	1	0	0	0	0	0	0	26	7.22	11.55		1,2,3,56
Dendropsophus giesleri	0	0	1	0	0	1	0	0	0	0	0	0	35.9	8.72	13.18		1,2,3,4
Dendropsophus haddadi	1	0	1	0	0	0	0	0	0	0	1	0	24	7.5	11.34		1,2,3,4
Dendropsophus jimi	0	0	1	0	0	1	0	0	0	0	0	0	22.3	6.05	9.85		1,2,3,9
Dendropsophus leucophyllatus	1	0	1	0	0	0	0	0	0	0	1	0	50	16	22.04	Head width and tibia length inferred	1,2,3
Dendropsophus melanargyreus	0	0	1	0	0	1	0	0	0	0	0	0	50	15.19	20.81	Head width and tibia length inferred	1,2,3
Dendropsophus meridianus	0	0	1	0	0	1	0	0	0	0	0	0	24	8.13	13.39		1,2,3,4
Dendropsophus microcephalus	0	0	1	0	0	1	0	0	0	0	0	0	32	10.15	13.68	Head width and tibia length inferred	1,2,3
Dendropsophus microps	0	0	1	0	0	1	0	0	0	0	0	0	33	22.5	8.5		1,2,3,4
Dendropsophus minutus	0	0	1	0	0	1	0	0	0	0	0	0	27.6	6.75	10.97		1,2,3,4
Dendropsophus nahdereri	0	0	1	0	0	1	0	0	0	0	0	0	50.5	14.73	21.18		1,2,3,4
Dendropsophus nanus	0	0	1	0	0	1	0	0	0	0	0	0	23.8	6	9.5		1,2,3,4
Dendropsophus novaisi	0	0	1	0	0	1	0	0	0	0	0	0	35	11.5	14.94	Tibia length inferred	1,2,3,115
Dendropsophus oliveirai	0	0	1	0	0	1	0	0	0	0	0	0	20	5.8	8.16		1,2,3,4
Dendropsophus pseudomeridianus	1	0	1	0	0	0	0	0	0	0	1	0	22.7	6.8	10.7		1,2,3,4
Dendropsophus rubicundulus	0	0	1	0	0	1	0	0	0	0	0	0	25.4	7.04	11.53	Head width and tibia length inferred	1,2,3
Dendropsophus ruschii	1	0	1	0	0	0	0	0	0	0	1	0	29	8.7	13.8		1,2,3,4
Dendropsophus sanborni	0	0	1	0	0	1	0	0	0	0	0	0	21.1	5.5	10		1,2,3,4
Dendropsophus seniculus	0	0	1	0	0	1	0	0	0	0	0	0	43	12.44	18.85		1,2,3,4
Dendropsophus soaresi	0	0	1	0	0	1	0	0	0	0	0	0	33	9	13.5		1,2,3,4
Dendropsophus werneri	0	0	1	0	0	1	0	0	0	0	0	0	23	6.5	10		1,2,3,4
Dermatonotus muelleri	0	0	1	0	0	1	0	0	0	0	0	0	74.15	21.31	27.29	Head width and tibia length inferred	1,2,3

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Elachistocleis bicolor	0	0	1	0	0	1	0	0	0	0	0	0	43	10.92	15.85	Head width and tibia length inferred	1,2,3
Elachistocleis cesarii	0	0	1	0	0	1	0	0	0	0	0	0	28.61	6.22	10.58		1,2,3,57
Elachistocleis ovalis	0	0	1	0	0	1	0	0	0	0	0	0	43.8	10.99	16.15	Head width and tibia length inferred	1,2,3
Elachistocleis piauiensis	0	0	1	0	0	1	0	0	0	0	0	0	22.5	5.8	8.2		1,2,3,58
Eleutherodactylus cubanus	1	1	0	1	0	0	0	0	0	1	0	0	14	5.48	7.31	Head width and tibia length inferred	1,2,3
Euparkerella brasiliensis	1	1	0	1	0	0	0	0	0	1	0	0	20	9.12	9.5	Head width and tibia length inferred	1,2,3
Euparkerella cochranae	1	1	0	1	0	0	0	0	0	1	0	0	20	9.12	9.5	Head width and tibia length inferred	1,2,3
Euparkerella tridactyla	1	1	0	1	0	0	0	0	0	1	0	0	20	9.12	9.5	Head width and tibia length inferred	1,2,3
Fritziana fissilis	1	0	1	0	0	0	0	0	0	0	0	1	38.7	13.65	18.22	Head width and tibia length inferred	1,2,3
Fritziana goeldii	1	0	1	0	0	0	0	0	0	0	0	1	34.8	12.45	16.79	Head width and tibia length inferred	1,2,3
Fritziana ohausi	1	0	1	0	0	0	0	0	0	0	0	1	34.7	12.42	16.75	Head width and tibia length inferred	1,2,3
Frostius pernambucensis	0	0	1	0	0	1	0	0	0	0	0	0	21	8.64	8.55	Head width and tibia length inferred	1,2,3
Gastrotheca albolineata	1	1	0	1	0	0	0	0	0	0	0	1	60	20.33	26.48	Head width and tibia length inferred	1,2,3
Gastrotheca ernestoi	1	1	0	1	0	0	0	0	0	0	0	1	75	24.96	31.98	Head width and tibia length inferred	1,2,3
Gastrotheca fissipes	1	1	0	1	0	0	0	0	0	0	0	1	68	22.85	29.64	Head width and tibia length inferred	1,2,3
Gastrotheca fulvorufa	1	1	0	1	0	0	0	0	0	0	0	1	77.2	25.64	32.78	Head width and tibia length inferred	1,2,3
Gastrotheca microdiscus	1	1	0	1	0	0	0	0	0	0	0	1	49	16.94	22.45	Head width and tibia length inferred	1,2,3
Gastrotheca pulchra	1	1	0	1	0	0	0	0	0	0	0	1	30.34	11.6	17.36		1,2,3,59
Haddadus binotatus	1	1	0	1	0	0	0	0	0	1	0	0	63.8	21.39	25.97	Head width and tibia length inferred	1,2,3
Holoaden luederwaldti	1	1	0	1	0	0	0	0	0	1	0	0	39.6	16.2	15.9		1,2,3,60
Holoaden pholeter	1	1	0	1	0	0	0	0	0	1	0	0	44.63	17.3	18.76		1,2,3,61
Hylodes amnicola	0	0	1	0	0	1	0	0	0	0	0	0	27.65	8.72	14.9		1,2,3,62
Hylodes asper	0	0	1	0	0	1	0	0	0	0	0	0	44.9	15.02	22.05	Head width and tibia length inferred	1,2,3
Hylodes babax	0	0	1	0	0	1	0	0	0	0	0	0	30.6	9.7	17.2		1,2,3,25
Hylodes cardosoi	0	0	1	0	0	1	0	0	0	0	0	0	40.72	13.65	22.5		1,2,3,63
Hylodes charadranaetes	0	0	1	0	0	1	0	0	0	0	0	0	34.4	10.4	17.3		1,2,3,21
Hylodes fredi	0	0	1	0	0	1	0	0	0	0	0	0	34.8	10.5	17.8		1,2,3,64
Hylodes heyeri	0	0	1	0	0	1	0	0	0	0	0	0	41.33	12.9	22.33		1,2,3,65
Hylodes lateristrigatus	0	0	1	0	0	1	0	0	0	0	0	0	40	13.56	20.28	Head width and tibia length inferred	1,2,3
Hylodes meridionalis	0	0	1	0	0	1	0	0	0	0	0	0	50	16.6	23.92	Head width and tibia length inferred	1,2,3
Hylodes nasus	0	0	1	0	0	1	0	0	0	0	0	0	38	19.17	23.59	Head width and tibia length inferred	1,2,3
Hylodes perere	0	0	1	0	0	1	0	0	0	0	0	0	25.35	7.72	13.94		1,2,3,66

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Hylodes perplicatus	0	0	1	0	0	1	0	0	0	0	0	0	45.1	15.08	22.13	Head width and tibia length inferred	1,2,3
Hylodes phyllodes	0	0	1	0	0	1	0	0	0	0	0	0	29.2	8.9	14.4		1,2,3,21
Hylodes pipilans	0	0	1	0	0	1	0	0	0	0	0	0	25.1	7.8	13.8		1,2,3,64
Hylodes sazimai	0	0	1	0	0	1	0	0	0	0	0	0	27.6	9.2	14.4		1,2,3,67
Hylomantis aspera	1	0	1	0	0	0	0	0	0	1	0	0	41.7	15.5	20.4		1,2,3,119
Hylomantis granulosa	1	0	1	0	0	0	0	0	0	0	1	0	37.4	14.5	17.2		1,2,3,134
Ischnocnema abdita	1	1	0	1	0	0	0	0	0	1	0	0	15.7	5.3	8.7		1,2,3,7
Ischnocnema bolbodactyla	1	1	0	1	0	0	0	0	0	1	0	0	15.3	5.71	9.03	Head width and tibia length inferred	1,2,3
Ischnocnema erythromera	1	1	0	1	0	0	0	0	0	1	0	0	26.5	9.43	14.58		1,2,3,68
Ischnocnema guentheri	1	1	0	1	0	0	0	0	0	1	0	0	30.8	11.08	19.86		1,2,3,68
Ischnocnema henselii	1	1	0	1	0	0	0	0	0	1	0	0	29.5	10.63	19.19	Head width and tibia length inferred	1,2,3
Ischnocnema hoehnei	1	1	0	1	0	0	0	0	0	1	0	0	32.2	8.83	20.33		1,2,3,120
Ischnocnema holti	1	1	0	1	0	0	0	0	0	1	0	0	19	7.5	10		1,2,3,121
Ischnocnema izecksohni	1	1	0	1	0	0	0	0	0	1	0	0	46.25	16.15	25.8		1,2,3,69
Ischnocnema juipoca	1	1	0	1	0	0	0	0	0	1	0	0	20.43	6.88	10.91		1,2,3,70
Ischnocnema lactea	1	1	0	1	0	0	0	0	0	1	0	0	32	11.24	14.77	Head width and tibia length inferred	1,2,3
Ischnocnema manezinho	1	1	0	1	0	0	0	0	0	1	0	0	34.8	11.76	16.79	Head width and tibia length inferred	1,2,3
Ischnocnema melanopygia	1	1	0	1	0	0	0	0	0	1	0	0	18.9	6.48	9.04		1,2,3,10
Ischnocnema nasuta	1	1	0	1	0	0	0	0	0	0	1	0	38.1	12.57	23.81		1,2,3,68
Ischnocnema nigriventris	1	1	0	1	0	0	0	0	0	1	0	0	21.9	7.67	10.9		1,2,3,122
Ischnocnema octavioi	1	1	0	1	0	0	0	0	0	1	0	0	31.25	12	15.51	Tibia length inferred	1,2,3
Ischnocnema oea	1	1	0	1	0	0	0	0	0	1	0	0	17.7	6.19	10.97		1,2,3,68
Ischnocnema parva	1	1	0	1	0	0	0	0	0	1	0	0	25.5	8.03	15.21	Head width and tibia length inferred	1,2,3
Ischnocnema sambaqui	1	1	0	1	0	0	0	0	0	1	0	0	36.89	13.96	19.16		1,2,3,71
Ischnocnema spanios	1	1	0	1	0	0	0	0	0	1	0	0	14.7	4.9	7.6		1,2,3,24
Ischnocnema surda	1	1	0	1	0	0	0	0	0	1	0	0	21.78	8.42	11.55		1,2,3,14
Ischnocnema verrucosa	1	1	0	1	0	0	0	0	0	1	0	0	24	9.16	12.63	Head width and tibia length inferred	1,2,3
Itapotihyla langsdorffii	0	0	1	0	0	1	0	0	0	0	0	0	112	21.72	40.45		1,2,3,4
Leptodactylus cunicularius	1	0	1	0	0	0	0	1	0	0	0	0	40	15	24		1,2,3,72
Leptodactylus cupreus	0	0	1	0	0	0	0	1	0	0	0	0	52.4	18	26.1		1,2,3,73
Leptodactylus elenae	1	0	0	1	0	0	0	0	0	1	0	0	43.5	14.3	20.6		1,2,3,74
Leptodactylus furnarius	0	0	1	0	0	0	0	1	0	0	0	0	35.4	11.6	18.76		1,2,3,72

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Leptodactylus fuscus	0	0	1	0	0	0	0	1	0	0	0	0	43.2	14.25	22.24		1,2,3,74
Leptodactylus gracilis	0	0	1	0	0	0	0	1	0	0	0	0	43	13.76	20.42		1,2,3,74
Leptodactylus jolyi	0	0	1	0	0	0	0	1	0	0	0	0	45.4	17	34.05		1,2,3,72
Leptodactylus labyrinthicus	0	0	1	0	0	0	0	1	0	0	0	0	117.73	37.24	49.37	Tibia length inferred	1,2,3,
Leptodactylus latinasus	0	0	1	0	0	0	0	1	0	0	0	0	32.1	10.91	14.44		1,2,3,74
Leptodactylus latrans	0	0	1	0	0	0	0	1	0	0	0	0	120	39.78	59.89	Head width and tibia length inferred	1,2,3
Leptodactylus macrosternum	0	0	1	0	0	0	0	1	0	0	0	0	80	25.99	35.82	Head width and tibia length inferred	1,2,3
Leptodactylus marambaiae	0	0	1	0	0	0	0	1	0	0	0	0	38.5	13.09	19.25		1,2,3,74
Leptodactylus mystaceus	0	0	1	0	0	0	0	1	0	0	0	0	43.15	14.67	21.79		1,2,3,74
Leptodactylus mystacinus	0	0	1	0	0	0	0	1	0	0	0	0	54.75	19.16	22.99		1,2,3,74
Leptodactylus natalensis	0	0	1	0	0	0	0	1	0	0	0	0	44	14.88	22.62	Head width and tibia length inferred	1,2,3
Leptodactylus notoaktites	0	0	1	0	0	0	0	1	0	0	0	0	48.25	15.92	26		1,2,3,74
Leptodactylus oreomantis	0	0	1	0	0	0	0	1	0	0	0	0	33.35	10.95	20.05		1,2,3,75
Leptodactylus plaumanni	0	0	1	0	0	0	0	1	0	0	0	0	46	14.92	22.05	Head width and tibia length inferred	1,2,3
Leptodactylus podicipinus	0	0	1	0	0	1	0	0	0	0	0	0	54	17.97	26.28	Head width and tibia length inferred	1,2,3
Leptodactylus pustulatus	0	0	1	0	0	0	0	1	0	0	0	0	40	13.65	21.15	Head width and tibia length inferred	1,2,3
Leptodactylus sertanejo	0	0	1	0	0	0	0	1	0	0	0	0	52.6	15.5	34.13		1,2,3,76
Leptodactylus spixi	0	0	1	0	0	0	0	1	0	0	0	0	43	14.5	21.5		1,2,3,77
Leptodactylus syphax	1	0	1	0	0	0	0	1	0	0	0	0	75.25	27.09	28.1		1,2,3,123
Leptodactylus troglodytes	0	0	1	0	0	0	0	1	0	0	0	0	49.35	16.77	19.74		1,2,3,74
Leptodactylus vastus	0	0	1	0	0	0	0	1	0	0	0	0	144.42	45.81	59.25	Head width inferred	1,2,3
Leptodactylus viridis	0	0	1	0	0	0	0	1	0	0	0	0	64.5	21.22	30.03	Head width and tibia length inferred	1,2,3
Limnomedusa macroglossa	0	0	1	0	0	1	0	0	0	0	0	0	49.5	18.27	23.2	Head width and tibia length inferred	1,2,3
Lithobates catesbeianus	0	0	1	0	0	1	0	0	0	0	0	0	203	62.61	75.83	Head width and tibia length inferred	1,2,3
Lithobates palmipes	0	0	1	0	0	1	0	0	0	0	0	0	126	38.86	47.61	Head width and tibia length inferred	1,2,3
Lysapsus limellum	0	0	1	0	0	1	0	0	0	0	0	0	24.8	7.69	14.75	Head width and tibia length inferred	1,2,3
Macrogenioglottus alipioi	0	0	1	0	0	1	0	0	0	0	0	0	113.8	41.79	39.03	Head width and tibia length inferred	1,2,3
Melanophryniscus alipioi	0	0	1	0	0	1	0	0	0	0	0	0	23.08	6.01	15.93		1,2,3,78
Melanophryniscus atroluteus	0	0	1	0	0	1	0	0	0	0	0	0	28	9.32	11.52	Head width and tibia length inferred	1,2,3
Melanophryniscus devincenzii	0	0	1	0	0	1	0	0	0	0	0	0	29	9.63	11.88	Head width and tibia length inferred	1,2,3
Melanophryniscus dorsalis	0	0	1	0	0	1	0	0	0	0	0	0	23.15	7.7	8.17		1,2,3,79
Melanophryniscus fulvoguttatus	0	0	1	0	0	1	0	0	0	0	0	0	25.6	7.7	8.15		1,2,3,79

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Melanophryniscus tumifrons	0	0	1	0	0	1	0	0	0	0	0	0	31	11.06	12.58	Head width and tibia length inferred	1,2,3
Melanophryniscus vilavelhensis	0	0	1	0	0	1	0	0	0	0	0	0	14.66	4.7	4.6		1,2,3,80
Myersiella microps	1	1	0	1	0	0	0	0	0	1	0	0	40	11	14.84	Head width and tibia length inferred	1,2,3
Nyctimantis bokermanni	0	0	1	0	0	1	0	0	0	0	0	0	81	21.2	34		1,2,3,81
Nyctimantis brunoi	0	0	1	0	0	1	0	0	0	0	0	0	81	20.5	25.64		1,2,3,4
Odontophrynus americanus	0	0	1	0	0	1	0	0	0	0	0	0	51	21.62	13.41		1,2,3,8
Odontophrynus carvalhoi	0	0	1	0	0	1	0	0	0	0	0	0	70	30.8	21.7		1,2,3,82
Odontophrynus cultripes	0	0	1	0	0	1	0	0	0	0	0	0	70	27.3	19.81		1,2,3,82
Odontophrynus maisuma	0	0	1	0	0	1	0	0	0	0	0	0	39.2	16.57	13.5		1,2,3,8
Paratelmatobius cardosoi	0	0	1	0	0	1	0	0	0	0	0	0	17.13	6.59	7.78		1,2,3,83
Paratelmatobius gaigeae	0	0	1	0	0	1	0	0	0	0	0	0	19	6.5	8.57	Tibia length inferred	1,2,3,83
Paratelmatobius poecilogaster	1	0	1	0	0	0	0	0	0	1	0	0	27.07	9.17	11.27		1,2,3,83
Phantasmarana apuana	1	0	0	0	1	0	0	0	0	1	0	0	90.5	38.57	44.25		1,2,3,84
Phantasmarana bocainensis	1	0	0	0	1	0	0	0	0	1	0	0	66.7	27	32.6		1,2,3,85
Phantasmarana boticariana	1	0	0	0	1	0	0	0	0	1	0	0	74.9	34.54	39.69		1,2,3,86
Phantasmarana massarti	1	0	0	0	1	0	0	0	0	1	0	0	112.25	46.95	55.55		1,2,3,85
Phasmahyla cochranae	1	0	1	0	0	0	0	0	0	0	1	0	46	15.5	21.66	Tibia length inferred	1,2,3,132
Phasmahyla cruzi	1	0	1	0	0	0	0	0	0	0	1	0	35.43	12.6	18.26		1,2,3,87
Phasmahyla exilis	1	0	1	0	0	0	0	0	0	0	1	0	34.5	12.09	17.49	Head width and tibia length inferred	1,2,3
Phasmahyla guttata	1	0	1	0	0	0	0	0	0	0	1	0	45	15.51	21.67	Head width and tibia length inferred	1,2,3
Phasmahyla jandaia	1	0	1	0	0	0	0	0	0	0	1	0	30.4	11.5	16.42	Tibia length inferred	1,2,3,133
Phasmahyla spectabilis	1	0	1	0	0	0	0	0	0	0	1	0	40.67	13.75	20.22		1,2,3,88
Phrynomedusa dryade	1	0	1	0	0	0	0	0	0	1	0	0	36.61	11.06	14.95		1,2,3,89
Phyllodytes acuminatus	0	0	1	0	0	1	0	0	0	0	0	0	24.5	7.93	11.73	Head width and tibia length inferred	1,2,3
Phyllodytes edelmoi	0	0	1	0	0	1	0	0	0	0	0	0	28.8	9.5	13.8		1,2,3,4
Phyllodytes gyrinaethes	0	0	1	0	0	1	0	0	0	0	0	0	27.9	9.7	13		1,2,3,4
Phyllodytes kautskyi	0	0	1	0	0	1	0	0	0	0	0	0	38	13.9	18.6		1,2,3,4
Phyllodytes luteolus	0	0	1	0	0	1	0	0	0	0	0	0	23	8.15	10.94		1,2,3,4
Phyllodytes maculosus	0	0	1	0	0	1	0	0	0	0	0	0	45.5	18.6	22.1		1,2,3,4
Phyllodytes melanomystax	0	0	1	0	0	1	0	0	0	0	0	0	26.6	8.9	11.7		1,2,3,4
Phyllodytes tuberculosus	0	0	1	0	0	1	0	0	0	0	0	0	26	8.6	11.2		1,2,3,4
Phyllomedusa bahiana	1	0	1	0	0	0	0	0	0	0	1	0	85	27.17	33.63	Head width and tibia length inferred	1,2,3

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Phyllomedusa burmeisteri	1	0	1	0	0	0	0	0	0	0	1	0	79	25.32	31.43	Head width and tibia length inferred	1,2,3
Phyllomedusa distincta	1	0	1	0	0	0	0	0	0	0	1	0	70	21	28		1,2,3,135
Phyllomedusa iheringii	1	0	1	0	0	0	0	0	0	0	1	0	75	24.1	29.96	Head width and tibia length inferred	1,2,3
Phyllomedusa sauvagii	1	0	1	0	0	0	0	0	0	0	1	0	96.6	30.74	37.88	Head width and tibia length inferred	1,2,3
Phyllomedusa tetraploidea	1	0	1	0	0	0	0	0	0	0	1	0	59.04	20.74	24.23		1,2,3,90
Physalaemus aguirrei	0	0	1	0	0	0	0	1	0	0	0	0	28.2	9.62	12.91	Head width and tibia length inferred	1,2,3
Physalaemus albifrons	0	0	1	0	0	0	0	1	0	0	0	0	25	7.99	12.02	Head width and tibia length inferred	1,2,3
Physalaemus albonotatus	0	0	1	0	0	1	0	0	0	0	0	0	34.1	10.8	15.35	Head width and tibia length inferred	1,2,3
Physalaemus atlanticus	0	0	1	0	0	0	1	1	0	0	0	0	21.77	7.1	10.57		1,2,3,91
Physalaemus biligonigerus	0	0	1	0	0	0	0	1	0	0	0	0	32.4	16.7	16.72	Tibia length inferred	1,2,3
Physalaemus bokermanni	0	0	1	0	0	0	1	1	0	0	0	0	19.46	6.29	9.72	Head width and tibia length inferred	1,2,3
Physalaemus caete	0	0	1	0	0	0	0	1	0	0	0	0	23	7.96	10.98	Head width and tibia length inferred	1,2,3
Physalaemus camacan	0	0	1	0	0	0	0	1	0	0	0	0	23.3	7.4	11.1		1,2,3,92
Physalaemus centralis	0	0	1	0	0	0	0	1	0	0	0	0	40	12.56	17.55	Head width and tibia length inferred	1,2,3
Physalaemus cicada	0	0	1	0	0	0	0	1	0	0	0	0	25.38	8.91	11.87	Head width and tibia length inferred	1,2,3
Physalaemus crombiei	0	0	1	0	0	0	1	1	0	0	0	0	20.3	7.7	9.3		1,2,3,22
Physalaemus cuvieri	0	0	1	0	0	0	0	1	0	0	0	0	36.5	11.48	16.26	Head width and tibia length inferred	1,2,3
Physalaemus erikae	0	0	1	0	0	0	0	1	0	0	0	0	23.62	7.47	11.25		1,2,3,93
Physalaemus erythros	0	0	1	0	0	0	0	1	0	0	0	0	25.33	7.8	10.46		1,2,3,94
Physalaemus evangelistai	0	0	1	0	0	0	0	1	0	0	0	0	23	7.96	10.98	Head width and tibia length inferred	1,2,3
Physalaemus feioi	0	0	1	0	0	0	0	1	0	0	0	0	25.7	9.2	12		1,2,3,95
Physalaemus gracilis	0	0	1	0	0	0	0	1	0	0	0	0	40	15.24	18.1	Head width and tibia length inferred	1,2,3
Physalaemus henselii	0	0	1	0	0	0	0	1	0	0	0	0	20.92	7.53	10.23	Head width and tibia length inferred	1,2,3
Physalaemus jordanensis	0	0	1	0	0	0	0	1	0	0	0	0	24	8.17	11.54	Head width and tibia length inferred	1,2,3
Physalaemus kroyeri	0	0	1	0	0	0	0	1	0	0	0	0	35	11.05	15.42	Head width and tibia length inferred	1,2,3
Physalaemus lateristriga	0	0	1	0	0	0	0	1	0	0	0	0	28.7	9	14		1,2,3,95
Physalaemus lisei	0	0	1	0	0	0	0	1	0	0	0	0	28.25	8.94	13.73	Head width and tibia length inferred	1,2,3
Physalaemus maculiventris	0	0	1	0	0	0	0	1	0	0	0	0	25	8.67	11.75	Head width and tibia length inferred	1,2,3
Physalaemus marmoratus	0	0	1	0	0	0	0	1	0	0	0	0	38.86	11.87	15.62		1,2,3,96
Physalaemus maximus	0	0	1	0	0	0	0	1	0	0	0	0	46.3	14.1	21.9		1,2,3,97
Physalaemus moreirae	0	0	1	0	0	0	0	1	0	0	0	0	25.4	8.8	11.9		1,2,3,24
Physalaemus nanus	0	0	1	0	0	0	1	1	0	0	0	0	20	7.03	9.88	Head width and tibia length inferred	1,2,3

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Physalaemus nattereri	0	0	1	0	0	0	0	1	0	0	0	0	56.4	18.26	23.22	Head width and tibia length inferred	1,2,3
Physalaemus obtectus	0	0	1	0	0	0	0	1	0	0	0	0	24.93	8.55	11.69	Head width and tibia length inferred	1,2,3
Physalaemus olfersii	0	0	1	0	0	0	0	1	0	0	0	0	41	13.51	17.57	Head width and tibia length inferred	1,2,3
Physalaemus orophilus	0	0	1	0	0	0	0	1	0	0	0	0	25.3	8.3	12.6		1,2,3,95
Physalaemus riograndensis	0	0	1	0	0	0	0	1	0	0	0	0	18.6	5.84	7.92		1,2,3,98
Physalaemus rupestris	0	0	1	0	0	0	0	1	0	0	0	0	17.8	5.2	7.1		1,2,3,124
Physalaemus signifer	0	0	1	0	0	0	1	1	0	0	0	0	26.72	9.44	11.89	Head width and tibia length inferred	1,2,3
Physalaemus soaresi	0	0	1	0	0	0	0	1	0	0	0	0	22.8	7.9	10.91	Head width and tibia length inferred	1,2,3
Physalaemus spiniger	0	0	1	0	0	0	1	1	0	0	0	0	22.7	7.56	11.49	Head width and tibia length inferred	1,2,3
Pipa carvalhoi	0	0	1	0	0	0	0	0	1	0	0	0	68	21.37	26.76	Head width and tibia length inferred	1,2,3
Pithecopus ayeaye	1	0	1	0	0	0	0	0	0	0	1	0	41	12.5	15.66		1,2,3,125
Pithecopus azureus	1	0	1	0	0	0	0	0	0	0	1	0	40.32	11.37	16		1,2,3,26
Pithecopus hypochondrialis	1	0	1	0	0	0	0	0	0	1	0	0	46	14.17	18.13	Head width and tibia length inferred	1,2,3
Pithecopus megacephalus	1	0	1	0	0	0	0	0	0	0	1	0	42.6	14.42	16.77		1,2,3,26
Pithecopus nordestinus	1	0	1	0	0	0	0	0	0	0	1	0	39.12	11.52	15.5		1,2,3,26
Pithecopus rohdei	1	0	1	0	0	0	0	0	0	0	1	0	36	11.57	14.37	Head width and tibia length inferred	1,2,3
Pithecopus rusticus	1	0	1	0	0	0	0	0	0	1	0	0	35.46	11.85	14.1		1,2,3,99
Pleurodema alium	0	0	1	0	0	0	1	1	0	0	0	0	33.8	11.6	13.9		1,2,3,100
Pleurodema bibroni	0	0	1	0	0	0	0	1	0	0	0	0	31	10.71	13.59	Head width and tibia length inferred	1,2,3
Pleurodema diplolister	0	0	1	0	0	0	0	1	0	0	0	0	20	7.34	9.01	Head width and tibia length inferred	1,2,3
Pristimantis paulodutrai	1	1	0	1	0	0	0	0	0	1	0	0	31.5	11.57	14.08	Head width and tibia length inferred	1,2,3
Pristimantis ramagii	1	1	0	1	0	0	0	0	0	1	0	0	30	11.11	13.53	Head width and tibia length inferred	1,2,3
Pristimantis vinhai	1	1	0	1	0	0	0	0	0	1	0	0	22	8.64	10.6	Head width and tibia length inferred	1,2,3
Proceratophrys appendiculata	0	0	1	0	0	1	0	0	0	0	0	0	52.8	27.8	23.2		1,2,3,11
Proceratophrys avelinoi	0	0	1	0	0	1	0	0	0	0	0	0	29.95	13.72	10.05		1,2,3,101
Proceratophrys belzebul	0	0	1	0	0	1	0	0	0	0	0	0	48	26	21		1,2,3,102
Proceratophrys bigibbosa	0	0	1	0	0	1	0	0	0	0	0	0	44.3	20.4	15.3		1,2,3,103
Proceratophrys boiei	0	0	1	0	0	1	0	0	0	0	0	0	56.47	28.65	21.22		1,2,3,11,13
Proceratophrys brauni	0	0	1	0	0	1	0	0	0	0	0	0	34.84	16.8	12.34		1,2,3,103
Proceratophrys cristiceps	0	0	1	0	0	1	0	0	0	0	0	0	50.2	22.34	18.76	Head width and tibia length inferred	1,2,3
Proceratophrys cururu	0	0	1	0	0	1	0	0	0	0	0	0	43.96	20.94	17.12		1,2,3,104
Proceratophrys laticeps	0	0	1	0	0	1	0	0	0	0	0	0	67.62	41.97	23.32		1,2,3,11

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Proceratophrys mantiqueira	0	0	1	0	0	1	0	0	0	0	0	0	40.37	20.42	17.62		1,2,3,16
Proceratophrys melanopogon	0	0	1	0	0	1	0	0	0	0	0	0	45	23.6	17.25		1,2,3,11,16
Proceratophrys minuta	0	0	1	0	0	1	0	0	0	0	0	0	24.65	11.96	9.3		1,2,3,105
Proceratophrys moratoi	0	0	1	0	0	1	0	0	0	0	0	0	32.07	13.7	11.2		1,2,3,126
Proceratophrys paviotii	0	0	1	0	0	1	0	0	0	0	0	0	49.82	22.95	17.82		1,2,3,11,13
Proceratophrys renalis	0	0	1	0	0	1	0	0	0	0	0	0	50.05	25.8	18.7		1,2,3,11
Proceratophrys schirchi	0	0	1	0	0	1	0	0	0	0	0	0	44.5	21.31	16.06	Head width and tibia length inferred	1,2,3
Proceratophrys subguttata	0	0	1	0	0	1	0	0	0	0	0	0	47	29	19		1,2,3,11
Proceratophrys tupinamba	0	0	1	0	0	1	0	0	0	0	0	0	56.62	29.12	24.17		1,2,3,11
Pseudis cardosoi	0	0	1	0	0	1	0	0	0	0	0	0	55.9	14.87	21.42		1,2,3,4
Pseudis fusca	0	0	1	0	0	1	0	0	0	0	0	0	53	16.65	25.4		1,2,3,4
Pseudis minuta	0	0	1	0	0	1	0	0	0	0	0	0	51.1	15.78	25.23		1,2,3,4
Pseudis paradoxa	0	0	1	0	0	1	0	0	0	0	0	0	56	19	32		1,2,3,19
Pseudis platensis	0	0	1	0	0	1	0	0	0	0	0	0	50	16	25		1,2,3,19
Pseudopaludicola falcipes	0	0	1	0	0	1	0	0	0	0	0	0	18.1	6.8	9.73	Head width and tibia length inferred	1,2,3
Pseudopaludicola mineira	0	0	1	0	0	1	0	0	0	0	0	0	14.7	5.8	7.36		1,2,3,106
Pseudopaludicola murundu	0	0	1	0	0	1	0	0	0	0	0	0	16	6.09	10.63	Head width and tibia length inferred	1,2,3
Pseudopaludicola mystacalis	0	0	1	0	0	0	0	1	0	0	0	0	14.8	5.55	7.47		1,2,3,17
Pseudopaludicola saltica	0	0	1	0	0	1	0	0	0	0	0	0	15.97	6.05	11.52		1,2,3,17
Pseudopaludicola ternetzi	0	0	1	0	0	1	0	0	0	0	0	0	20	7.39	10.43	Head width and tibia length inferred	1,2,3
Rhinella abei	0	0	1	0	0	1	0	0	0	0	0	0	83.9	28.33	28.86	Head width and tibia length inferred	1,2,3
Rhinella achavali	0	0	1	0	0	1	0	0	0	0	0	0	60.85	21.95	20.68	Tibia length inferred	1,2,3,116
Rhinella arenarum	0	0	1	0	0	1	0	0	0	0	0	0	84.34	30.25	29.67	Tibia length inferred	1,2,3,116
Rhinella azarai	0	0	1	0	0	1	0	0	0	0	0	0	50	15.5	14		1,2,3,18
Rhinella crucifer	0	0	1	0	0	1	0	0	0	0	0	0	130	42.56	45.76	Head width and tibia length inferred	1,2,3
Rhinella dorbignyi	0	0	1	0	0	1	0	0	0	0	0	0	66	21	17.5		1,2,3,136
Rhinella fernandezae	0	0	1	0	0	1	0	0	0	0	0	0	60	20	19		1,2,3,136
Rhinella granulosa	0	0	1	0	0	1	0	0	0	0	0	0	55	18	19		1,2,3,18
Rhinella henseli	0	0	1	0	0	1	0	0	0	0	0	0	63.9	22.16	21.52	Head width and tibia length inferred	1,2,3
Rhinella hoogmoedi	0	0	1	0	0	1	0	0	0	0	0	0	47.9	17.7	19.3		1,2,3,107
Rhinella icterica	0	0	1	0	0	1	0	0	0	0	0	0	190	61.95	68.08	Head width and tibia length inferred	1,2,3
Rhinella jimi	0	0	1	0	0	1	0	0	0	0	0	0	140.64	51.37	47.45		1,2,3,137

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Rhinella ornata	0	0	1	0	0	1	0	0	0	0	0	0	84.29	28.45	29	Head width and tibia length inferred	1,2,3
Rhinella pombali	0	0	1	0	0	1	0	0	0	0	0	0	119	39.16	41.72	Head width and tibia length inferred	1,2,3
Rhinella pygmaea	0	0	1	0	0	1	0	0	0	0	0	0	29	11	9		1,2,3,138
Rhinella rubescens	0	0	1	0	0	1	0	0	0	0	0	0	130	43.51	46.11	Head width and tibia length inferred	1,2,3
Rhinella schneideri	0	0	1	0	0	1	0	0	0	0	0	0	250	84.68	87.71	Head width and tibia length inferred	1,2,3
Rhinella scitula	0	0	1	0	0	1	0	0	0	0	0	0	44.07	15.85	17.22		1,2,3,20
Rupirana cardosoi	1	0	1	0	0	0	0	0	0	0	1	0	30.47	11.45	14.34		1,2,3,108
Scinax agilis	0	0	1	0	0	1	0	0	0	0	0	0	19.5	6	9		1,2,3,4
Scinax albicans	0	0	1	0	0	1	0	0	0	0	0	0	46.94	12.5	19.16		1,2,3,4
Scinax alter	0	0	1	0	0	1	0	0	0	0	0	0	32	9.3	14.1		1,2,3,4
Scinax angrensis	0	0	1	0	0	1	0	0	0	0	0	0	39.2	9.51	14.14		1,2,3,139
Scinax arduous	0	0	1	0	0	1	0	0	0	0	0	0	26.2	8.38	13.67		1,2,3,4
Scinax argyreornatus	0	0	1	0	0	1	0	0	0	0	0	0	23	6.68	11.05		1,2,3,4
Scinax aromothyella	0	0	1	0	0	1	0	0	0	0	0	0	31.8	7.4	12.5		1,2,3,4
Scinax auratus	0	0	1	0	0	1	0	0	0	0	0	0	24.7	7.4	13		1,2,3,4
Scinax belloni	0	0	1	0	0	1	0	0	0	0	0	0	37.5	10.4	15.3		1,2,3,4
Scinax berthae	0	0	1	0	0	1	0	0	0	0	0	0	25	4.36	8.79	Head width and tibia length inferred	1,2,3
Scinax brieni	0	0	1	0	0	1	0	0	0	0	0	0	40	11.39	17.6		1,2,3,4
Scinax caldarum	0	0	1	0	0	1	0	0	0	0	0	0	35	8.82	16		1,2,3,4
Scinax camposseabrai	0	0	1	0	0	1	0	0	0	0	0	0	35.9	10.42	16.26	Head width and tibia length inferred	1,2,3
Scinax canastrensis	0	0	1	0	0	1	0	0	0	0	0	0	38	11.06	17.03	Head width and tibia length inferred	1,2,3
Scinax catharinae	0	0	1	0	0	1	0	0	0	0	0	0	45.5	15.3	22.39		1,2,3,4
Scinax constrictus	0	0	1	0	0	1	0	0	0	0	0	0	28.25	9.2	15.93		1,2,3,109
Scinax cosenzai	0	0	1	0	0	1	0	0	0	0	0	0	21.23	7.28	10.93		1,2,3,110
Scinax cretatus	0	0	1	0	0	1	0	0	0	0	0	0	30.96	10.44	15.98		1,2,3,111
Scinax crospedospilus	0	0	1	0	0	1	0	0	0	0	0	0	37.6	9.92	15.81		1,2,3,4
Scinax curicica	0	0	1	0	0	1	0	0	0	0	0	0	31.5	9.06	14.65	Head width and tibia length inferred	1,2,3
Scinax cuspidatus	0	0	1	0	0	1	0	0	0	0	0	0	32.5	9	15.5		1,2,3,4
Scinax duartei	0	0	1	0	0	1	0	0	0	0	0	0	37	11	18		1,2,3,4
Scinax eurydice	0	0	1	0	0	1	0	0	0	0	0	0	53.8	14	23		1,2,3,4
Scinax flavoguttatus	0	0	1	0	0	1	0	0	0	0	0	0	45.4	15	21		1,2,3,4
Scinax fuscomarginatus	0	0	1	0	0	1	0	0	0	0	0	0	26.7	5.7	9.9		1,2,3,4

Species	**OT**	**Dev**	**Aquatic**	**Terrestrial**	**Semiterrestrial**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**BL**	**HW**	**TL**	**Obs**	**Ref**
Scinax fuscovarius	0	0	1	0	0	1	0	0	0	0	0	0	55.3	12.5	22		1,2,3,4
Scinax granulatus	0	0	1	0	0	1	0	0	0	0	0	0	43	12	18		1,2,3,4
Scinax hayii	0	0	1	0	0	1	0	0	0	0	0	0	53	15.84	24.96		1,2,3,4
Scinax heyeri	0	0	1	0	0	1	0	0	0	0	0	0	35.6	12.41	19.38		1,2,3,4
Scinax hiemalis	0	0	1	0	0	1	0	0	0	0	0	0	34.4	9.39	14		1,2,3,4
Scinax humilis	0	0	1	0	0	1	0	0	0	0	0	0	40.9	9.91	15.77		1,2,3,4
Scinax imbegue	0	0	1	0	0	1	0	0	0	0	0	0	31.85	10.57	15.9		1,2,3,112
Scinax juncae	0	0	1	0	0	1	0	0	0	0	0	0	24.1	8.2	12.9		1,2,3,127
Scinax littoralis	0	0	1	0	0	1	0	0	0	0	0	0	39.9	9	16.5		1,2,3,4
Scinax littoreus	0	0	1	0	0	1	0	0	0	0	0	0	25.5	4.95	9.65		1,2,3,4
Scinax longilineus	0	0	1	0	0	1	0	0	0	0	0	0	48	15	25		1,2,3,4
Scinax luizotavioi	0	0	1	0	0	1	0	0	0	0	0	0	30	7.7	12.2		1,2,3,4
Scinax melanodactylus	0	0	1	0	0	1	0	0	0	0	0	0	14.62	5.12	8.05		1,2,3,128
Scinax nasicus	0	0	1	0	0	1	0	0	0	0	0	0	30.21	9.55	15.02	Tibia length inferred	1,2,3
Scinax nebulosus	0	0	1	0	0	1	0	0	0	0	0	0	40	12.84	19.81		1,2,3,4
Scinax obtriangulatus	0	0	1	0	0	1	0	0	0	0	0	0	39	7.46	12.35		1,2,3,4
Scinax pachycrus	0	0	1	0	0	1	0	0	0	0	0	0	33	10	19		1,2,3,4
Scinax perereca	0	0	1	0	0	1	0	0	0	0	0	0	42.2	13.2	20		1,2,3,4
Scinax perpusillus	0	0	1	0	0	1	0	0	0	0	0	0	25	6.53	10.1		1,2,3,4
Scinax ranki	0	0	1	0	0	1	0	0	0	0	0	0	28.7	9.25	14.95		1,2,3,4
Scinax rizibilis	0	0	1	0	0	0	0	1	0	0	0	0	34	10	16.79		1,2,3,4
Scinax rogerioi	0	0	1	0	0	1	0	0	0	0	0	0	30.05	10.32	15.15		1,2,3,129
Scinax ruber	0	0	1	0	0	1	0	0	0	0	0	0	45	12.75	20.15	Head width and tibia length inferred	1,2,3
Scinax similis	0	0	1	0	0	1	0	0	0	0	0	0	41	11	16.5		1,2,3,4
Scinax squalirostris	0	0	1	0	0	1	0	0	0	0	0	0	29	9	14		1,2,3,4
Scinax strigilatus	0	0	1	0	0	1	0	0	0	0	0	0	38.3	9.3	12.4		1,2,3,4
Scinax trapicheiroi	0	0	1	0	0	1	0	0	0	0	0	0	40	13.75	21.08		1,2,3,4
Scinax tripui	0	0	1	0	0	1	0	0	0	0	0	0	30.92	10.77	16.47		1,2,3,130
Scinax tymbamirim	0	0	1	0	0	1	0	0	0	0	0	0	25.37	8.05	13.37		1,2,3,112
Scinax uruguayus	0	0	1	0	0	1	0	0	0	0	0	0	25.8	8.3	12.8		1,2,3,4
Scinax v-signatus	0	0	1	0	0	1	0	0	0	0	0	0	27	7.7	12.8		1,2,3,4
Scinax x-signatus	0	0	1	0	0	1	0	0	0	0	0	0	48	13.6	21.25		1,2,3,4

Species	OT	Dev	Aquatic	Terrestrial	Semiterrestrial	S1	S2	S3	S4	S5	S6	S7	BL	HW	TL	Obs	Ref
Scythrophrys sawayae	0	0	1	0	0	1	0	0	0	0	0	0	17.5	6	9		1,2,3
Sphaenorhynchus caramaschii	0	0	1	0	0	1	0	0	0	0	0	0	29.3	8.38	13		1,2,3,4
Sphaenorhynchus palustris	0	0	1	0	0	1	0	0	0	0	0	0	36	10.47	15.5	Head width and tibia length inferred	1,2,3
Sphaenorhynchus planicola	0	0	1	0	0	1	0	0	0	0	0	0	24	7	12		1,2,3,4
Sphaenorhynchus prasinus	0	0	1	0	0	1	0	0	0	0	0	0	31	9.8	13.94		1,2,3,4
Sphaenorhynchus surdus	0	0	1	0	0	1	0	0	0	0	0	0	28	7.75	12.53		1,2,3,4
Stereocyclops incrassatus	0	0	1	0	0	1	0	0	0	0	0	0	57.8	16.45	21.35	Head width and tibia length inferred	1,2,3
Stereocyclops parkeri	0	0	1	0	0	1	0	0	0	0	0	0	51	14.35	18.86	Head width and tibia length inferred	1,2,3
Thoropa megatympanum	1	0	0	0	1	0	0	0	0	1	0	0	41.8	17.92	21.95		1,2,3,113
Thoropa miliaris	1	0	0	0	1	0	0	0	0	1	0	0	58.5	25.2	31.9		1,2,3,140
Thoropa taophora	1	0	0	0	1	0	0	0	0	1	0	0	102.1	38.43	47.48	Head width and tibia length inferred	1,2,3
Trachycephalus atlas	0	0	1	0	0	1	0	0	0	0	0	0	107	30	27.13		1,2,3,4
Trachycephalus dibernardoi	0	0	1	0	0	1	0	0	0	0	0	0	84.4	25.38	39.47		1,2,3,4
Trachycephalus imitatrix	0	0	1	0	0	1	0	0	0	0	0	0	53	16	26		1,2,3,4
Trachycephalus mesophaeus	0	0	1	0	0	1	0	0	0	0	0	0	80.5	21	32		1,2,3,4
Trachycephalus nigromaculatus	0	0	1	0	0	1	0	0	0	0	0	0	91.05	26	36		1,2,3,4
Trachycephalus typhonius	0	0	1	0	0	1	0	0	0	0	0	0	105	30.28	38.71	Head width and tibia length inferred	1,2,3
Vitreorana eurygnatha	1	0	1	0	0	0	0	0	0	0	1	0	23	8.68	11	Head width and tibia length inferred	1,2,3
Vitreorana uranoscopa	1	0	1	0	0	0	0	0	0	0	1	0	25.8	9.54	12.03	Head width and tibia length inferred	1,2,3
Xenohyla eugenioi	0	0	1	0	0	1	0	0	0	0	0	0	35.74	11.34	14.46		1,2,3,114
Xenohyla truncata	0	0	1	0	0	1	0	0	0	0	0	0	42	11.83	15.42		1,2,3,4

S4 File. References of dataset of life-history traits of Atlantic Forest anurans.

Number	**Reference**
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Number	Reference
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S6 File – Result of piecewiseSEM model. Direct and indirect effects of predictor variables on proportion of direct developing species of Atlantic Forest anuran communities. Goodness of fit: Fischer’s C = 2.635; P-value = 0.268; DF =2.Standard error (St. Error); degrees of freedom (DF); critical value (Crit. Value); and standardized estimate (St. Estimate)

Response	Predictor	Estimate	St. Error	DF	Crit.Value	P. Value	St. Estimate
PCPS1	**BIO4**	**-9.26E-02**	**0.038**	**766**	**-2.421**	**0.016**	**-0.092**
PCPS1	BIO12	5.86E-02	0.036	766	1.616	0.107	0.059
PCPS1	**ET0**	**-4.19E-01**	**0.041**	**766**	**-10.261**	**0.000**	**-0.419**
SES.FD	**PCPS1**	**-3.23E-01**	**0.037**	**766**	**-8.740**	**0.000**	**-0.323**
SES.FD	BIO4	2.13E-02	0.060	766	0.358	0.721	0.021
SES.FD	**BIO12**	**1.30E-01**	**0.054**	**766**	**2.393**	**0.017**	**0.130**
SES.FD	ET0	-5.17E-02	0.077	766	-0.671	0.502	-0.052
SES.FD	**Slope**	**2.09E-01**	**0.044**	**766**	**4.715**	**0.000**	**0.208**
PROP.DD	**SES.FD**	**2.31E-01**	**0.029**	**766**	**8.049**	**0.000**	**0.231**
PROP.DD	**PCPS1**	**-1.75E-01**	**0.031**	**766**	**-5.637**	**0.000**	**-0.175**
PROP.DD	**BIO4**	**-3.05E-01**	**0.063**	**766**	**-4.872**	**0.000**	**-0.305**
PROP.DD	BIO12	0.0847	0.061	766	1.383	0.167	0.085
PROP.DD	**Slope**	**0.1612**	**0.040**	**766**	**4.041**	**0.000**	**0.161**
PROP.DD	**ET0**	**-0.4512**	**0.082**	**766**	**-5.492**	**0.000**	**-0.451**

Endogenous variable R^2 (R-squared).

Response	R-squared
PCPS1	0.17
SES.FD	0.13
PROP.DD	0.36

S3 Appendix

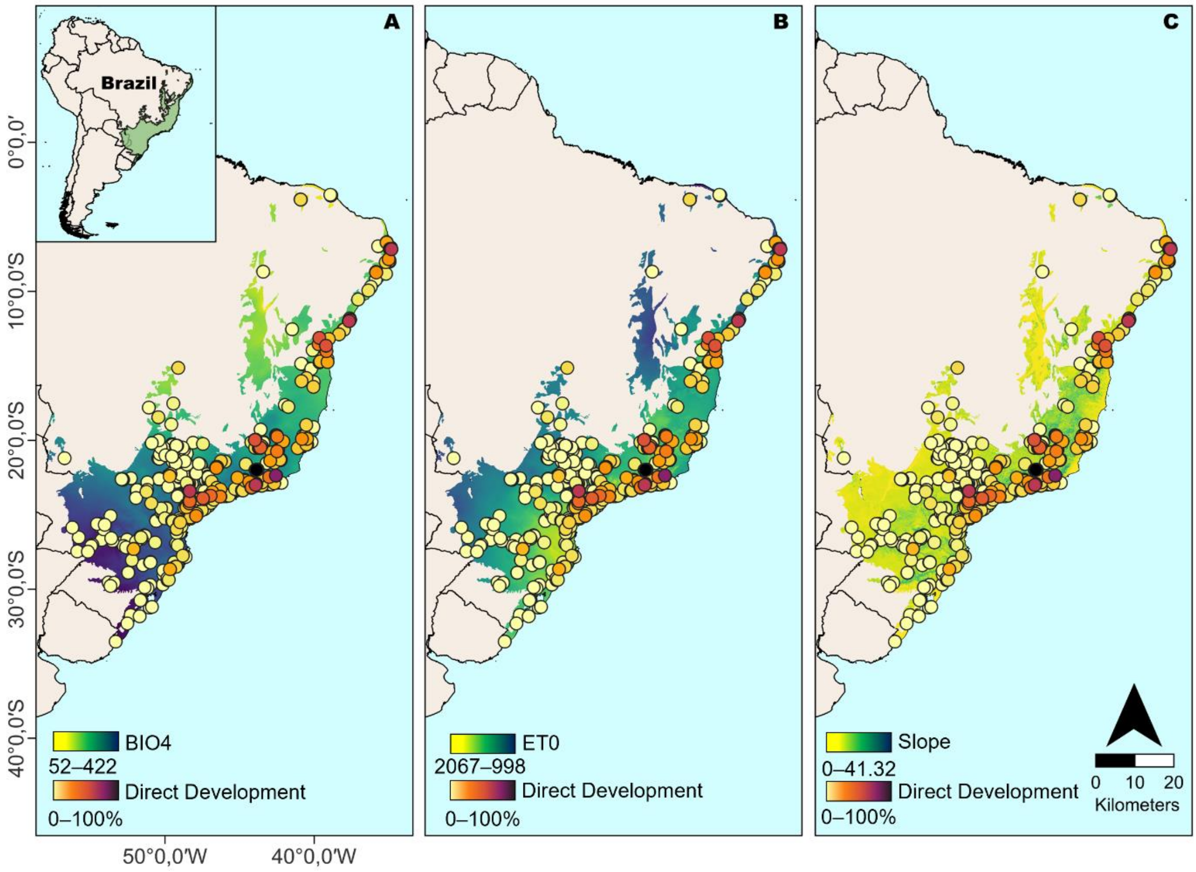

Fig S1. Variation in the proportion of direct developing species in anuran Atlantic Forest communities and the environment. A – temperature seasonality; B – potential evapotranspiration; and C – terrain slope. Base layer sources: South America shape file retrieved from the Database of Global Administrative Areas (GADM) under an open license (CC-BY): https://gadm.org/license.html; Atlantic Forest limits shape file from Muylaert et al. 2018 [34] under the GNU General Public License (https://github.com/LEEClab/ATLANTIC-limits/blob/master/LICENSE); communities (points) distributions were mapped based on records retrieved from Vancine et al. 2018 [30]; raster layers sources: temperature seasonality (BIO4) from WorldClim [35] (https://www.worldclim.org/data/worldclim21.html); ET0 from Global Aridity Index and Potential Evapotranspiration Climate Database [36] (https://figshare.com/articles/dataset/Global_Aridity_Index_and_Potential_Evapotranspiration_ET0

_Climate_Database_v2/7504448/3) under license CC BY 4.4; and Slope from EarthEnv database [37]. Modified from Vancine et al. 2018 [30].

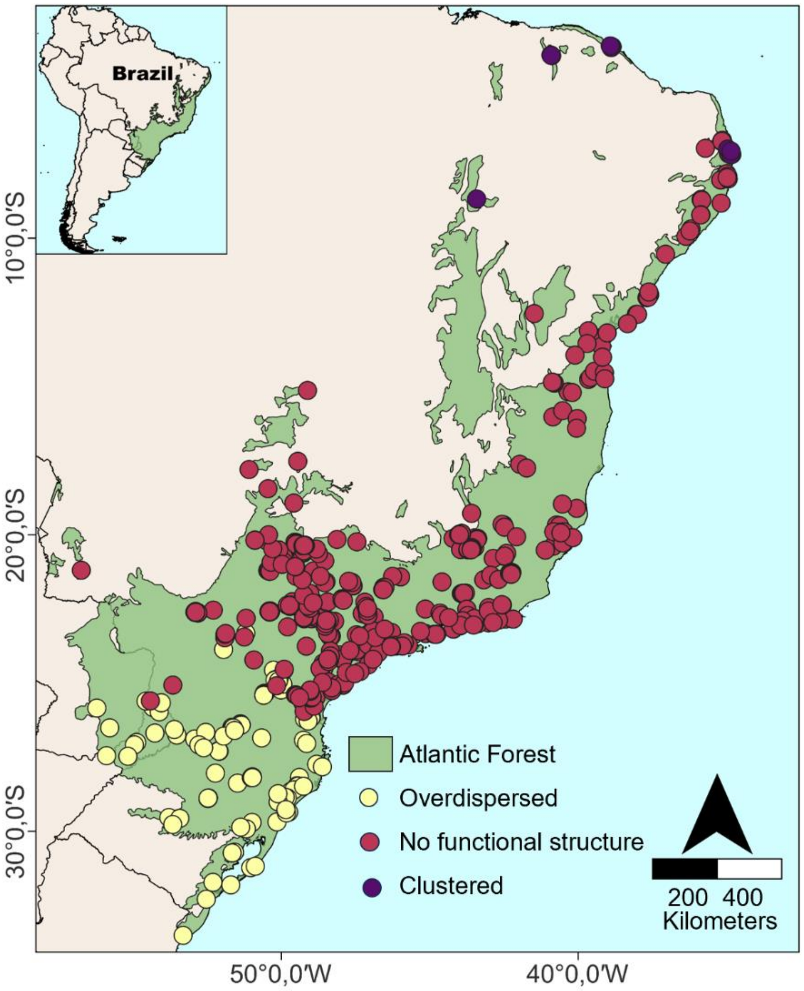

Fig S2. Pattern of functional structure in anuran communities from the Atlantic Forest. Light yellow points represent communities with FD values (functional diversity) lower than expected (functional overdispersion), dark purple points represent communities with FD values higher than expected (functional clustering), and magenta points represent communities with random functional structure. Base layer sources: South America shape file retrieved from the Database of Global Administrative Areas (GADM) under an open license (CC-BY): https://gadm.org/license.html; Atlantic Forest limits shape file from Muylaert et al. 2018 [34] under the GNU General Public License (https://github.com/LEEClab/ATLANTIC-limits/blob/master/LICENSE); communities (points) distributions were mapped based on records retrieved from Vancine et al. 2018 [30]. Modified from Vancine et al. 2018.

CAPÍTULO III

FROM EVOLUTIONARY HISTORY TO ENVIRONMENTAL CONDITIONS: THE DETERMINANTS OF DIRECT DEVELOPMENT IN NEW WORLD ANURANS

Capítulo com previsão de submissão para a revista *Global Ecology and Biogeography*

From evolutionary history to environmental conditions: The determinants of direct development in New World anurans

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Biosketch

Rodrigo B. Fontana is interested in the ecology, evolution, and conservation of amphibians. His primary focus is understanding the ecological and evolutionary aspects associated with direct development in anuran amphibians on a macroecological scale. Additionally, he investigates the conservation panorama of the group in the Atlantic Forest as well as how these species will respond to future climate changes.

From evolutionary history to environmental conditions: The determinants of direct development in New World anurans

Running title: New World direct-developing Anurans

Abstract

Aim: Among the high reproductive diversity of amphibians, some species deviate from the classical reproductive mode with a biphasic life cycle and exhibit direct development, characterized by the absence of a free-living larval form and egg-hatching in miniature adults. Here, we investigated how biotic (phylogenetic composition and functional diversity) and abiotic factors (climate and topography) are related to the evolution and occurrence of direct-developing anurans in the New World and across the biomes from this region.

Location: New World.

Time period: Current.

Major taxa studied: Anurans.

Methods: Using data on reproductive mode and distribution maps of 2,534 amphibian species from the New World, we estimated the proportion of direct-developing anurans per 0.5° cell. Then, we used structural equation models (SEM) to investigate the relationships among the abiotic (temperature, precipitation, humidity, and topography) and biotic (phylogenetic composition and functional diversity) factors with the proportion of direct development in 9,522 New World anuran communities. We also explored if and how these relationships vary across 12 New World biomes.

Results: Phylogenetic composition was the main predictor of the proportion of direct-developing species in the New World anuran communities. We verified that relationships among abiotic and biotic factors with direct development are dependent on biome type. There was a tendency of the biotic component (phylogenetic composition) to strongly predict the proportion of direct-developing anurans in tropical biomes. In contrast, abiotic factors (temperature and humidity) were the most related to direct development in temperate biomes.

Main conclusions: The high reproductive diversity of amphibians is the result of distinct selective forces. In the case of direct development, the synergism between the abiotic and biotic factors led to the evolution of this specialized reproductive mode in diverse ways depending on the biogeographic region.

Keywords: amphibians; climate; functional diversity; direct-developing amphibians; phylogenetic composition; structural equation model; topography

1. INTRODUCTION

One of the central topics in ecology is understanding how distinct factors have influenced the evolution of species and how these elements are related to the current patterns of biodiversity. Among those that received the most attention is the influence of abiotic factors, like environmental conditions to which the species are subjected. In this context, climatic conditions, such as patterns of temperature, precipitation, and humidity, can restrict the species distribution according to their specific requirements, as well as ignite their evolution (Gomez-Mestre et al., 2012; Lion et al. 2019). Additionally, structural variations, such as topographic heterogeneity, can hinder the occurrence and survival of some individuals/species in particular environments that can become harsh environments for them (Liedtke et al., 2017; Lion et al. 2019). Notably, the biotic component also plays a significant role in the evolutionary processes, distribution of species, and assembly of ecological communities (Wisz et al., 2013).

Biotic factors can shape the composition, structure, and dynamics of communities through mechanisms of species coexistence, such as predation, competition, parasitism, and other interactions (Wisz et al., 2013). For example, predation can reduce the fitness of prey species, resulting in shifts in community composition (Buxton & Sperry, 2017). Similarly, if species with similar requirements occur in the same space, the strength of the competition can result in coexistence or in competitive exclusion of one species from the community (MacArthur & Levins, 1967). In these cases, restrictions imposed by biotic and abiotic factors can also promote the evolution of novel characteristics, or traits, enabling the colonization of new environments, such as distinct niches, where different environmental conditions exert influence (Crump, 2015; Zamudio et al., 2016). A notable example of how abiotic and biotic factors lead to the evolution of new traits can be verified through the reproductive diversity presented by amphibians.

Amphibians exhibit the greatest reproductive diversity among tetrapods, with at least 74 reproductive modes (RM) having been described (Nunes-de-Almeida et al., 2021). Among this vast reproductive diversity and differing from the ancestral and usual RM with a biphasic life cycle, there is direct development, which represents a profound evolutionary transition within the group (Gomez-Mestre et al., 2012; Nunes-de-Almeida et al., 2021). This RM, primarily defined by the absence of the free-living larval form (*i.e.*, tadpole; Haddad & Prado, 2005). Although there is a growing literature on the evolution of amphibian reproductive modes, the influence of ecological mechanisms in this context is still limited (Fontana et al. 2022).

The main hypothesis predicts that direct development has evolved in response to both abiotic and biotic factors (Crump, 2015; Zamudio et al., 2016; Fontana et al., 2022). Indeed, the whole transition from aquatic to terrestrial reproductive modes is considered as an example of repeated adaptations of amphibians to the same set of specific environmental conditions (Liedtke et al., 2017). However, very few studies have effectively assessed the role of abiotic factors in reproductive diversification. Previous studies uncovered that climatic conditions, such as temperature, precipitation, and humidity were correlated to terrestrial reproduction, including direct development (Gomez-Mestre et al., 2012; Lion et al., 2019). Müller et al. (2013), investigated the influence of habitat type and found an association of terrestrial oviposition with forested environments and the complete terrestrial development, including direct development, with montane forests. Liedtke et al. (2017) summed the geophysical structure of the environments. The authors attributed the evolution of terrestrial reproduction of bufonids as a result of the topographic conditions, represented by the steep terrain and low availability of accumulated water sources, in Africa.

Although biotic factors, such as predation and competition, are listed as the main promoters of the evolution of direct development, knowledge about their real influence is still scarce. On a local scale, both Magnusson and Hero (1991) and Touchon and Worley (2015) verified high mortality rates of eggs and larvae in response to predation in the aquatic environment. Whereas due to studies limitations, do not permit extrapolations and generalizations for these authors, these findings agree with the hypothesis that predation acts as a selective force in the evolution of terrestrial RM. Moving to a broader scale, Zamudio et al. (2016) found that sexual selection contributed to the evolution of reproductive terrestriality of hylids and leptodactylids, resulting in reduced polyandry. In this case, sexual selection favored the reproductive diversification in these lineages through the reduction of the loss of fitness due to male-male competition and avoidance of polyandry.

Comprehending how direct development has emerged in the anuran tree of life is a fundamental step in understanding how life evolved from aquatic systems and conquered the terrestrial environment. Few studies effectively evaluated hypotheses regarding the evolution of this specialized RM (Fontana et al., 2023), especially considering different spatial scales, distinct biomes, and communities, and most importantly integrating the analyses of the importance of biotic and abiotic factors. In a recent study (Fontana et al., 2023) we identified that, although biotic factors were related to the proportion of species with this RM in communities in the Atlantic Forest, abiotic factors, such as low evapotranspiration and low-temperature seasonality, were the main factors associated with this RM. Here, we aim to expand the comprehension about the evolution of direct development and the occurrence of species which have direct development. For this purpose, we created a conceptual model that illustrates the relationships and influences of the abiotic and biotic factors with the proportion of direct-developing in the New World anuran communities (Figure 1) and evaluated it using structural equation models (SEM). We have assessed this model for the entire New World region and for each biome separately. Additionally, we also investigated the patterns of distribution of direct-developing anurans in the New World biomes.

With a complex geological history, the New World is known for its vast climatic, environmental, and structural heterogeneity providing a set of varied biomes, ranging from deserts and grasslands to forests, in lowland or mountain regions (Olson et al., 2001; Woodward, 2009). In turn, these conditions contributed to the elevated taxonomic diversity of varied species groups in the region. Similarly, this region encompasses distinctive evolutionary histories, represented by phylogenetic diversity, and multiple functional forms, characterized by the functional diversity, of different taxa, such as the case of amphibians (Duarte et al., 2014; Ochoa-Ochoa et al., 2019; Ochoa-Ochoa et al., 2020). The New World harbors the greatest diversity of anuran species in the world and important endemism centers for direct-developing anurans (IUCN, 2022; Gomez-Mestre et al., 2012). In turn, these patterns of diversity promote a wide range of possible biotic interactions among species. Hence, the New World is an ideal study system to investigate how abiotic and biotic factors are related to direct development in anurans.

In ecological studies, scale is a critical aspect of the analysis of patterns. Although there is no consensus, it is frequently recognized that the biotic factors act at finer/smaller scales (site or local), while on larger/broader scales (regional, continental) abiotic factors are more preponderant in shaping species distribution (King et al., 2021). Furthermore, phylogenetic and functional metrics reveal fundamental evolutionary and ecological patterns that occur in communities, serving as proxies for biological processes related to the response of species to biotic interactions, such as past competition and predation (in communities that exhibit phylogenetic and/or functional overdispersion), as well as the influence of environmental filters (in communities with phylogenetic and/or functional clustering) (Webb, 2002; Cavender-Bares et al., 2006; Fontana et al., 2023). Thus, we expect to find: i) a greater influence of abiotic factors on the proportion of direct-developing anurans, compared to the biotic component, when considering the model for the entire New World; ii) variations in the relationships between abiotic and biotic factors with the proportion of species in direct development, when analyzing biome models; and iii) a more intense association between higher functional diversity values and the proportion of direct-developing anurans in the communities, a result of coexistence mechanisms, such as past competition and predation.

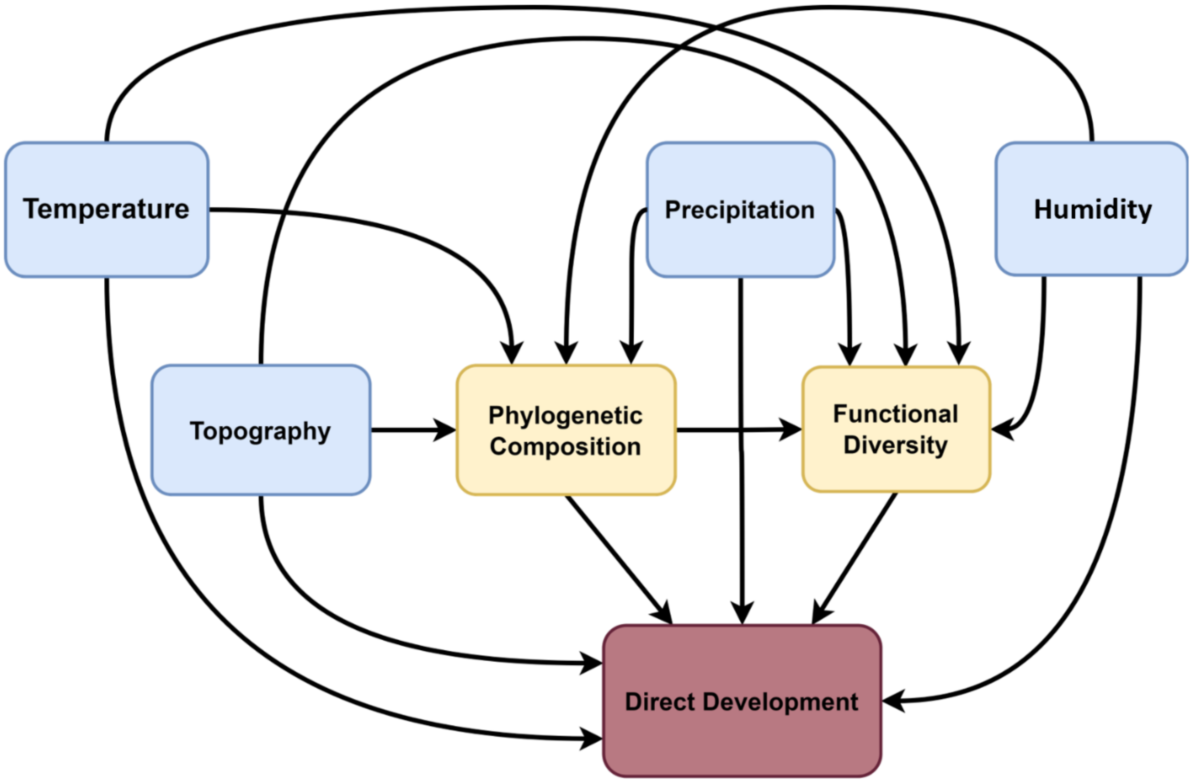

Figure 1. Conceptual representation of the relationships of abiotic and biotic factors with direct-developing anurans in the New World. The blue boxes represent abiotic factors, the yellow boxes represent biotic factors, and the brown box represents the proportion of direct-developing species in New World anuran communities.

2. METHODS

2.1 Community data

To evaluate the effects of biotic and abiotic variables on the proportion of direct-developing species in New World anuran communities, we organized a matrix of species by communities at a resolution of 0.5º First, in order to obtain data for characterize each community, we used data of species distributions from the 2022 International Union for Conservation of Nature and Natural Resources Red List (https://www.iucnredlist.org/resources/spatial-data-download). We created a grid map of the New World with a resolution of 0.5º and extracted the occurrence matrix (presence/absence matrix) for each grid cell using the package 'letsR' (Vilela & Villalobos, 2015) within the R environment (R Core Team, 2022). We considered the group of species occurring in each grid cell as an individual community. Second, we overlaid the anuran community data onto the shapefiles representing the biomes of Neotropical and Nearctic realms according to Olson et al. (2001, Figure S1). Subsequently we checked and updated the species nomenclature according to Frost (2023), resulting in a total of 2,534 anuran species.

Recognizing that species occurrence and distribution can exert an influence on the average trait values within communities (Duarte et al., 2018), we controlled the effect of species composition on the proportion of direct-developing species in the communities using null models (Pillar & Duarte, 2010; Peres-Neto et al., 2017). To do this, we constructed a **D** matrix containing the development mode for each species present in the communities. Subsequently, we computed the observed proportion of direct-developing species within each community. Following this, we generated 999 null proportions through randomization of the **D** matrix and calculated the mean and standard deviation of these null proportions. Finally, employing standardized effect size metrics, we used the observed proportions in conjunction with the means and standard deviations of the null proportions to calculate the proportion of direct-developing species that were independent of the composition effect for each community. Our comprehensive database, subject to analysis, encompassed a total of 9,522 communities distributed across the New World (Figure S1, Figure 2,

Appendix 1). To generate models for each biome, we subdivided this database into sets corresponding to individual New World biomes.

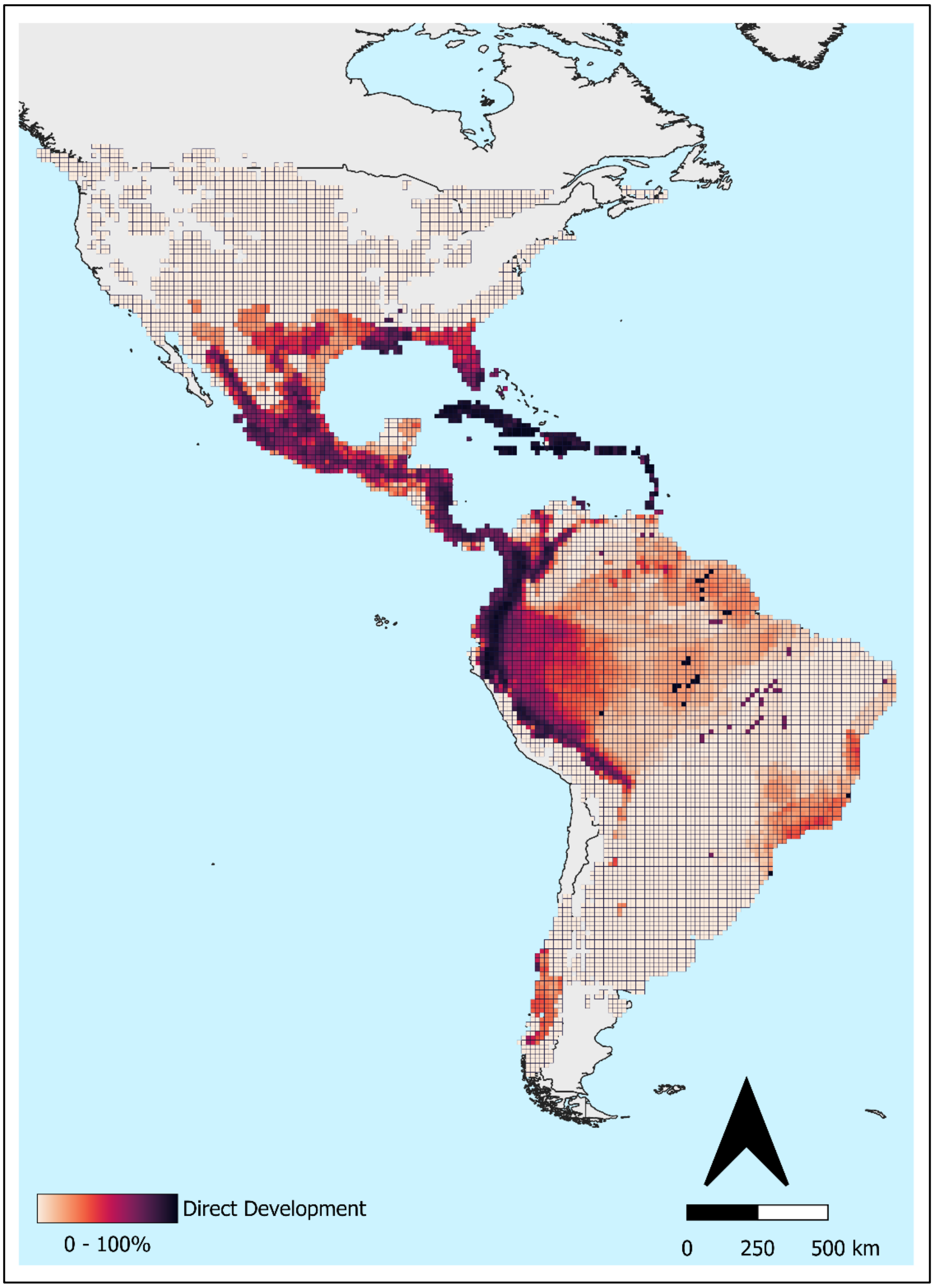

Figure 2. Spatial distribution of the observed proportion of direct-developing frogs in the New World. Data based on the **D** matrix.

2.2 Abiotic factors

To assess the influence of abiotic variables on the proportion of direct-developing anurans of the New World, we gathered a set of 21 environmental variables, encompassing: the 19 bioclimatic variables sourced from WorldClim 2.1 (Fick & Hijmans, 2017) related to the temperature and precipitation; the potential evapotranspiration (ET0) retrieved from Global Aridity Index and Potential Evapotranspiration Climate Database (Zomer et al., 2022); and the terrain slope obtained from the EarthEnv database (Amatulli et al., 2018). After downloading the data, we adjusted the extent of all raster files to align with the geographical boundaries of the New World. This process allowed us to derive the environmental variables of individual communities (cell grid). The raster files were originally obtained at a resolution of 30 arc-sec and were subsequently transformed to a resolution of 0.5°. To simplify the climate complexity data, we separated the bioclimatic variables related to temperature and to the precipitation and performed two principal component analyses (PCA), one for each variable type.

2.3 Biotic factors

In our conceptual model, we integrated two biotic factors as proxies for coexistence mechanisms: phylogenetic composition and functional diversity (FD). To establish the phylogenetic composition, we constructed a phylogenetic tree of our species pool (sub-tree, Figure S2) using Jetz and Pyron's (2018) consensus phylogenetic hypothesis as our base. We then pruned and checked the correspondence of our species pool with the consensus phylogenetic hypothesis and identified the absent species (n = 100), commonly referred to as phylogenetically uncertain taxa (PUTs). To incorporate PUTs into the sub-tree, we used relevant information from the literature to define the most derived consensus clade (MDCC), representing the basal node containing the closest living relative. We used the PAM v0.9 software to add the PUTs to our sub-tree (Rangel et al., 2015).

Subsequently, we conducted a principal coordinates of phylogenetic structure (PCPS) analysis, a method based on a principal coordinates analysis (PCoA) of a matrix containing phylogeny-weighted species composition (**P** matrix). This method generated a series of eigenvectors that illustrate orthogonal gradients of phylogenetic structure (Duarte, 2011; Duarte et al., 2012). The primary PCPS eigenvector, characterized by higher eigenvalues, captures deeper phylogenetic relationships (basal nodes of the phylogenetic tree), while the subsequent PCPS eigenvectors describe relationships between more recent lineages (terminal nodes) (Duarte et al., 2014). For the phylogenetic composition calculation, we used 'geiger' (Pennel et al., 2014) and 'PCPS' packages (Debastiani & Duarte, 2014).

Regarding functional diversity (FD), we compiled six anuran life-history and ecological traits, drawing information from the databases of amphibian traits provided by Oliveira et al. (2017) and Huang et al. (2023). We considered the following traits: i) habitat (seven categories: aquatic; arboreal; fossorial; semi-arboreal; semi-fossorial; semi-terrestrial; and terrestrial); ii) diel (three categories: diurnal, nocturnal, or both); iii) development mode (three categories: larval; direct development; and viviparous); iv) body size (mean value in mm); v) head width (mean value in mm); and vi) tibia length (mean value in mm) (Figure S3). We selected these traits due to their potential to unveil the effects of species coexistence, as they are connected with resource complementarity, distinctions in reproductive niches, and habitat utilization (Oliveira et al., 2018, Huang et al., 2023), as well as by their availability. In cases where information on these traits was not available for all species, we inferred missing traits using the package 'missForest' (Appendix 2; Stekhoven, 2022).

Subsequently, to address the influence of phylogenetic autocorrelation on functional traits, we employed a phylogenetic eigenvector regression (PVR) approach. This method involves the calculation of a phylogenetic distance matrix, followed by a principal coordinates analysis (PCoA) to generate a set of independent orthogonal eigenvectors that remain unaffected by the underlying phylogenetic structure (Diniz-Filho et al., 1998). Furthermore, we chose to employ the standardized effect size of functional diversity (SES.FD) to minimize the influence of species richness on the FD metric, thus facilitating comparisons among locations characterized by varying levels of species richness. SES metrics derived from null model analyses provide a means to correct potential biases associated with species richness, encompassing both observed and null model-generated values. Moreover, they possess the capacity to unveil patterns in phylogenetic or functional community structure (Swenson, 2014). In this context, communities influenced by biotic factors such as competition will exhibit functional overdispersion, indicated by positive SES.FD values, while those strongly affected by abiotic factors like environmental filters will manifest functional clustering, indicated by negative SES.FD values (Fontana et al., 2023).

To obtain SES.FD values, we initially generated a distance matrix based on the phylogenetic eigenvectors obtained through the previous PVR analysis, which was subsequently transformed into a dendrogram. Using this dendrogram, we calculated observed FD following the metric proposed by Petchey and Gaston (2002). This metric derives from Faith's phylogenetic diversity (PD; Faith, 1992) and is founded on the sum of branch lengths of a dendrogram. We employed “taxa.labels” as the null model, which shuffles the species names at the dendrogram's terminal nodes along with 999 randomizations. All of these analyses were performed within the R environment and used the ‘daee’ (Debastiani, 2021), picante (Kembel et al., 2010), PVR (Santos, 2018), and stats (R Core Team, 2022) packages.

2.4 Data analysis

In our analysis, we used the first PCPS eigenvector (PCPS 1), which captured 22.89% of the phylogenetic composition data variation, and the standardized effect size of FD (SES.FD, referred to as functional diversity) as indicators of biotic factors. We chose these metrics due to their ability to investigate the influence of evolutionary history and aspects related to species co-occurrence. For abiotic factors, we used the first principal component of temperature (TPC1) and the first principal component of precipitation (PPC1) as indicators of temperature and precipitation in our model. TPC1 explained 68.14% of the temperature variation data, while PPC1 explained 20.78% of the precipitation variation data. For humidity, we considered potential evapotranspiration (ET0), and for topography, we incorporated the terrain slope.

We investigated the relationships between biotic and abiotic factors with the proportion of direct-developing species in New World anuran communities, using the SEM with a piecewise approach (Lefcheck, 2016). SEM are valuable for investigating and confirming direct and indirect causal relationships outlined in a conceptual model derived from a priori based on specific knowledge of the studied system (Lefcheck, 2016). To accomplish our first prediction, which considers the entire New World region, we created three global SEM: i) a model without spatial autocorrelation structure and biomes as random effects; ii) a model with spatial autocorrelation structure and without random effects; and iii) a model with spatial autocorrelation structure and biomes as random effects. Three linear models formulated SEM: a) the first model establishes the connection between abiotic factors to the phylogenetic composition; b) the second model links abiotic and phylogenetic composition to FD; and c) the last model correlates abiotic and biotic factors with the proportion of direct-developing species in New World anuran communities. For the SEM (iii), we used linear mixed models due to the inclusion of the biomes as random effects (Supporting Information). We selected the best SEM through the lowest AIC (Table S1-S3).

Furthermore, to investigate variations in these relationships across different biomes in this continental region, we formulated 12 SEM sub-models, one for each of the New World biomes. Whereas in some biomes the relationship among specific variables was slightly changed to the model acceptance, the general structure of SEM sub-models was maintained the same as the global SEM. All predictors exhibited a noncollinearity relationship (variance inflation factor <3.0). The validity of the SEM was assessed through statistical significance ($p > 0.05$). All variables were standardized in advance, and the analyses were performed in R (R Core Team, 2022) using 'nlme' (Pinheiro et al., 2022), 'lme4' (Bates et al., 2015), and 'piecewiseSEM' (Lefcheck, 2016) packages.

3. RESULTS

We analyzed 9,522 communities, which harbor 2,534 anuran species of 28 families distributed across the New World. Within these communities, species richness exhibited a wide range, varying from 3 to 149 (mean = 33.79, SD = 30.98). We observed that slightly over one-third (34.32%) of the analyzed anuran species have direct development as their reproductive mode. Additionally, half of the evaluated communities (50.48%) present direct developing species. The prevalence of anuran communities with direct-developing species ranged from 0 to 100%, with an average of 7.12% (SD = 12.37). The highest recorded species richness of direct-developing anurans within a single community reached 61 (Fig. 2).

The Tropical and Subtropical Coniferous Forests; Tropical and Subtropical Dry Broadleaf Forests; and Tropical and Subtropical Moist Broadleaf Forests, located in the southern regions of Mexico, Central America, the Western Amazon, and Brazilian Southern had the highest proportions of direct-developing species (Fig. 2, Table 1). In contrast, the Mediterranean Forests, Woodlands, Scrub; Temperate Grasslands, Savanna, and Shrublands; and Tropical and Subtropical Grasslands, Savannas, and Shrublands, showed the lowest proportions of these species (Table 1).

Table 1 – Mean proportion of direct-developing anurans in each New World biome.

Biome	**Mean Proportion of DD Species (%)**
Tropical and Subtropical Coniferous Forests	19.14
Tropical and Subtropical Dry Broadleaf Forests	16.26
Tropical and Subtropical Moist Broadleaf Forests	11.64
Montane Grasslands and Shrublands	10.84
Mangroves	10.75
Flooded Grasslands and Savannas	8.87
Deserts and Xeric Shrublands	4.54
Temperate Conifer Forests	3.89
Temperate Broadleaf and Mixed Forests	2.5
Tropical and Subtropical Grasslands, Savannas, and Shrublands	2.4
Temperate Subtropical Grasslands, Savannas, and Shrublands	0.72
Mediterranean Forests, Woodlands, and Scrub	0.46

The SEM with no spatial autocorrelation structure and with biomes as random effect was the best model describing the relationships among environmental and biotic characteristics, and the proportion of direct-developing species in the New World anuran communities. Together, biotic and abiotic factors explained 48% of this data (*AIC* = 46.273, *Fisher's* C_2 = 0.273, *p* = 0.872, Fig. 3,

Table S1). Both the phylogenetic composition (PCPS 1) and functional diversity were explained by temperature (TPC1) (r = 0.503, r = -0.510, respectively). The proportion of direct-developing anurans in the New World communities was directly influenced by all factors, being the most important variables in explaining this data, the phylogenetic composition (PCPS 1) with a negative effect (r = -0.660), topography (slope), and temperature (TPC1), both with positive effects (r = 0.170, and r = 0.132, respectively). Although biomes have influenced the investigated relationships, both biotic and abiotic factors were responsible in explaining the amount of the variation in the proportion of direct-developing anurans in the New World communities ($R^2m = 0.48$, $R^2c = 0.60$, Figure 3).

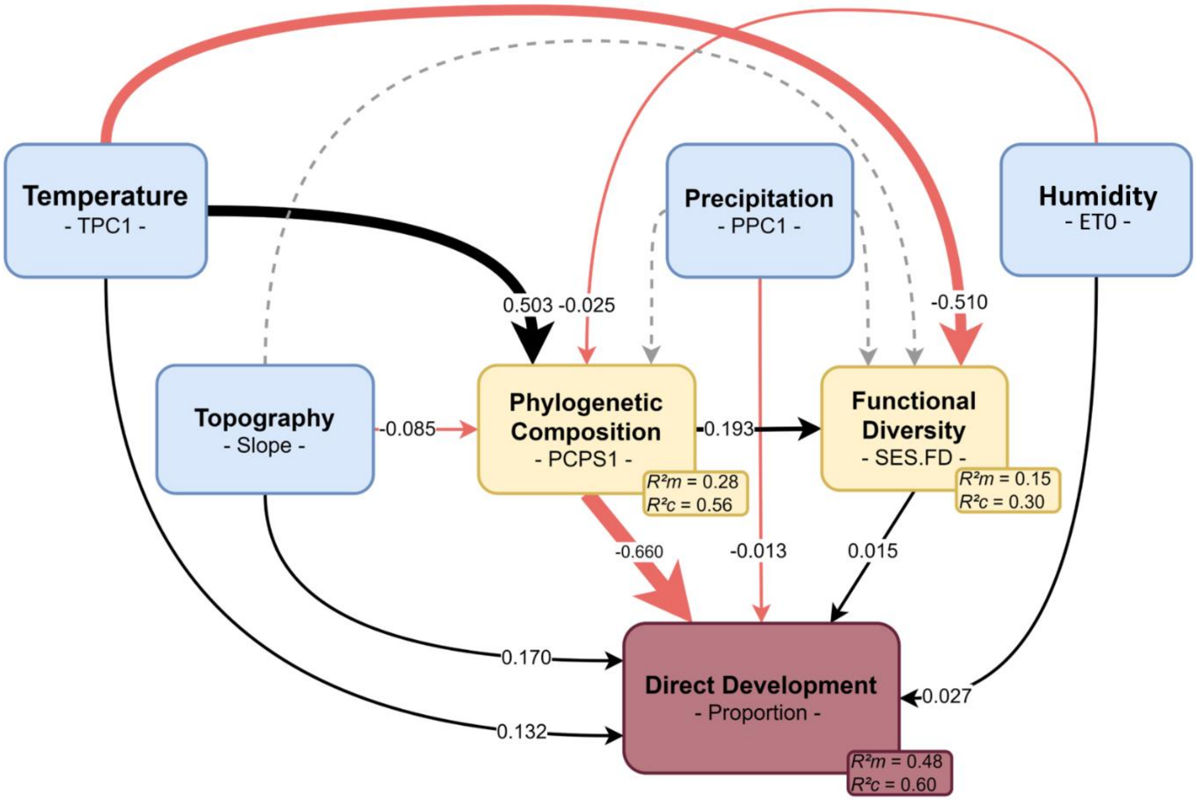

Figure 3. Piecewise SEM relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. R^2 marginal (R^2m) and R^2

conditional (R^2c) values for endogenous variables are presented in the small boxes. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

Regarding the SEM for biomes (sub-models), biotic and abiotic factors explained between 20% (in Temperate Broadleaf and Mixed Forest) and 95% (Flooded Grasslands and Savannas) of the proportion of direct-developing anurans in the communities (Figures S4-S15). We observed a pattern in the relationships of the evaluated factors with the proportion of direct-developing anurans, in which the proportion of these species in tropical and subtropical biomes was more influenced by phylogenetic composition. In contrast, in temperate biomes, abiotic factors, such as temperature and humidity, were the most predominant (Table 2, Figures S4-S15). The SEM for Deserts and Xeric Shrublands was the only one that did not include functional diversity as a predictor of the proportion of direct-developing species in the anuran communities.

Table 2 – Standardized path coefficients of the direct causal links between biotic and abiotic factors and the proportion of direct-developing frogs in anuran communities in the New World biomes. Significant relationships are bolded.

Biome	TPC1	PPC1	ET0	Slope	PCPS	SES.FD
Tropical and Subtropical Moist Broadleaf Forests	**-0.137**	-0.008	-0.001	**0.105**	**-0.830**	**0.073**
Tropical and Subtropical Dry Broadleaf Forests	**0.211**	-0.030	**0.076**	**0.158**	**-0.889**	**0.069**
Tropical and Subtropical Coniferous Forests	**0.458**	**-0.292**	-0.028	**0.281**	**-0.498**	0.030
Temperate Broadleaf and Mixed Forests	**-0.003**	-0.157	0.008	**-0.318**	**0.192**	**0.245**
Temperate Conifer Forests	**0.741**	-0.036	**-0.299**	0.021	**-0.188**	**0.341**
Tropical and Subtropical Grasslands, Savannas, and Shrublands	**-0.192**	**0.246**	**-0.324**	**-0.144**	**-0.547**	0.007
Temperate Subtropical Grasslands, Savannas, and Shrublands	**-0.547**	**0.398**	**-0.547**	-0.015	**-0.193**	**-0.102**
Flooded Grasslands and Savannas	**0.101**	0.014	**-0.342**	0.008	**-0.853**	**0.060**
Montane Grasslands and Shrublands	0.132	**-0.219**	-0.036	**-0.205**	**-0.654**	**0.091**
Mediterranean Forests, Woodlands, and Scrub	**-0.589**	**0.379**	0.057	-0.321	-0.002	**0.447**
Deserts and Xeric Shrublands	**0.271**	**-0.159**	**-0.115**	0.091	**-0.877**	NE
Mangroves	**0.228**	-0.0008	**-0.106**	**0.100**	**-0.954**	**0.119**

4. DISCUSSION

Direct development is a widespread reproductive mode among New World anurans. Our study comprehends a large set of species corresponding to more than 80% of those from the New

World and one-third of the world's anuran species (Frost, 2023; IUCN, 2023). Interestingly, the three biomes harboring the largest proportion of direct-developing anurans species in the New World - Tropical and Subtropical Coniferous Forests, Dry Broadleaf Forests, and Moist Broadleaf Forests - contrast in their climatic and topographical conditions (Corrales et al., 2015). Moreover, the spatial distribution of the proportion of direct-developing species in the New World anuran communities that we showed here, is similar to that mapped for terrestrial breeder amphibians by Lion et al. (2019). Although not every direct developer is a terrestrial breeder, and *vice versa*, these reproductive strategies are strongly correlated (Furness et al., 2022; Liedtke et al., 2022), thus these species can present similar responses to environmental conditions.

Partially contradicting our first expectation, the biotic component, represented by the phylogenetic composition had a stronger influence on the proportion of direct-developing anurans in the New World than the abiotic factors. This result indicates that in this macroecological context, although evolutionary history is also an outcome of abiotic factors, it had a crucial role in assembling these communities, and consequently can be considered as the main driver of the evolution of direct development in the New World anurans. Historical facets of biodiversity, such as the biogeographical history of amphibian clades, can strongly influence the species distributions (Duarte et al., 2013). On the other hand, functional diversity had a weaker effect on the proportion of such species compared to the abiotic factors. Thus, if this metric reflects a measure of coexistence mechanisms, as proposed (see Fontana et al., 2023), this result corroborates with abiotic factors being more predominant in broader scales than the biotic ones (King et al., 2021).

Our comparison of the relationships between abiotic and biotic factors with the proportion of species with direct development across biomes is consistent with our second prediction, once we have found variations in these relationships. The same abiotic characteristics can govern patterns of species occurrence among distinct regions and scales in distinct ways (Lion et al., 2019). Similarly, the New World biomes differ strongly in their abiotic and biotic conditions, and therefore reflect different relationships among these factors, as we found. Thus, the specificities of the distinct biomes and their interaction seem to have influenced the evolution of this RM in diverse ways and led to a reproductive convergence in these biomes (Müller et al., 2013). This result may also explain the fact that direct development is not structured in the phylogeny of anurans, appearing widely disseminated across distinct lineages of New World anurans, as well as having evolved multiple times (Gomez-Mestre et al., 2012, Furness et al., 2022).

As verified through the spatially unstructured model, there was a tendency of the biotic component, represented by phylogenetic composition, to strongly predict the proportion of direct-developing anurans in tropical biomes. In contrast, abiotic factors, such as temperature and humidity, were the most related to direct development in temperate biomes. Tropical regions possess a higher diversity of species which can promote more interaction opportunities among species, and consequently, more diversification (Mittelbach et al., 2007). On the other hand, the higher climatic seasonality and environmental unpredictability of temperate regions can determine and restrict the survival and occurrence of some amphibians (Zamudio et al., 2016). Thus, abiotic factors appear to function as environmental filters selecting only specific reproductive modes adapted to the specific conditions of these regions. Also, this can explain why our SEM for Deserts and Xeric Shrublands did not encompass functional diversity since these environments can present severe and hostile conditions for most amphibians (Warburg 2012).

Therefore, considering the main evolutionary theories linked to the evolution of reproductive modes in anurans, our results confirm that the evolution of direct development in the New World follows a similar pattern proposed by Dobzhansky (1950) to species diversity. This means that, while in tropical regions coexistence mechanisms (e.g., competition and predation) would be the main promoters of the diversity of reproductive modes and, consequently, the evolution of direct development, in temperate regions reproductive diversification would be guided by abiotic factors. The influence of abiotic factors, most specifically climatic variables on the distribution of biodiversity, including anurans, is already well known. Patterns of spatial distribution of biodiversity are frequently related to patterns of temperature, precipitation, and humidity (Gomes-Mestre et al., 2012; Lion et al., 2019; Ochoa-Ochoa et al., 2019).

Our third expectation was partially corroborated. We verified that biomes with the highest proportions of direct-developing anurans were most influenced by the phylogenetic composition, revealing the importance of such factor to this RM. As demonstrated by our results, direct-developing anurans are highly associated with forested environments, those located in mountain regions (Liedtke et al., 2018). Nonetheless, the functional diversity was weakly related to direct development in most of the biome models. It is important to note that our communities were established as a set of species cooccurring in grids of 0.5° resolution. Thus, this measure may be diluting or failing to represent interactions among species that are only apparent at finer scales (Godsoe et al., 2015) as viewed at the local community scale by Fontana et al. (2023), or even through the use of species abundance data. While our models have explained a considerable amount of data variation, there are some parts of the data that remain unexplained. This can be associated with other non-evaluated conditions, such as those related to micro-environmental factors (Fontana et al., 2023).

Investigating evolutionary processes and understanding the relationships between factors related to these processes can be challenging tasks, even more so considering the context of biological communities and macroecological scales. However, using metrics and approaches that can, in a certain way, reflect and represent the patterns originated through these processes proves to be an important ally. The association between ecological particularities and the vast reproductive diversity of amphibians provides us with a range of hypotheses to be assessed and questions to be answered. Our results indicate that the evolution of direct development in anurans and the distribution of such species throughout the New World is a result of the geographic synergy of different forces and mechanisms. Additionally, we highlight the importance of investigating evolutionary processes at different scales, perspectives, and regions. Finally, by associating different selective forces related to the evolution of direct development in anurans in the new world, our results take a fresh look and bring new perspectives to the knowledge of reproductive specialization in amphibians.

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APPENDICES

Appendix 1. New World anuran communities. Database of New World anuran communities distributed in in 9,522 grids of 0.5º.[1]

Appendix 2. Dataset of life-history traits of New World anurans.[1]

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[1] Arquivos disponibilizados como material anexo.

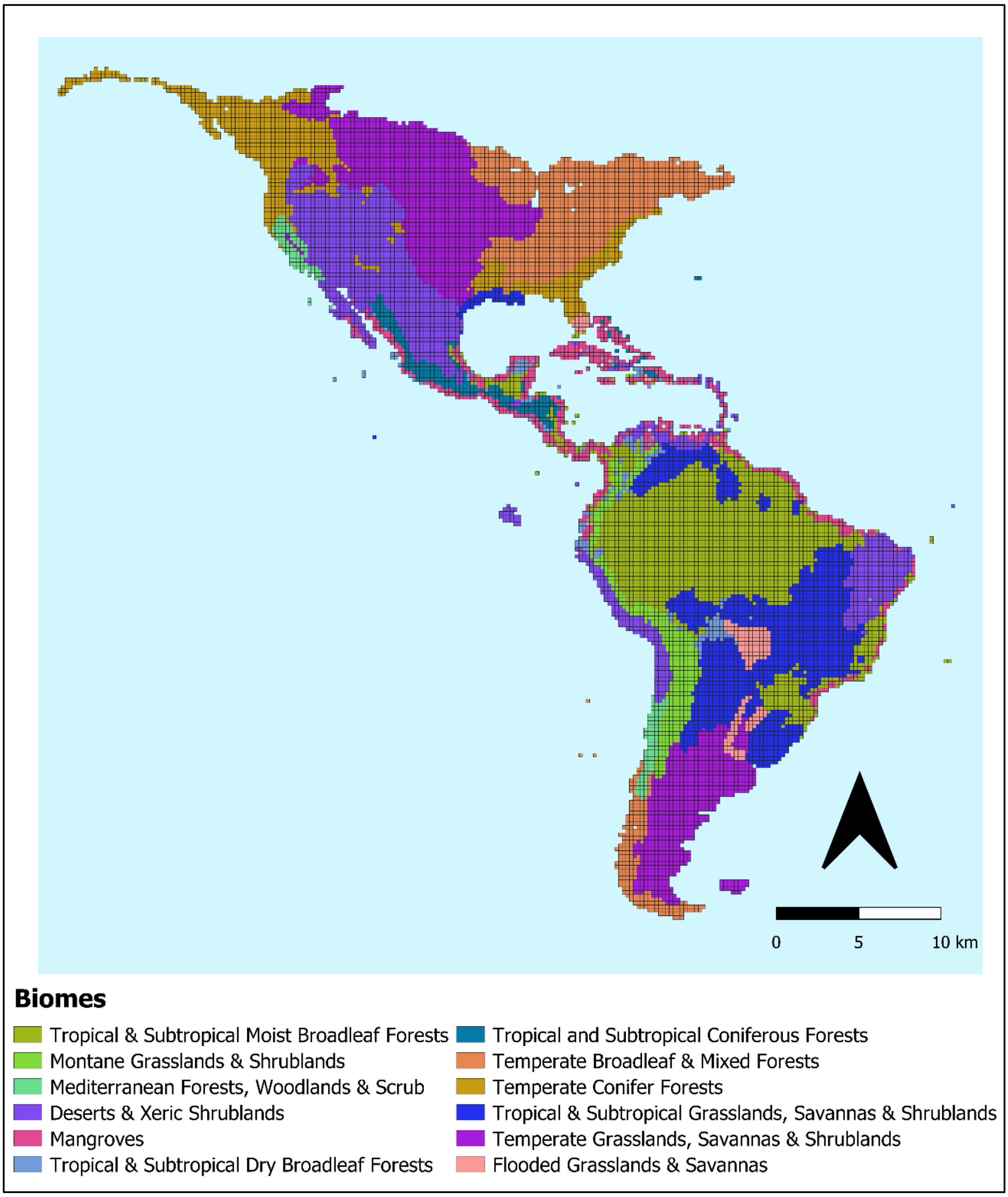

Figure S1. New World biomes according to Olson et al. (2002) and the grid used for the analysis. Cell size of 0.5°.

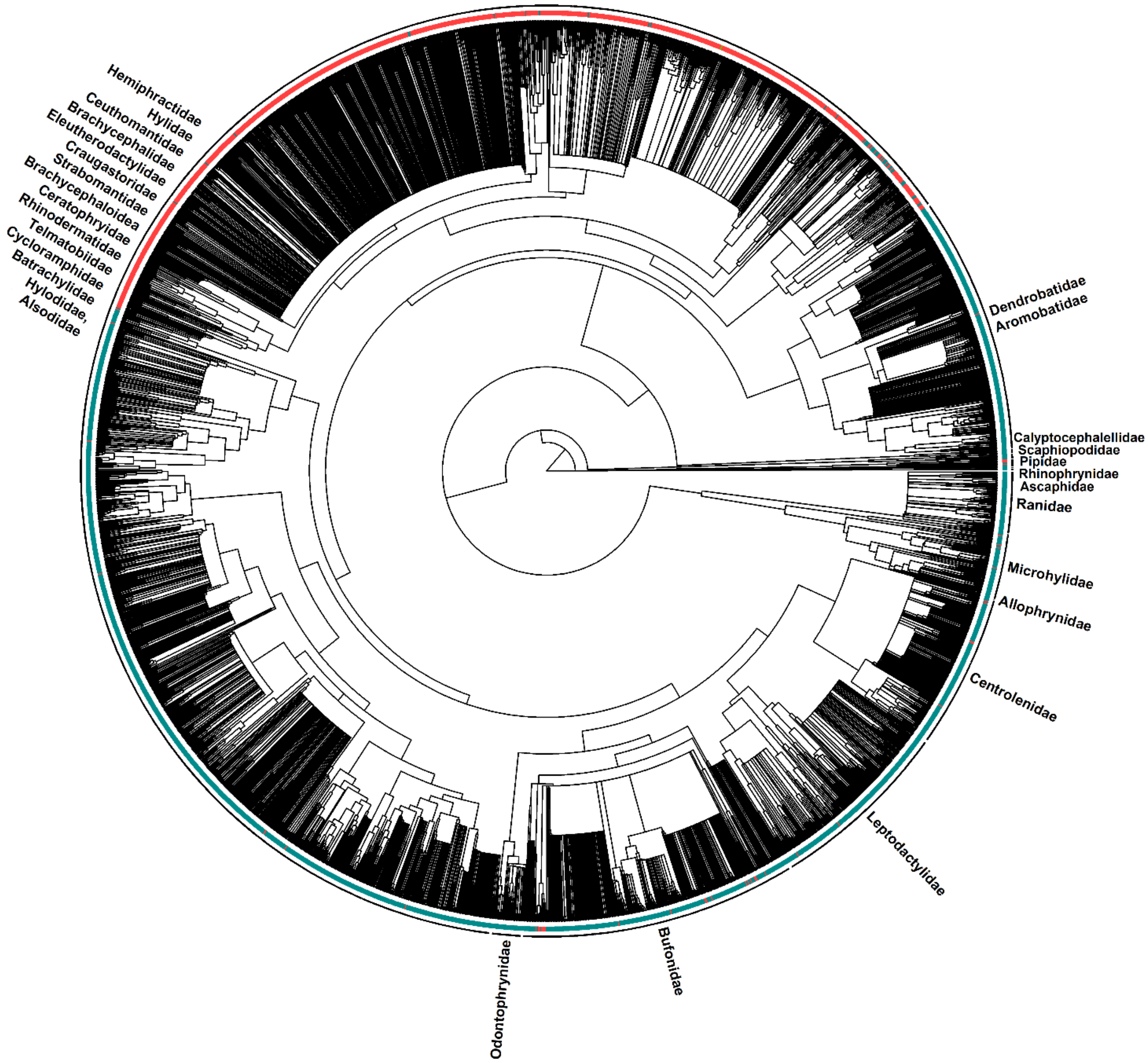

Figure S2. Phylogenetic distribution of development mode in 2,534 anuran species from the New World. Species outlined in blue comprise species with biphasic development (n = 1,663), while species highlighted in red encompass species with direct development (n = 870) and in green species with viviparous development mode (only one species, *Eleutherodactylus jasperi*). Species relationships were based on the consensus phylogenetic tree of Jetz & Pyron (2018).

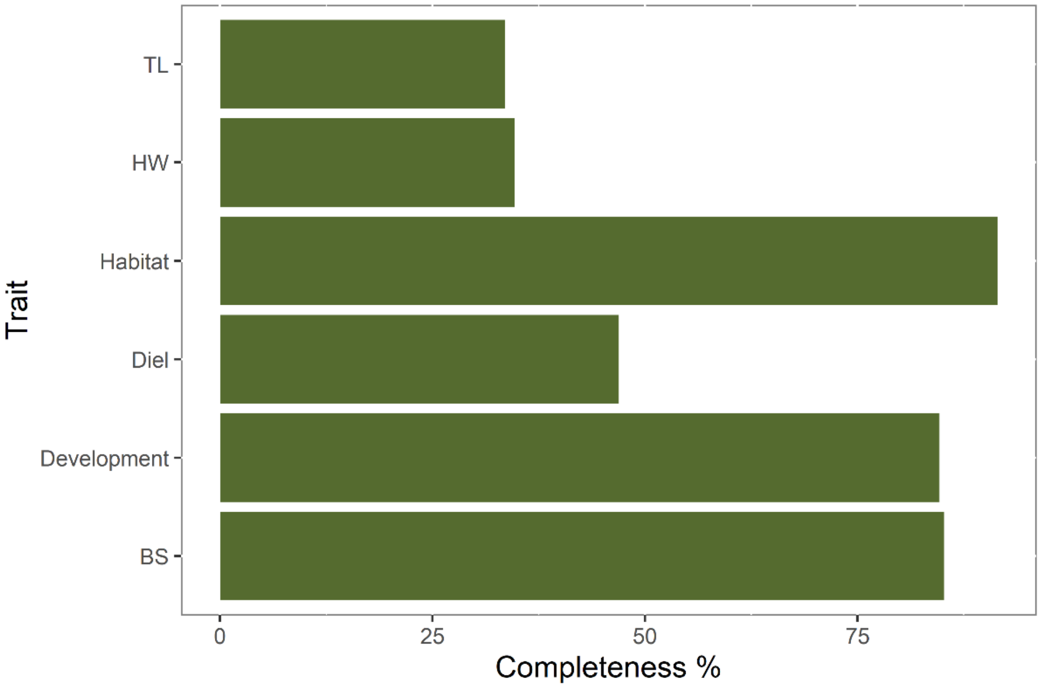

Figure S3. Percentage of data completeness for each gathered trait. Habitat (aquatic; arboreal; fossorial; semi-arboreal; semi-fossorial; semi-terrestrial; and terrestrial); Diel (diurnal, nocturnal, or both); Development mode (larval; direct development; and viviparous); BS - body size (mean value in mm); HW - head width (mean value in mm); TL - tibia length (mean value in mm).

S1 Table. Result of piecewiseSEM (i - model without spatial autocorrelation structure and biomes as random effects). Direct and indirect effects of predictor variables on the proportion of direct-developing species of New World anuran communities. Goodness of fit: *Fischer's C* = 0.273; *p-value* = 0.872; *DF* =2; *AIC* = 46.273. Standard error (St. Error); degrees of freedom (DF); critical value (Crit. Value); and standardized estimate (St. Estimate).

Response	Predictor	Estimate	St. Error	DF	Crit.Value	P.Value	St. Estimate
PCPS1	PPC1	0.0086	0.0067	9506	1.2912	0.1967	0.0086
PCPS1	**TPC1**	**0.5039**	**0.0126**	**9506**	**39.9332**	**0**	**0.5039**
PCPS1	**PET**	**-0.0251**	**0.0067**	**9506**	**-3.7596**	**0.0002**	**-0.0251**
PCPS1	**Slope**	**-0.0856**	**0.0078**	**9506**	**-10.9379**	**0**	**-0.0856**
SES.FD	**PCPS1**	**0.1937**	**0.0144**	**9506**	**13.4855**	**0**	**0.1937**
SES.FD	**TPC1**	**-0.5106**	**0.0191**	**9506**	**-26.769**	**0**	**-0.5106**
SES.FD	PPC1	-0.0099	0.0094	9506	-1.0523	0.2927	-0.0099
SES.FD	Slope	0.0144	0.011	9506	1.3074	0.1911	0.0144
Proportion	**SES.FD**	**0.015**	**0.0066**	**9504**	**2.2627**	**0.0237**	**0.015**
Proportion	**PCPS1**	**-0.6605**	**0.0094**	**9504**	**-70.5763**	**0**	**-0.6605**
Proportion	**TPC1**	**0.1323**	**0.0128**	**9504**	**10.3634**	**0**	**0.1323**
Proportion	**PPC1**	**-0.0133**	**0.0061**	**9504**	**-2.2019**	**0.0277**	**-0.0133**
Proportion	**Slope**	**0.1702**	**0.0071**	**9504**	**23.8861**	**0**	**0.1702**
Proportion	**PET**	**0.0272**	**0.0061**	**9504**	**4.484**	**0**	**0.0272**

Variance explained by fixed (Marginal) and fixed + random (Conditional) effects of relationships established in the structural equation model.

Response	**Marginal**	**Conditional**
PCPS1	0.28	0.56
SES.FD	0.15	0.30
Proportion	0.48	0.60

S2 Table. Result of piecewiseSEM (ii - model with spatial autocorrelation structure and without random effects). Direct and indirect effects of predictor variables on the proportion of direct-developing species of New World anuran communities. Goodness of fit: *Fischer's C* = 0.273; *p-value* = 0.872; *DF* =2; AIC = 48.650. Standard error (St. Error); degrees of freedom (DF); critical value (Crit. Value); and standardized estimate (St. Estimate).

Response	Predictor	Estimate	St. Error	DF	Crit.Value	P.Value	St. Estimate
PCPS1	**TPC1**	**0.1184**	**0.0268**	**9522**	**4.4105**	**0**	**0.1184**
PCPS1	PPC1	-0.0002	0.0019	9522	-0.1064	0.9152	-0.0002
PCPS1	PET	0.0013	0.0017	9522	0.7296	0.4657	0.0013
PCPS1	**Slope**	**-0.0298**	**0.0048**	**9522**	**-6.2812**	**0**	**-0.0298**
SES.FD	PCPS1	0.0094	0.0242	9522	0.3906	0.6961	0.0094
SES.FD	**TPC1**	**-0.2111**	**0.0504**	**9522**	**-4.1917**	**0**	**-0.2111**
SES.FD	PPC1	-0.0032	0.0047	9522	-0.6707	0.5024	-0.0032
SES.FD	Slope	0.0016	0.0114	9522	0.1439	0.8856	0.0016
Proportion	**SES.FD**	**0.0276**	**0.0037**	**9522**	**7.5322**	**0**	**0.0276**
Proportion	**PCPS1**	**-0.2534**	**0.0089**	**9522**	**-28.3214**	**0**	**-0.2534**
Proportion	**TPC1**	**-0.2708**	**0.0235**	**9522**	**-11.5332**	**0**	**-0.2708**
Proportion	**PPC1**	**-0.0039**	**0.0017**	**9522**	**-2.3045**	**0.0212**	**-0.0039**
Proportion	PET	-0.0025	0.0015	9522	-1.6305	0.103	-0.0025
Proportion	**Slope**	**0.0467**	**0.0042**	**9522**	**11.2377**	**0**	**0.0467**

Variance explained (R^2) by fixed effects of relationships established in the structural equation model.

Response	**R^2**
PCPS1	0.02
SES.FD	0.04
Proportion	0.30

S3 Table. Result of piecewiseSEM (iii - model with spatial autocorrelation structure and the biomes as random effects). Direct and indirect effects of predictor variables on the proportion of direct-developing species of New World anuran communities. Goodness of fit: *Fischer's C* = 0.830; *p-value* = 0.660; *DF* =2; *AIC* = 52.830. Standard error (St. Error); degrees of freedom (DF); critical value (Crit. Value); and standardized estimate (St. Estimate).

Response	Predictor	Estimate	St. Error	DF	Crit.Value	P.Value	St. Estimate
PCPS1	**TPC1**	**0.1457**	**0.025**	**9506**	**5.8364**	**0**	**0.1457**
PCPS1	PPC1	0.0002	0.0021	9506	0.0737	0.9413	0.0002
PCPS1	PET	0	0.0022	9506	-0.0218	0.9826	0
PCPS1	**Slope**	**-0.0312**	**0.0049**	**9506**	**-6.3446**	**0**	**-0.0312**
SES.FD	PCPS1	0.032	0.0231	9506	1.3828	0.1667	0.032
SES.FD	**TPC1**	**-0.2484**	**0.0452**	**9506**	**-5.5009**	**0**	**-0.2484**
SES.FD	PPC1	-0.0039	0.005	9506	-0.7771	0.4371	-0.0039
SES.FD	Slope	0.0021	0.0115	9506	0.1836	0.8543	0.0021
Proportion	**SES.FD**	**0.0258**	**0.0037**	**9504**	**6.9603**	**0**	**0.0258**
Proportion	**PCPS1**	**-0.2414**	**0.0089**	**9504**	**-27.2216**	**0**	**-0.2414**
Proportion	**TPC1**	**-0.228**	**0.0218**	**9504**	**-10.4728**	**0**	**-0.228**
Proportion	**PPC1**	**-0.0042**	**0.0018**	**9504**	**-2.3014**	**0.0214**	**-0.0042**
Proportion	**PET**	**0.0048**	**0.0019**	**9504**	**2.576**	**0.01**	**0.0048**
Proportion	**Slope**	**0.0581**	**0.0043**	**9504**	**13.6148**	**0**	**0.0581**

Variance explained by fixed (Marginal) and fixed + random (Conditional) effects of relationships established in the structural equation model.

Response	**Marginal**	**Conditional**
PCPS1	0.02	0.03
SES.FD	0.05	0.07
Proportion	0.18	0.18

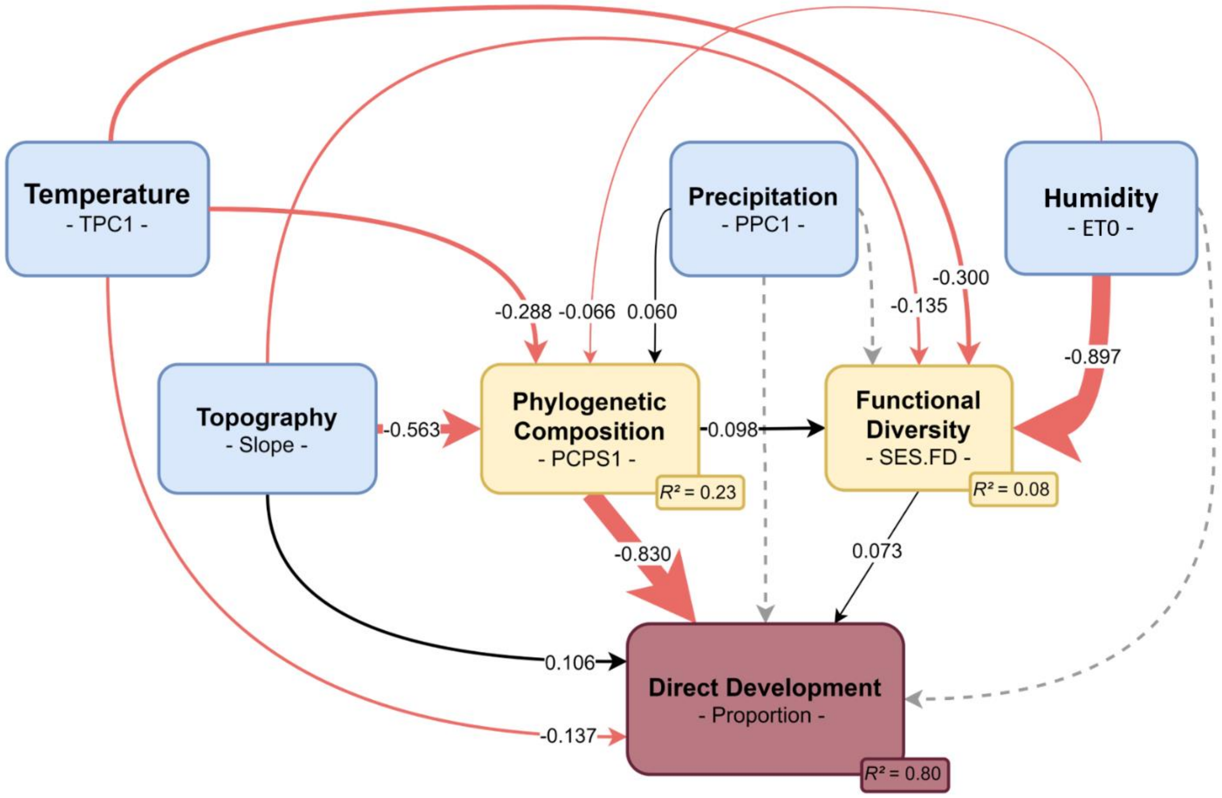

Figure S4. Piecewise SEM (*Fisher's C* = 0.539, *p* = 0.764, *AIC* = 0.764) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Tropical and Subtropical Moist Broadleaf Forest of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

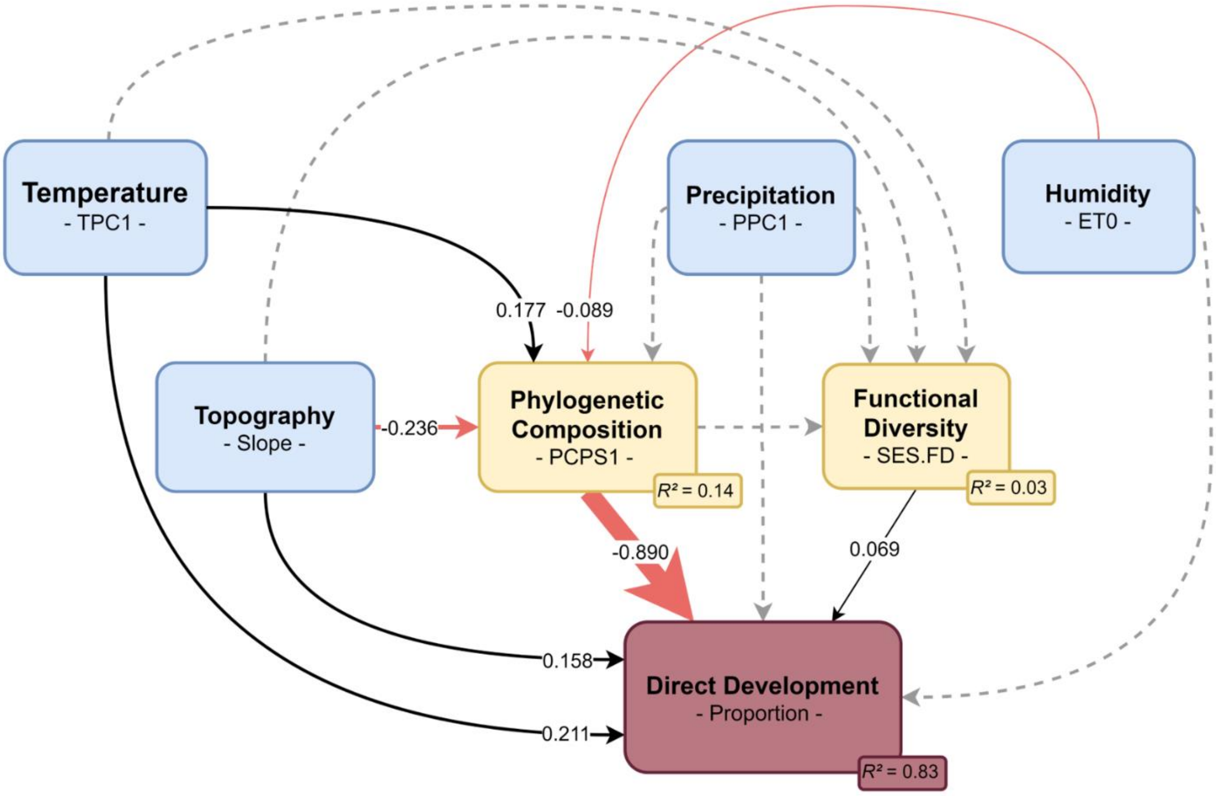

Figure S5. Piecewise SEM (*Fisher's C* = 1.863, *p* = 0.394, *AIC* = 41.863) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Tropical and Subtropical Dry Broadleaf Forest of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

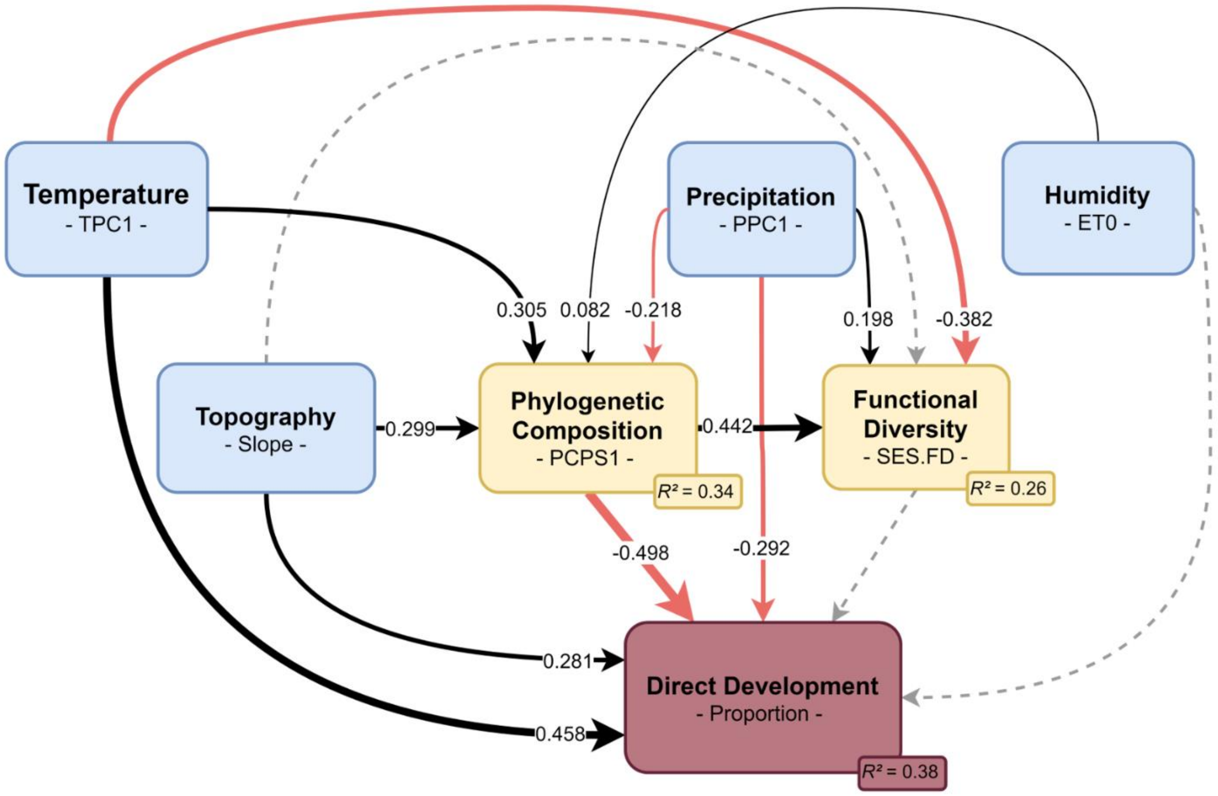

Figure S6. Piecewise SEM (*Fisher's C* = 0.107, *p* = 0.948, *AIC* =40.107) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Tropical and Subtropical Coniferous Forest of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

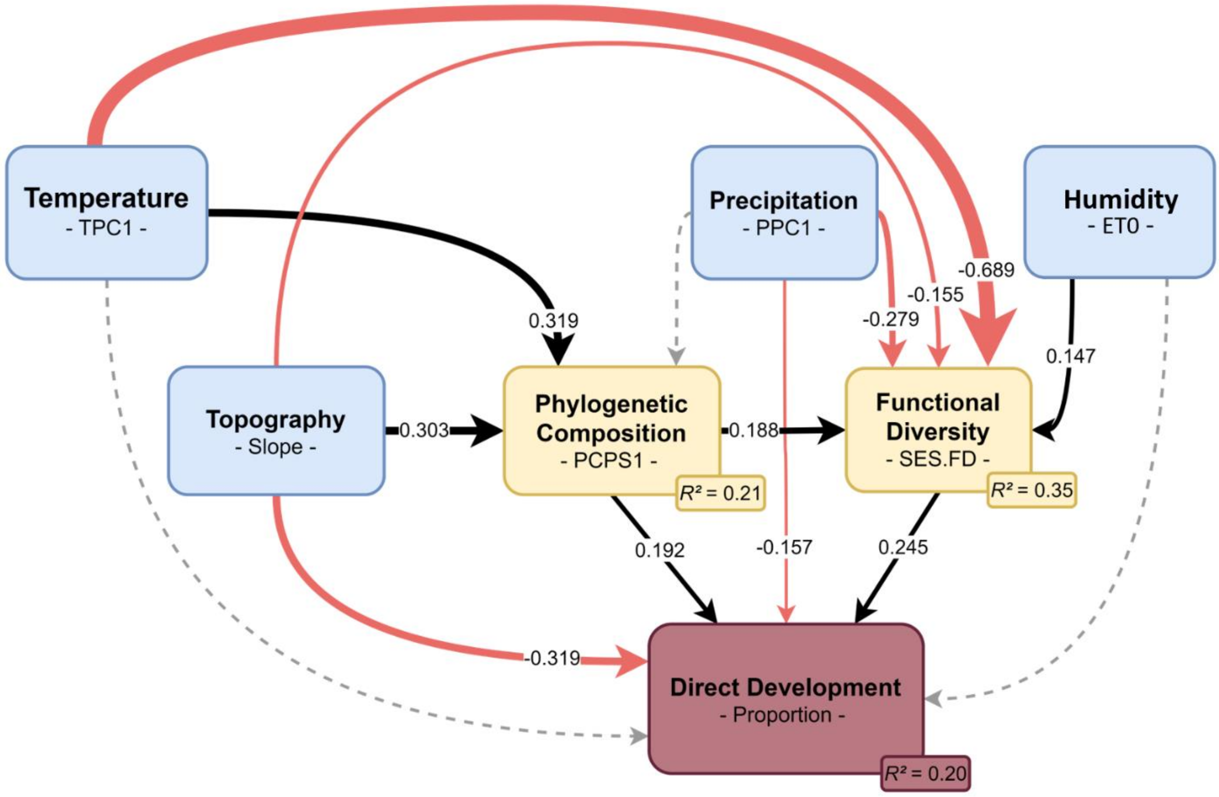

Figure S7. Piecewise SEM (*Fisher's C* = 0.343, *p* = 0.842, *AIC* = 40.343) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Temperate Broadleaf and Mixed Forest of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

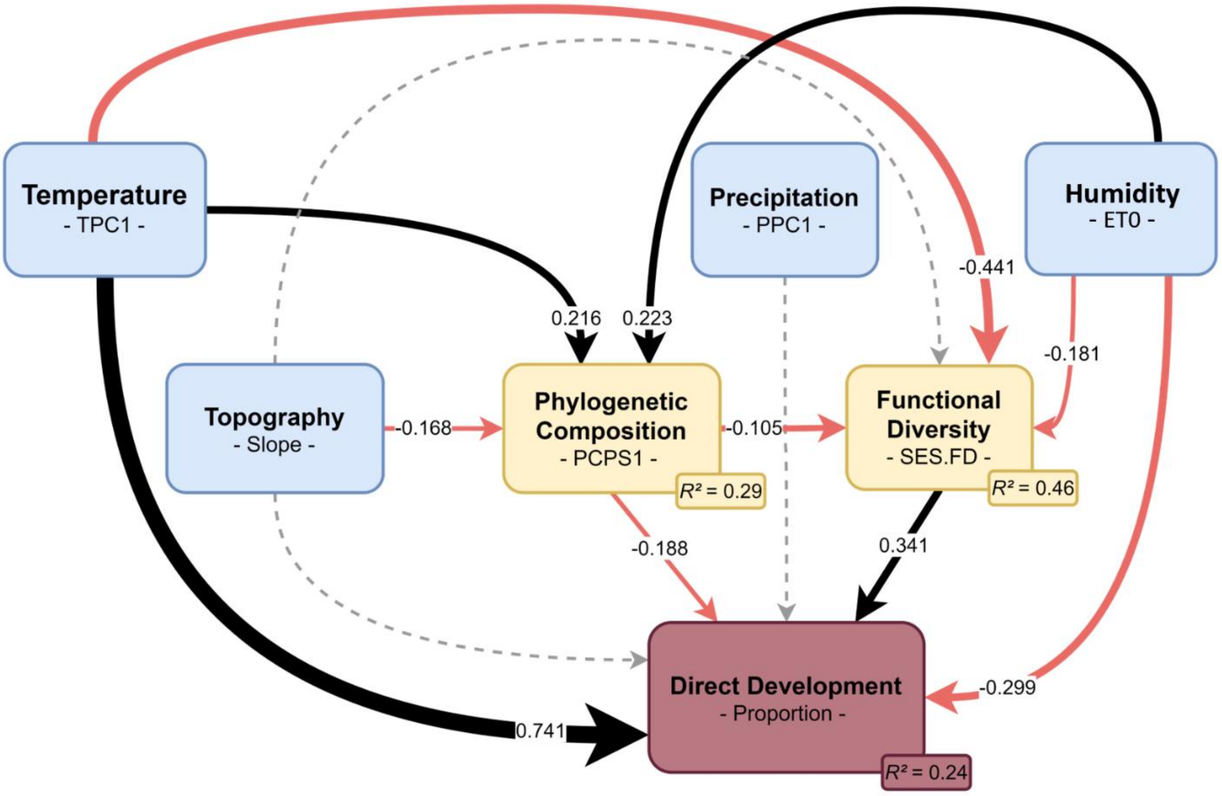

Figure S8. Piecewise SEM (*Fisher's C* = 0.639, *p* = 0.959, *AIC* = 38.639) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Temperate Conifer Forests of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

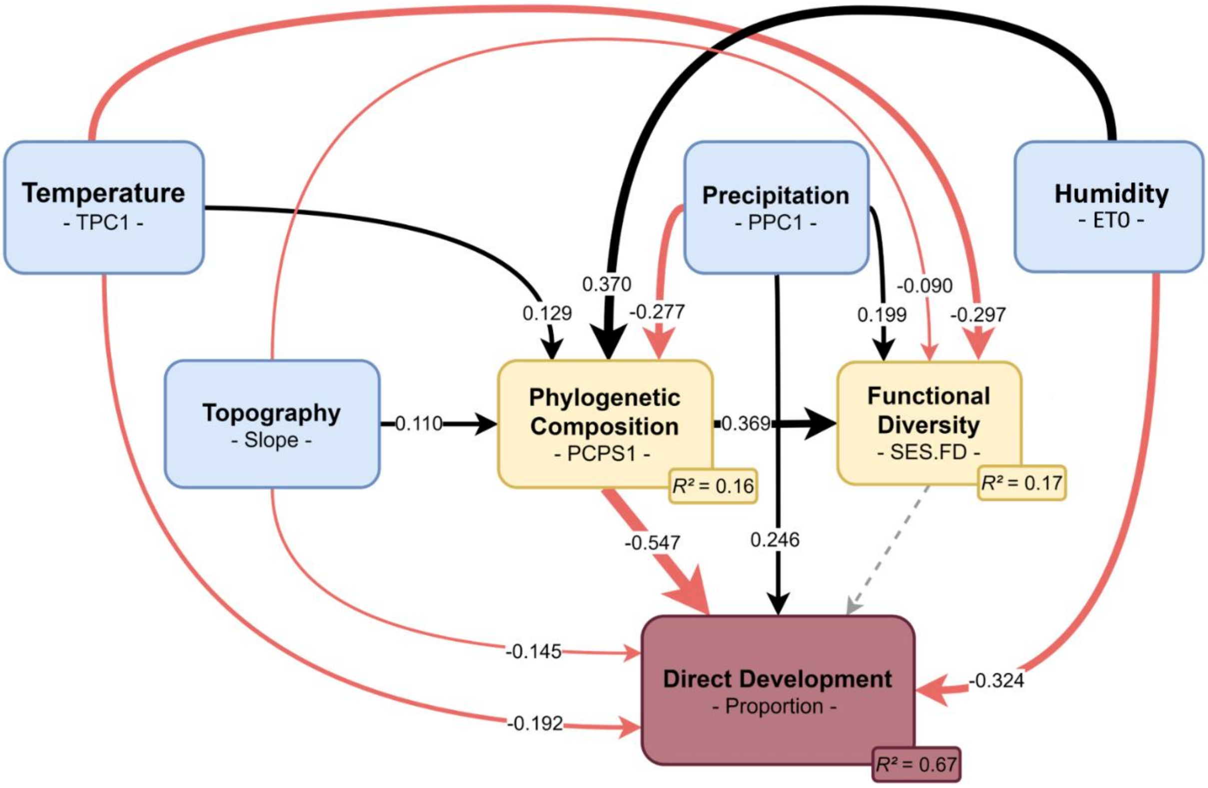

Figure S9. Piecewise SEM (*Fisher's C* = 2.554, *p* = 0.279, *AIC* = 42.554) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Tropical and Subtropical Grasslands, Savannas and Shrublands of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

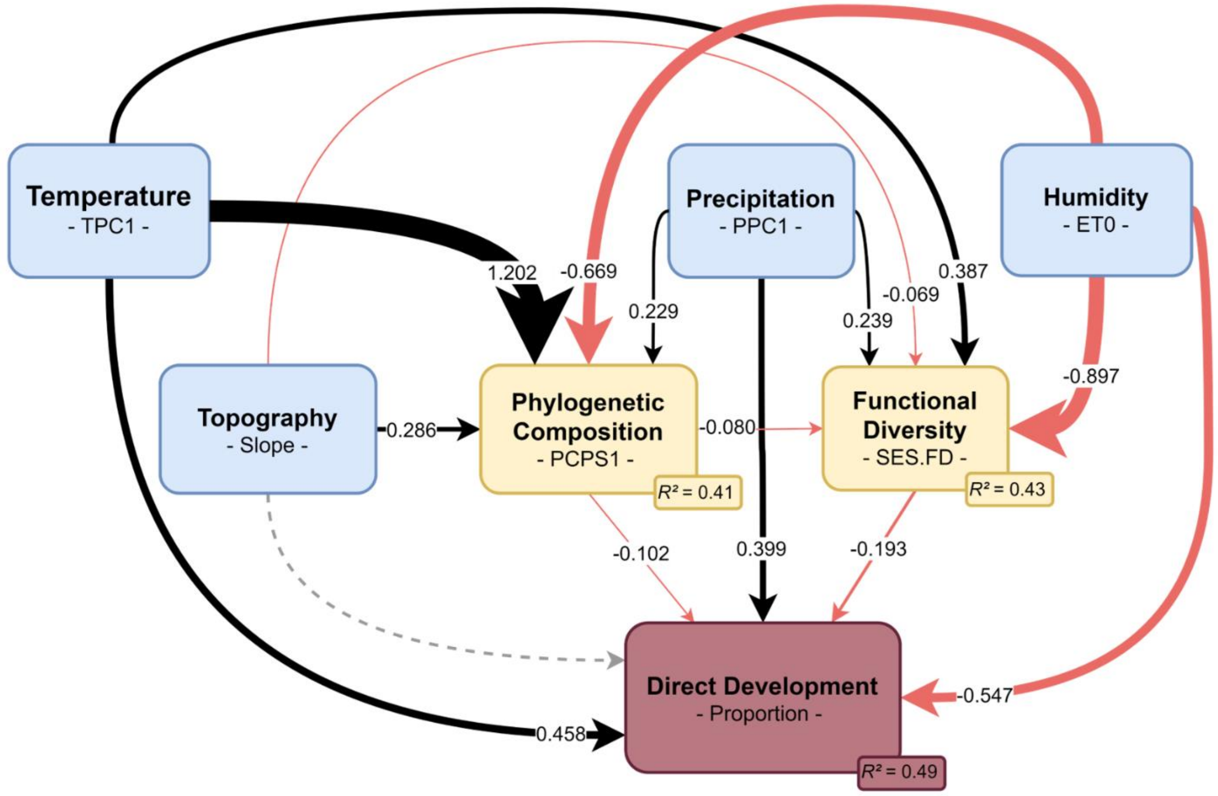

Figure S10. Piecewise SEM (*Fisher's C* = 0.318, *p* = 0.853, *AIC* = 40.318) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Temperate Grasslands, Savannas, and Shrublands of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

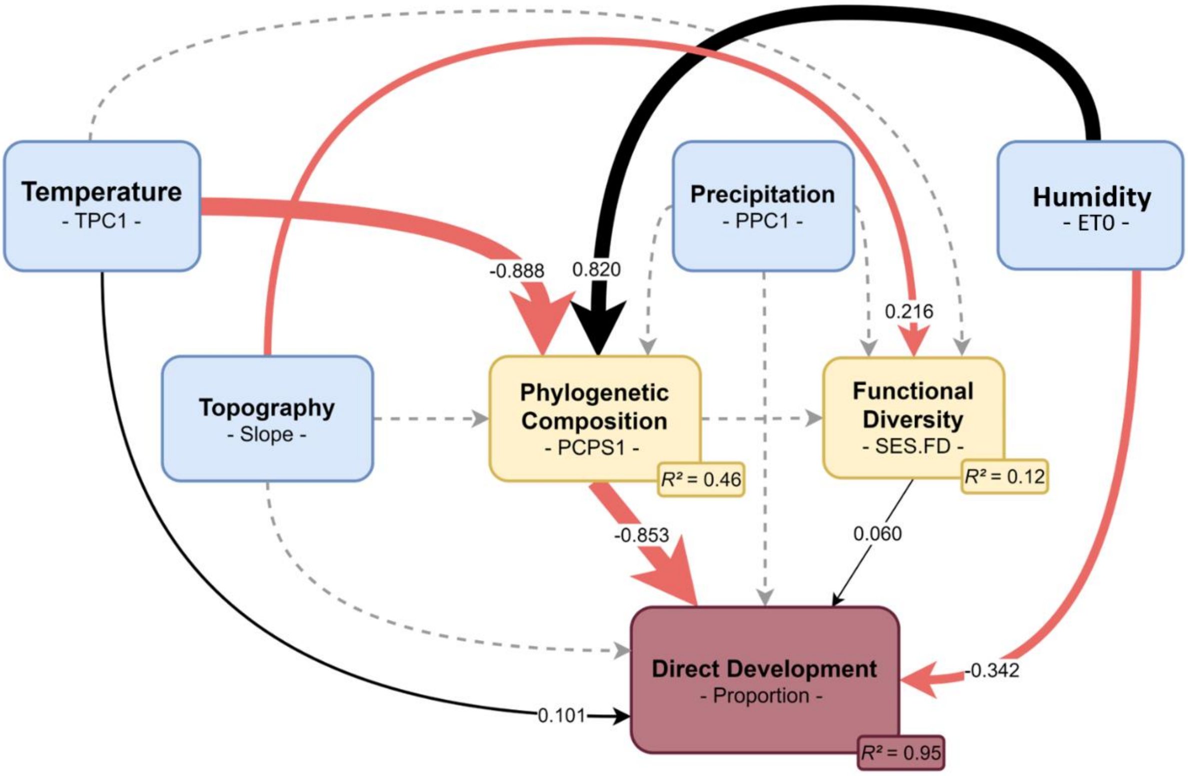

Figure S11. Piecewise SEM (*Fisher's* $C = 1.442$, $p = 0.486$, $AIC = 41.442$) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Flooded Grasslands and Savannas of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

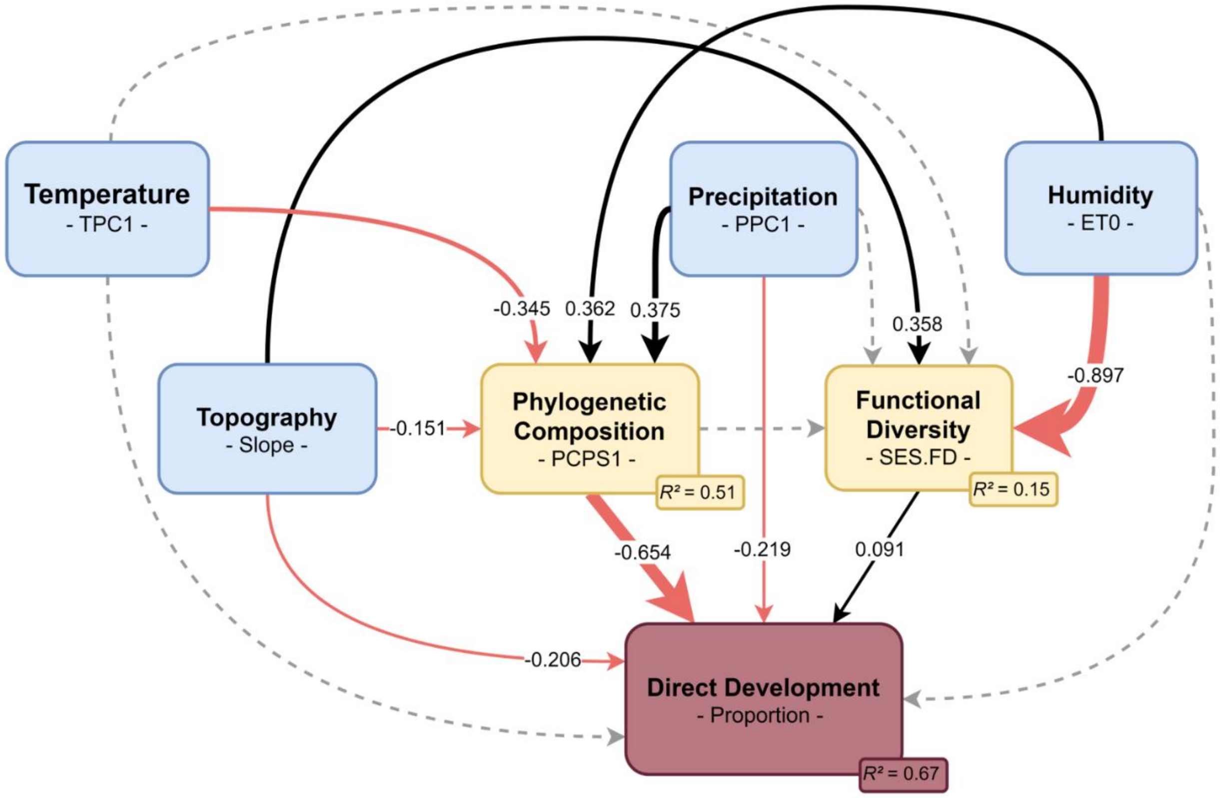

Figure S12. Piecewise SEM (*Fisher's C* = 0.842, *p* = 0.657, *AIC* = 40.842) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Montane Grasslands and Shrublands of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

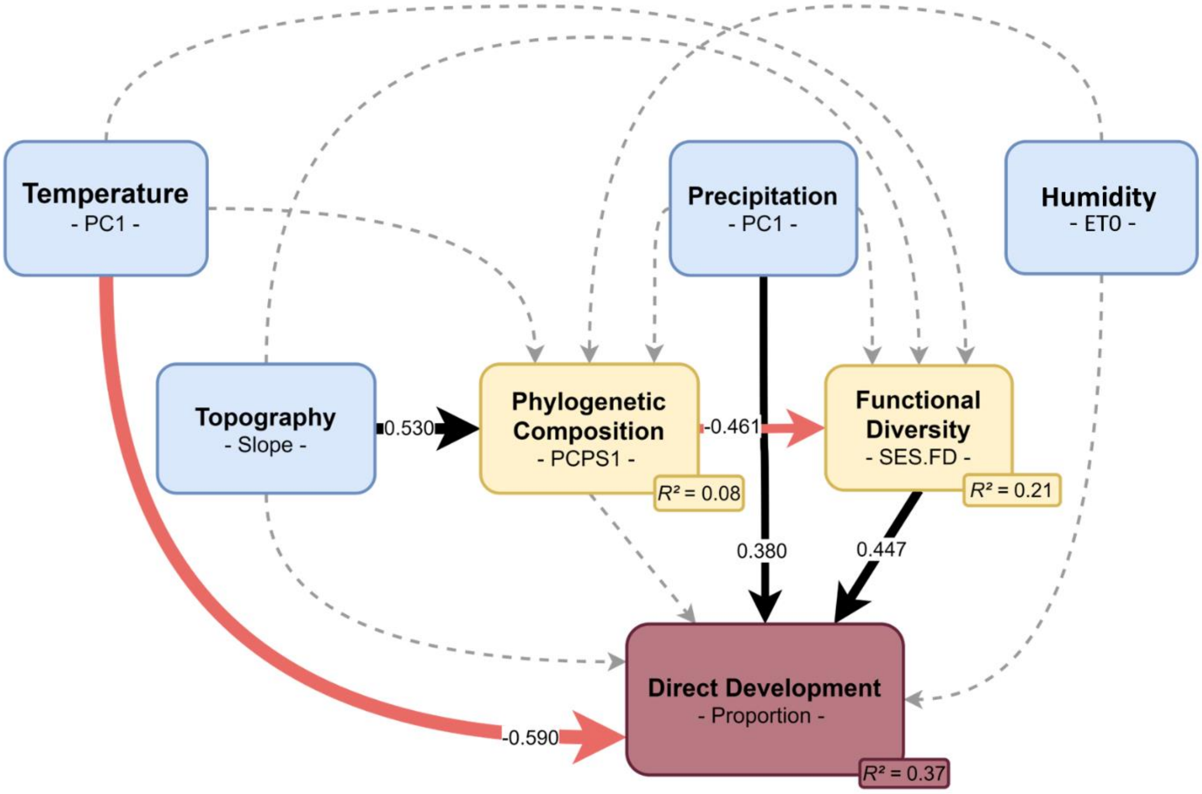

Figure S13. Piecewise SEM (*Fisher's* $C = 1.052$, $p = 0.591$, $AIC = 41.052$) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Mediterranean Forests, Woodlands and Scrub of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

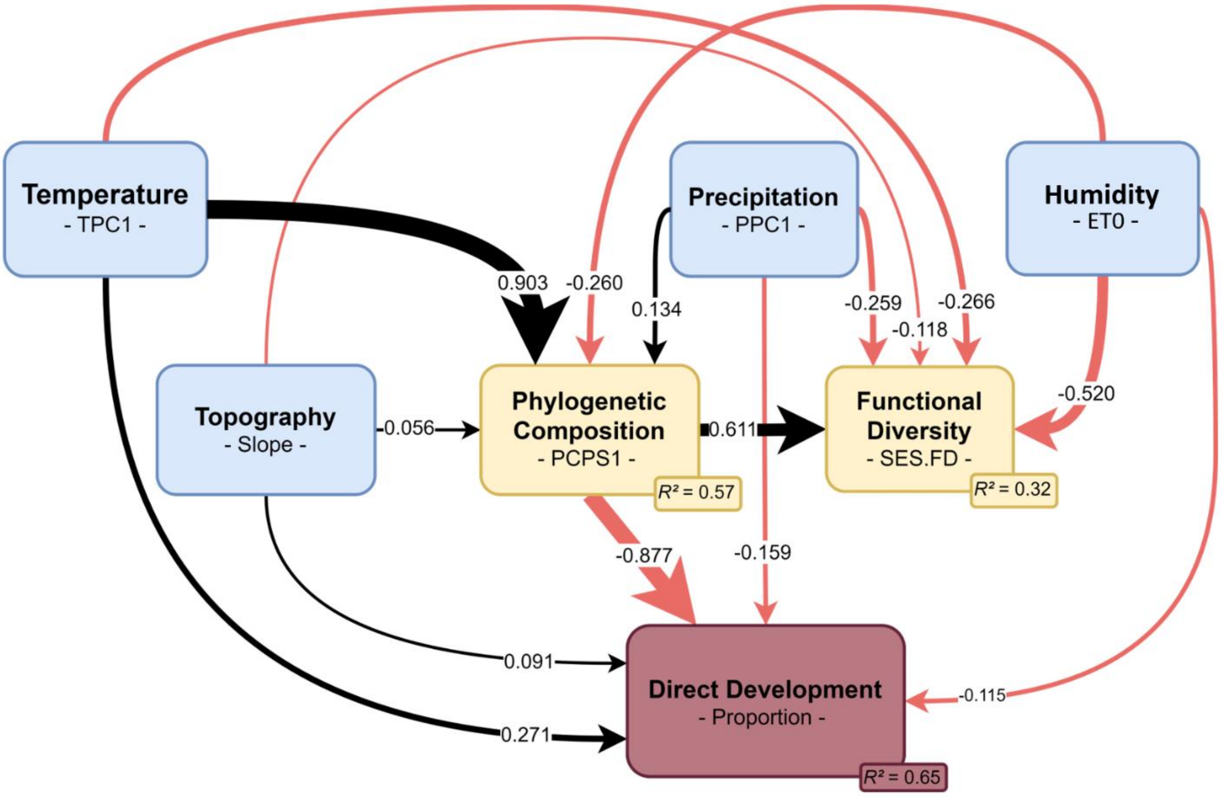

Figure S14. Piecewise SEM (*Fisher's C* = 0.455, *p* = 0.797, *AIC* = 40.455) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Desert and Xeric Shrublands of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

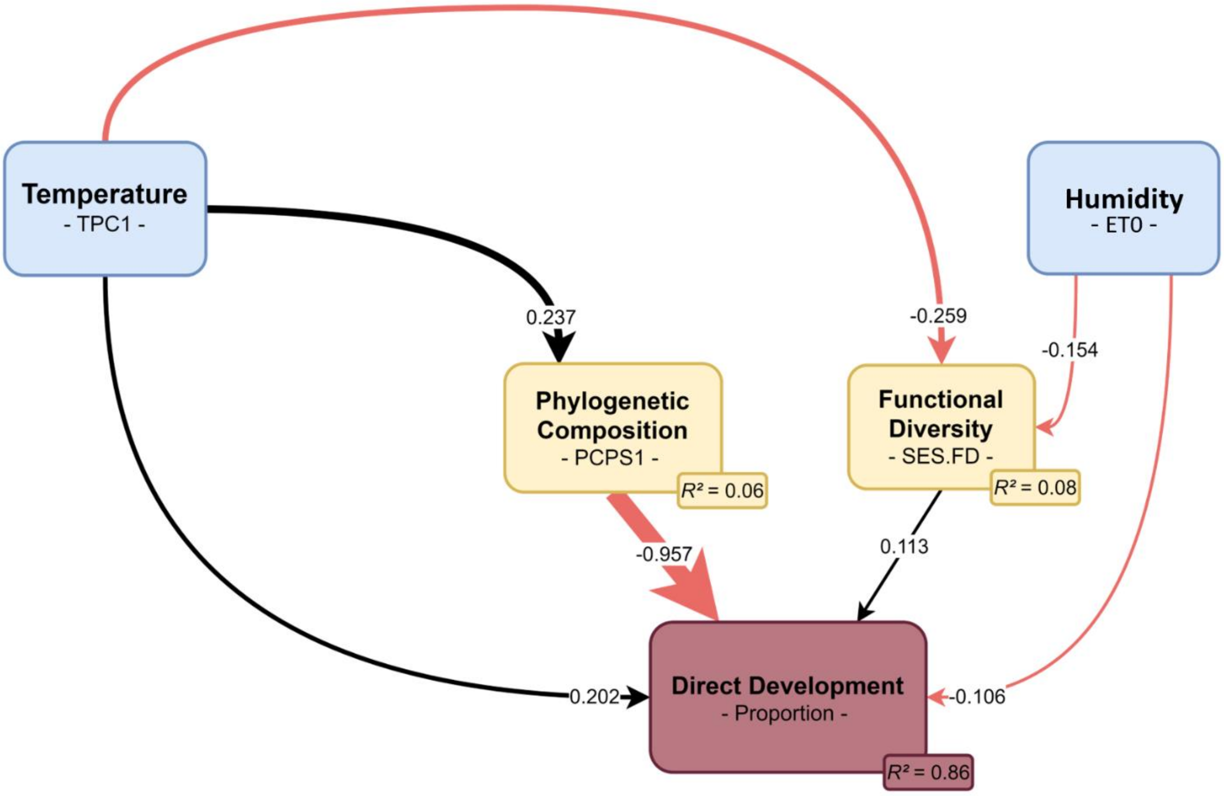

Figure S15. Piecewise SEM (*Fisher's C* = 5.259, *p* = 0.262, *AIC* = 31.259) relating biotic the indirect and direct effects of abiotic factors (blue boxes) and biotic factors (yellow boxes) on the proportion of direct-developing species (the brown box) in anuran communities of the Mangroves of the New World. Solid arrows represent significant relationships, being positive relationships represented by the black arrows and negative relationships by the red ones. Values on arrows correspond to standardized coefficients. The thickness of the arrows is proportional to the magnitude of the standardized coefficients.

CAPÍTULO IV

AMPHIBIAN STRONGHOLDS: PROTECTED AREAS AND THE FUTURE OF DIRECT-DEVELOPING FROGS OF GENUS ISCHNOCNEMA IN THE ATLANTIC FOREST UNDER CLIMATE CHANGE

Capítulo com previsão de submissão para a revista Biological Conservation

Amphibian strongholds: Protected areas and the future of direct-developing frogs of genus *Ischnocnema* in the Atlantic Forest under climate change

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Highlights

- *Ischnocnema* species are expected to show contractions in their distributions
- Atlantic Forest PAs can be considered as refugees for direct-developing frogs
- Future of *Ischnocnema* frogs is highly dependent of the Atlantic Forest PAs

Abstract

Among the highly diverse amphibian species from the Atlantic Forest (AF) and deviating from the usually biphasic anuran reproductive mode, are the direct-developing frogs. Predicting how species will face climate change scenarios and knowing the effectiveness of the protected areas (PAs) are essential and useful tools for planning different conservation strategies. In this study, we seek to: i) model the current and future distributions of 18 direct-developing frogs of the genus *Ischnocnema* distributed in the AF; ii) predict possible changes in species distributions in the face of two climate change scenarios for 2050 and 2090; and iii) evaluate the protection degree of such species in the AF. For this, through the ensemble of small models approach, using four different algorithms and five general circulation models, we generated *Ischnocnema* species distribution models. We evaluated the protection degree of direct-developing anurans through the mean percentage overlay. We verified that the southeast AF harbors most of the direct-developing species. We predict a linear and accentuated reduction in the distribution areas of these species. Regarding the protection degree, we verified that the PAs are effective in protecting the distribution area of all *Ischnocnema* frogs in the present, indicating that these areas already serve as true strongholds for these species and that with the possible future losses in the distribution areas, they will have even greater importance for the conservation of AF direct-developing frogs.

Keywords: anurans; future predictions; protection degree; species distribution modeling

1. Introduction

Several initiatives can be taken to protect natural ecosystems and biodiversity, one of them is the establishment of protected areas (PAs; Leclère et al., 2020). With more than 1,500 PAs and less than 12% of its total extension protected, the Atlantic Forest holds almost 60% of Brazilian PAs (MMA, 2023). This forest has a huge environmental heterogeneity, with considerable topographic variations, a wide gradient of climatic and microclimatic conditions, and a variety of environments and ecosystems, reflecting in one of the world’s highest diversities of plants and animals, being considered a biodiversity hotspot (Marques et al., 2021; Myers et al., 2000). Among vertebrates, amphibians stand out as one of the most representative taxonomic groups of the Atlantic Forest, with more than 700 species of which many (~70%%) are endemic (Figueiredo et al., 2021). Also, amphibians have a distinct evolutionary history, resulting in a great diversity of morphologies, behaviors, and reproductive modes (Wells, 2007).

Amidst the high reproductive diversity, direct development is characterized by the absence of the larval form known as a tadpole, which is the hatching of eggs directly into miniature versions of adults (Haddad and Prado, 2005; Nunes-de-Almeida et al., 2021). Distinct factors are listed as drivers of the evolution of direct development in amphibians (Fontana et al., 2022). Among the abiotic factors, climate and topography are the major forces related to the evolution of the terrestrial reproductive modes, which are also associated with the distribution of such species (Liedtke et al., 2017; Lion et al., 2019). Additionally, the occurrence of amphibians with specialized reproductive modes, such as direct development, along the Atlantic Forest coast can be attributed to the climate stability during the Pleistocene era, as well as the high topographic complexity of this environment (Benício et al., 2021; Carnaval et al., 2009; Haddad and Prado, 2005). On the other hand, although this specialized reproductive mode has enabled a certain independence of the water bodies for reproduction, direct-developing frogs still rely on moisture-rich environments for survival, particularly living in tropical and subtropical forests (Wells, 2007).

Belonging to the family Brachycephalidae, the genus *Ischnocnema* is recognized as one of the most prominent lineages of direct-developing amphibians in the Atlantic Forest with almost 40 described species, many of which are considered endemic (Figueiredo et al., 2021; Frost, 2023; Pie et al., 2013; Thomé et al., 2020). Brachycephalids are distributed along the entire coast of the Atlantic Forest, mainly in the highlands of the southeastern portion of the Serra do Mar mountain system (Bornschein et al., 2016; Siqueira et al., 2011). This region, known for being one of the leading centers of endemism and harboring one of the greatest biodiversity in the Atlantic Forest, especially of amphibians, also contains the most significant fragments of dense Atlantic Forest, where many of the Atlantic Forest PAs were implemented (Campos and Lourenço-de-Moraes, 2017; Carlucci et al., 2021; de Castro et al., 2021). Whereas these areas actually serve as strongholds for biodiversity, many species can become threatened in the future, especially by climate change.

Several studies have already predicted the effects of climate change on distinct species groups in the Atlantic Forest (Bogoni and Tagliari, 2021; Lourenço-de-Moraes et al., 2019a; Mota et al., 2022). Possible outcomes of such effects on native species can vary from adaptation to the new conditions, to shifts in their geographic range (displacement, expansions, or contraction) or local extinctions (Diniz-Filho and Bini, 2008; Román-Palacios and Wiens, 2020). In the case of amphibians, it is frequently expected that reductions of climatically suitable areas will affect most species, but especially those with specialized reproductive modes (Loyola et al., 2014; Vasconcelos et al., 2018; Lourenço-de-Moraes et al., 2019b), such as direct development. These distinct responses of species to climate change and environmental modification are highly mediated by their intrinsic characteristics (Alves-Ferreira et al., 2022; Aragón et al., 2010).

Amphibians have specific characteristics and distinct life-history traits that can be linked to population decline and extinction risk (Fontana et al., 2021; Sodhi et al., 2008). Some of these characteristics, such as the strong dependence on moist environments (Wells, 2007), reduced clutch size, small body length (Callery et al., 2001), and higher sensitivity to environmental alterations and susceptibility to infections by the chytrid fungus *Bd* (Mesquita et al., 2017; Nowakowski et al.,

2017) are common for direct-developing species. However, this relationship may be further intensified by climate change, once alterations in the temperature, precipitation regimes, and the availability of moist environments can trigger negative impacts on the survival of individuals, reproduction, development, and population maintenance, leading to a greater extinction risk of amphibians (Blaustein et al., 2010; Ficetola and Maiorano, 2016). Therefore, the use of approaches that can predict the potential effects of climate change on species distribution, such as the Species Distribution Models (SDM), has become an important tool for understanding the future of biodiversity on a changing planet (Guisan et al., 2013).

The increasing use of SDM has been valuable in identifying potentially suitable and unsuitable areas for species occurrence and survival in the present and future, guiding conservation strategies by pinpointing key areas for protection (Guisan et al., 2013). In addition, although the maintenance of environmental services and the protection of different ecosystems and taxonomic groups are the main objectives of the PAs, the real effectiveness of these areas deserves to be better understood so that the management of the current PAs becomes more effective, as well as the implementation of new ones (Rodríguez-Rodríguez and Martínez-Vega, 2022). Thus, in this study, using SDM approaches, we aim to: i) model the current and future distributions of 18 direct-developing anuran species of the genus *Ischnocnema*; ii) predict possible changes in the distributions of these species under two different future climate projections (moderate and extreme) for 2050 and 2090; and iii) evaluate the protection degree of such species by the Atlantic Forest PAs at the present and the distinct future scenarios.

2. Material and Methods

2.1 Direct-developing frogs occurrences

We initially gathered species occurrences of 36 species of genus *Ischnocnema* using open-access data sources and published articles that gathered occurrence data for species from biological surveys and museum collections: the Global Biodiversity Information Facility (GBIF.org);

SpeciesLink (https://www.splink.org.br/); Vancine e al. (2018); and Vasconcelos et al. (2018). After compiling the occurrence data of species, we excluded all duplicate points. Once the occurrence data can be biased by spatial autocorrelation, we performed a spatial thinning approach to control these sampling biases using the 'spThin' package (Aiello-Lammens et al., 2015) in the R environment (R Core Team, 2023), selecting one random occurrence point per 10 km with 50 replications. We considered only species represented by at least 5 occurrence points, totaling 18 species and 440 single records to build the models (Table A1). As we do not have real absence data, we generated pseudo-absences (background data, Barbet-Massin et al., 2012) for each species. They were composed of 10,000 random points distributed in the Atlantic Forest. Since all evaluated *Ischnocnema* species are endemic to the Atlantic Forest, we considered the limits of the AF as their accessible area (M) for model calibration.

2.2 Environmental variables and future scenarios

To contemplate our first objective of modeling the distribution of direct-developing anurans of genus *Ischnocnema* in the Atlantic Forest, we compiled as environmental predictors the 19 bioclimatic variables from WorldClim (Fick and Hijmans, 2017), the potential evapotranspiration (ET0) from the Global Aridity Index and Potential Evapotranspiration Climate Database (Zomer et al., 2022), the terrain slope (slope), and the profile curvature (pcurv) from the EarthEnv database (Amatulli et al., 2018), and topographic wetness index (TWI) from ENVIREM dataset (Title and Bemmels, 2017). We choose to use these variables due to the strong dependence of anurans on environmental conditions (Haddad and Prado, 2005; Lion et al., 2019). To avoid multicollinearity among the environmental variables in our models and retain only the independent ones, we calculated the correlation among the variables using a correlation threshold of $r>0.7$ at the 'usdm' package (Naimi et al., 2014). Thus, we retained 10 environmental variables that were used in our models, eight bioclimatic: mean diurnal range (bio2); temperature seasonality (bio4); mean temperature of wettest quarter (bio8); mean temperature of warmest quarter (bio9); annual precipitation (bio12); precipitation of wettest month (bio13); precipitation of warmest quarter (bio18); precipitation of coldest quarter (bio19), and two topographic variables: pcurv; and TWI.

To create future projections of species distributions, we used the same 10 environmental variables. We gathered the future bioclimatic variables from two representative concentration pathways (RCP): the moderate scenario (RCP 4.5) and the extreme scenario (RCP 8.5) of the Coupled Model Intercomparison Project Phase 6 (CMIP6), under five randomly chosen distinct general circulation models (Atmosphere-Ocean General Circulation-AOGCM) from WorldClim (Fick and Hijmans, 2017). These AOGCMs are: Access-CM2; GISS-E2-1-H; HadGEM3-GC31-LL; IPSL-CM6A-LR; and MIROC6. For each AOGCM used, we considered two future periods: 2050 (period ranging from 2041 to 2060) and 2090 (period ranging from 2081 to 2100). Since we do not expect major changes in topography over the analyzed period, we kept these variables constant in both the present and future scenarios. We gathered all variables at a spatial resolution of 2.5 min (~4.5 km).

2.3 Species distribution modeling

For modeling the potential distribution of *Ischnocnema* species, we used the approach of the ensemble of small models (ESM). The use of ESM is indicated for modeling the distribution of species with few occurrence records and considers an ensemble model generated from a combination of predictor variables fitted by a sequence of bivariate models (Breiner et al., 2015). We generate our models based on four algorithms – one enveloping method (surface range envelope (SRE); Busby (1991)) which predicts an environmental space suitable for species occurrence based on the association between environment and species occurrence, one regression-based method: generalized linear model (GLM; McCullagh and Nelder (1989)) which is based on linear or non-linear relationships between species occurrence and their environmental space, and two machine-learning methods: maximum entropy (MaxEnt; Phillips et al. (2006)); and random forest (RF;

Breiman (2001)) which use trained data to predict the environmental space of the species occurrence.

For model calibration, we used 80% of our data for model training and 20% for model testing, repeated this process ten times for each species, and weighted the models by Area Under the Receiver-Operator Curve (AUC) and Somers' D (Breiner et al., 2015). We evaluated the predictive performances of models using the AUC and the True Skill Statistic (TSS; Breiner et al., 2015). Finally, to construct our final ensembles for the present and future scenarios, we converted all projected maps of habitat suitability into binary maps containing the presence and absence of the species using a threshold of minimal predicted area (MPA) equal to 1.0. Thus, we generate five binary projections for each species, being: i) for the current distribution area; ii) two for 2050 – one for moderate scenario (RCP 4.5) and one for extreme scenario (RCP 8.5); and two for 2090 – one for moderate scenario (RCP 4.5) and one for extreme scenario (RCP 8.5) (Figs. A1-A18). To perform our models, we used 'biomod2' (Thuiller et al. 2023) and 'ecospat' (Broennimann et al., 2022) packages on the R environment (R Core Team, 2023).

2.4 Shifts in direct-developing anurans distribution

To assess our second aim of predicting shifts (gain or loss) in the distribution areas of *Ischnocnema* species, we first determined the current total distribution area of each species using the binary projections for the present. Then, we used the binary projections for future scenarios and calculated the change proportion in the total distribution area for the species.

2.5 Protection degree of the Ischnocnema species from the Atlantic Forest

Finally, to evaluate the protection degree of *Ischnocnema* species, we used the approach of mean percentage overlap (MPO) proposed by Sánchez-Fernández and Abellán (2015) that measures the level of representation of species by PAs. To do this, we first gathered the boundaries of all the PAs of strict protection and sustainable use (national and state administrative levels), available at

Painel Unidades de Conservação Brasileiras from Centro Nacional de Unidades de Conservação (CNUC; MMA, 2023). After the PAs data collection, we filtered those that were inserted within the limits of the integrative boundaries of Atlantic Forest proposed by Muylaert et al. (2018). Using the binary ESM of each species and the boundaries of PAs, we calculate the percentage of overlap of the cells occupied by each species and the PAs, here named as observed MPO (obsMPO).

Subsequently, we compared the obsMPO with null MPO (nullMPO) values obtained from the calculation of MPO for 1,000 random species with the same distribution size (number of occupied cells). Then, we obtained the level of representation of each species by PAs. If a species has a value of obsMPO lower than nullMPO (and therefore lower than expected by chance) it means that PAs significantly under-represents the species, whereas if obsMPO is higher than nullMPO (higher than expected by chance) it means that PAs significantly over-represents the species, (Sánchez-Fernández and Abellán, 2015). To obtain the MPO for species we used QGIS and R software (QGIS Development Team, 2019; R Core Team, 2023), and a significance level of $p<0.05$.

3. Results

3.1 A current overview of the distribution and the conservation of direct-developing anurans in the Atlantic Forest

In general, our modeling algorithms exhibited a good predictive power, with GLM presenting the highest mean AUC (0.91±0.04; mean±SD) and TSS (0.83±0.10; mean±SD) values, followed by MaxEnt (AUC = 0.88±0.06; TSS = 0.80±0.10; mean±SD), SRE (AUC = 0.82±0.08; TSS = 0.69±0.14; mean±SD), and finally RF (AUC = 0.79±0.11; TSS = 0.30±0.18; mean±SD Table A2). Temperature seasonality (bio4) was the variable that most contributed to the final ensemble for most of the species (7 species), followed by TWI (4 species) and pcurv (2 species; Table A3).

Our projections for the present showed a suitable area for the occurrence of direct-developing frogs of the genus *Ischnocnema*, especially in the southeastern Atlantic Forest, where we predict a high range overlap for most species from the genus (Fig. 1, Figs. A1-A18). With a predicted distribution of 644,073 km², *Ischnocnema parva* is the most widespread species along the Atlantic Forest, followed by *I. guentheri* and *I. manezinho* (Table 1). Contrary, *Ischnocnema penaxavantinho*, *I. vizottoi*, and *I. izecksohni* are the species with more restricted distributions (Table 1). Half of the species are not evaluated or have deficient data for the classification of extinction risk, while more than half (55.5%) have unknown population trends (Table A1).

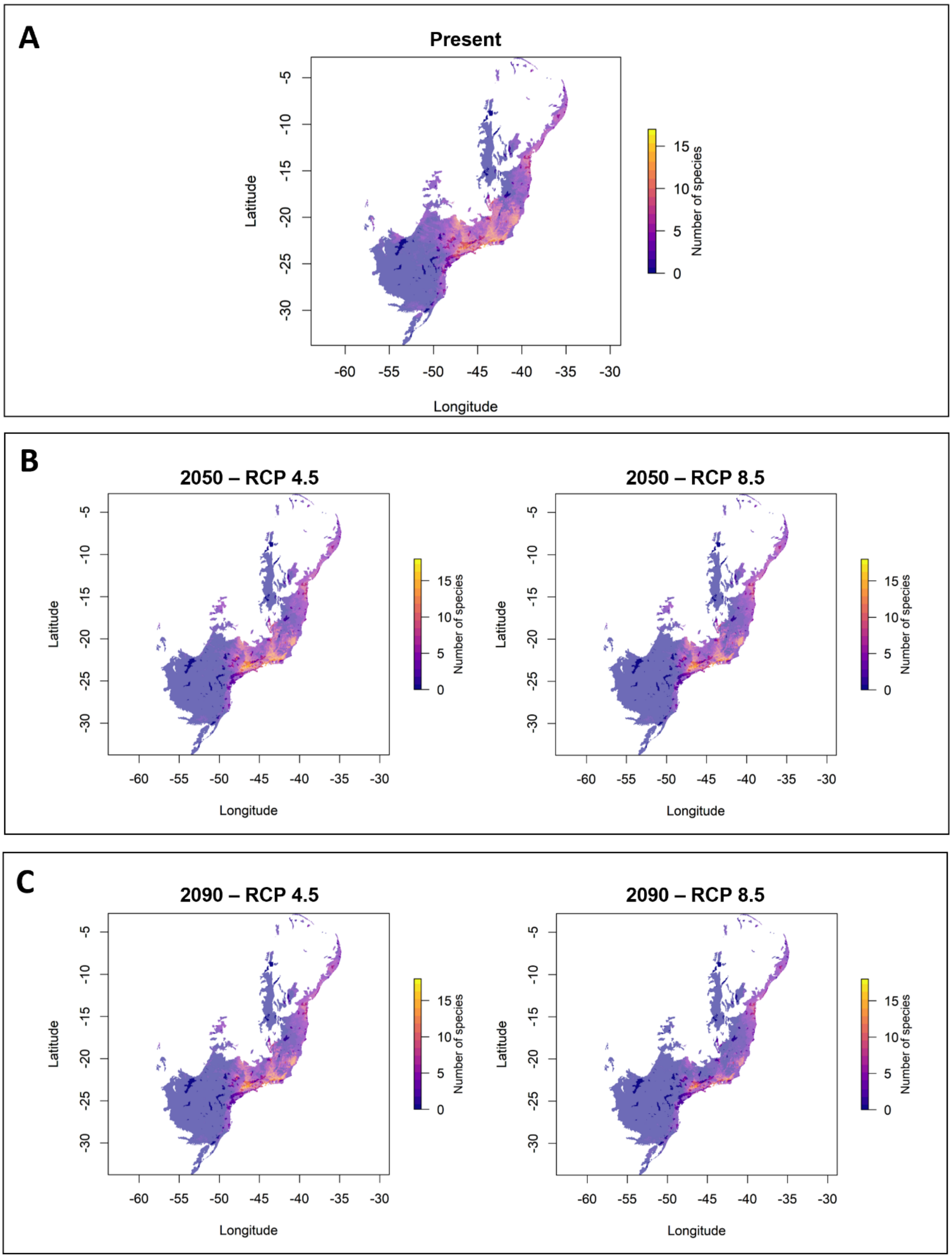

Fig. 1 - Predicted spatial distribution of species richness for genus *Ischnocnema* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Atlantic Forest PA are represented by the absence of transparency (more colorful gradient).

Table 1 – Current and future predicted distribution areas of *Ischnocnema* species and percentage of loss of their range according to the different scenarios (RCP 4.5 and RCP 8.5) in the two future time horizons evaluated.

	Current	**2050**				**2090**			
		RCP 4.5	**RCP 8.5**	**Loss RCP 4.5**	**Loss RCP 8.5**	**RCP 4.5**	**RCP 8.5**	**Loss RCP 4.5**	**Loss RCP 8.5**
I.abdita	5383	3880	2887	27.92	46.37	3122	934	42.00	82.65
I.bolbodactyla	20917	18196	16748	13.01	19.93	17470	15140	16.48	27.62
I.guentheri	25947	14438	10884	44.36	58.05	11106	5297	57.20	79.59
I.henselii	14260	10535	9339	26.12	34.51	9885	9878	30.68	30.73
I.holti	13118	6556	5124	50.02	60.94	5072	2547	61.34	80.58
I.izecksohni	3204	1865	1521	41.79	52.53	1362	230	57.49	92.82
I.juipoca	17892	12249	9953	31.54	44.37	10276	5383	42.57	69.91
I.manezinho	24955	15796	13891	36.70	44.34	14680	8453	41.17	66.13
I.nasuta	7290	5397	4774	25.97	34.51	5006	2343	31.33	67.86
I.nigriventris	4471	3572	2771	20.11	38.02	3415	2428	23.62	45.69
I.octavioi	20551	13463	11609	34.49	43.51	11477	2912	44.15	85.83
I.oea	21714	14722	12777	32.20	41.16	13423	5954	38.18	72.58
I.parva	30660	29019	24811	5.35	19.08	25908	20087	15.50	34.48
I.penaxavantinho	660	422	379	36.06	42.58	336	192	49.09	70.91
I.randorum	7658	3849	2976	49.74	61.14	2868	1385	62.55	81.91
I.sambaqui	3540	2407	2009	32.01	43.25	2171	1357	38.67	61.67
I.verrucosa	12982	8922	7272	31.27	43.98	6833	2847	47.37	78.07
I.vizottoi	1838	944	695	48.64	62.19	704	317	61.70	82.75

The values express the number of cells occupied by the evaluated species. Each cell equals ~ 21.6 km²

Regarding the protection degree of direct-developing frogs in the present, we observed that PA significantly over-represents all species, with MPO ranging from 7.79% to 43.55% (17.97±10.27; mean±SD; Table A4). We also observed an almost negative linear pattern of representation of species by PAs, where species with more restricted distributions are the most represented by these areas, such as the case of *I. vizottoi*, *I. penaxavantinho*, and *I.sambaqui* (Fig. 2A).

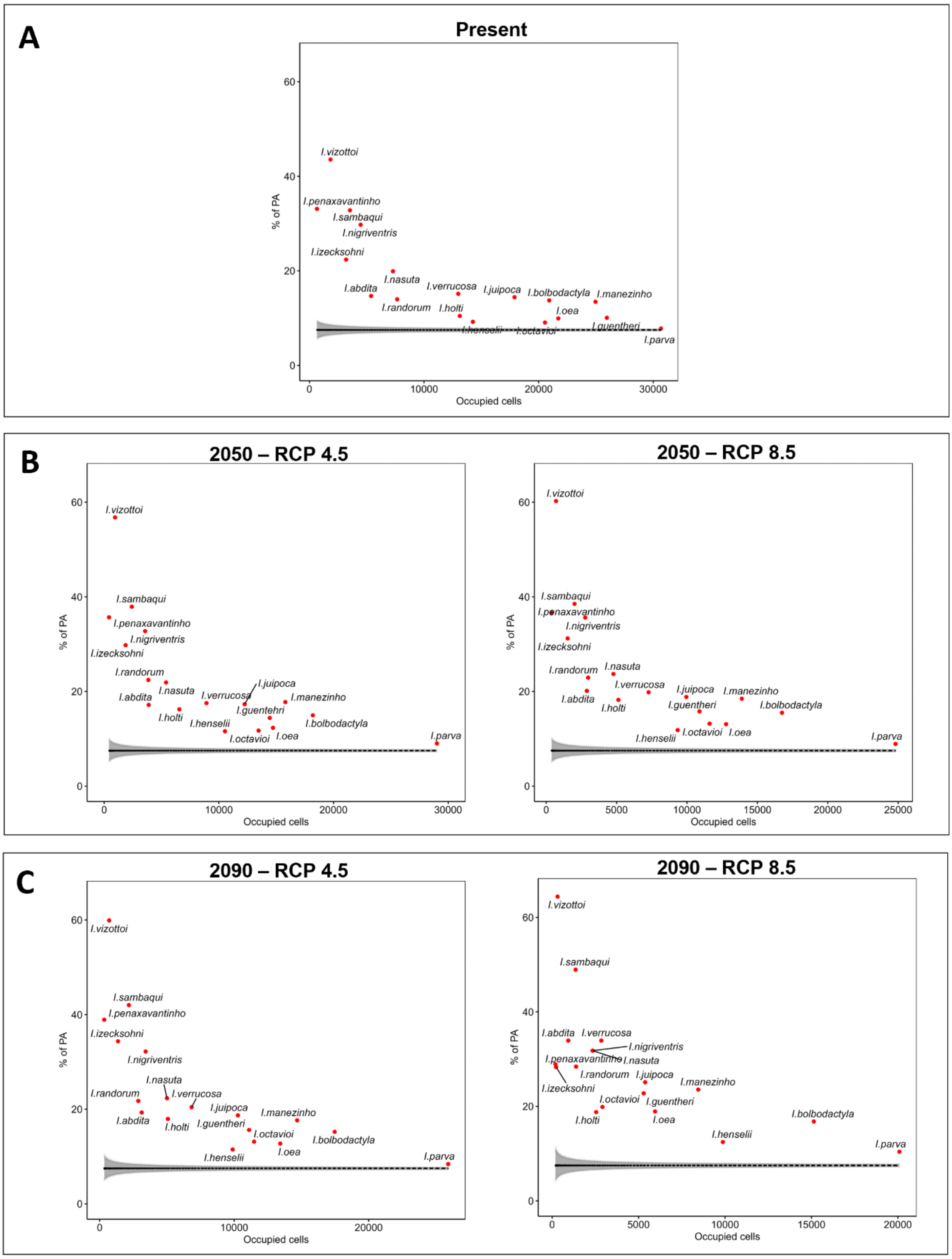

Fig. 2 – Mean percentage overlap (MPO) between direct-developing frogs from genus *Ischnocnema* distribution (number of occupied cells) and the proportion of their range covered by the Atlantic Forest PAs. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios The dashed

line represents the MPO from 1,000 randomizations at each range size level (number of cells), the grey shadow indicates the random range (range of the 95th percentile of the randomized data). For a more detailed vision see the supplemental materials.

3.2 Future perspectives of the direct-developing anurans in the face of environmental changes in the Atlantic Forest

In both predictions of future scenarios of the distribution of *Ischnocnema* species, highlands in southeastern Atlantic Forest, such as Serra do Mar, will be the most important regions for the maintenance and protection of the genus, safeguarding most species (Fig. 2). In the moderate scenario (RCP 4.5) for 2050 we observed a mean loss in the distribution area for all species of 32.63%, where *I. holti* will be the most affected species with a reduction of half of its current distribution area (Table 1). At the extreme scenario (RCP 8.5) for 2050, we projected an average loss of almost 44% of species geographic distributions, with *I. vizottoi* losing about 62.19% of its current distribution (Table 1). On the other hand, when we evaluated the moderate scenario (RCP 4.5) for 2090 we observed a mean loss of 42% of species distributions, with *I. randorum* as the species with the greatest loss under this scenario (Table 1). The loss of distribution area of the species in the worst scenario (RCP 8.5) of 2090 can reach a mean of more than two-thirds and may exceed more than 90% as in the case of *I. izecksohni* (Table 1).

While we can expect a decrease in the distribution area of all species, we also perceive an increase in the relative species range covered by PAs in both future scenarios (Fig. 3). For both scenarios in the two future times, we also observed a significantly over-representation of all species by PAs. Additionally, we observed the continuity of the pattern of distribution vs percentage covered by PAs, which indicates that species with smaller ranges will be more represented by these areas (Figure 2B-C; Tables A4-A6).

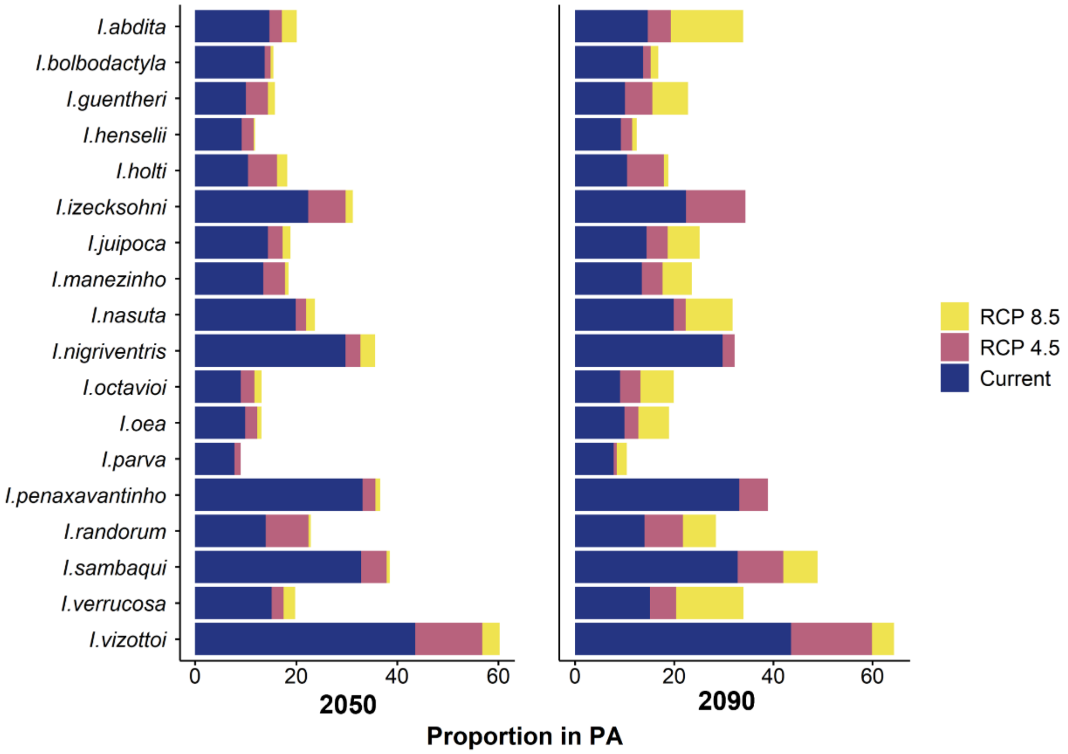

Fig. 3 – Proportion of range of direct-developing frogs of genus *Ischnocnema* covered by Atlantic Forest protected areas (PA) at the present (blue), at the moderate scenario (magenta), and the extreme scenario (yellow). A – for 2050 and B – for 2090. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

4. Discussion

4.1 A current overview of the distribution and the conservation of direct-developing anurans in the Atlantic Forest

With an estimated average loss of almost a third of the distribution area in the moderate scenario of 2050, with the possibility of reaching more than 40% reduction by 2100, the future of direct-developing frogs of genus *Ischnocnema* in the Atlantic Forest is under threat. As viewed by Vasconcelos et al. (2018), our results demonstrate a loss of anuran species in inland regions of the Atlantic Forest, with the regions with higher species richness being restricted to the coastal regions. Alves-Ferreira et al. (2022) found that amphibians that occur exclusively in forest habitats in higher altitudes will be more impacted by climate change, with a greater loss of their ranges. On the other hand, although amphibians with smaller geographic range sizes will tend to have proportionally smaller losses in their range in response to climate change than widespread species (Alves-Ferriera et al., 2022), these species tend to have greater vulnerability to extinction risk and population decline (Sodhi et al., 2008).

Species range loss does not represent just a contraction in the distribution area of species but also can represent a threat to the maintenance of populations and further to the survival of species, which may become extinct in the future (Ceballos and Ehrlich, 2002; Channell and Lomolino, 2000; Dubos et al., 2022). With a substantial contraction of their ranges, some species may be restricted to suboptimal habitats, becoming refugee species (Kerley et al., 2012). Likewise, the ecological marginalization caused by being restricted to ecologically extreme habitats at the periphery of their historic niche raises the extinction risk for some species, as demonstrated for mammals by Britnell et al. (2023). Also, the contraction in the species range can enhance negative effects to the remaining populations, such as those effects of ... genetic drift and inbreeding (REFS). Nonetheless, the perspective of the future of direct-developing frogs of the genus *Ischnocnema* can be much more worrying if the extreme scenario becomes a reality, where there is an estimated average loss of the distribution area of up to two-thirds in the extreme scenario.

Direct-developing frogs of the genus *Ischnocnema* are not expected to expand their range in the Atlantic Forest. This finding supports the idea that amphibians with more specialized reproductive modes are more negatively affected by climate change, essentially by their specific requirements (Loyola et al., 2014). With the shift from aquatic to terrestrial habitats direct-developing species became dependent on the humidity supplied mainly by the moist forests in which they live (Haddad and Prado, 2005). However, the alterations in temperature and precipitation regimes, the increase in the rates of evapotranspiration, and the loss of soil moisture that are expected for the Atlantic Forest (Follador et al., 2018), the requirement for humidity by these species, may hamper their reproduction and survival (Alcala et al., 2011). Thus, ensuring relatively intact environments for these species becomes an important tool for the conservation of the group.

4.2 Direct-developing frogs are truly protected by the Atlantic Forest Protected Areas?

Frogs of the genus *Ischnocnema* seem to be indirectly benefited by the PAs in the Atlantic Forest at present. Similarly, Loyola et al. (2008) observed the favoring of amphibians with terrestrial development by the prioritization of areas. When considering the distinct ecomorph groups, terrestrial species appear as the group with the highest representativeness of protection, with an average of 10% species distribution covered by PAs (Bolochio et al, 2020). Bolochio et al. (2020) viewed that among the distinct types of ecomorph groups, terrestrial amphibians present the lowest percentage of overlap between their range and human-modified areas either in the present or in the future. In general, amphibians are well represented in PAs, with most species having between 10 and 25% of their range included in PA (Nori et al., 2015). Also, among the species most represented by PAs, are those with a more restricted range (Nori et al., 2015), a characteristic of terrestrial amphibians, such as direct-developing species (Brooks and Kindsvater, 2022).

Nonetheless, it is important to note that the protection degree provided by PAs can vary according to the species, specific focal group, and region. For example, Bailly et al. (2021) found that PAs located in the Paraná-Paraguay Basin are not effective in the protection of migratory fishes in the region, Toranza et al. (2016) also detected a poor efficiency of PAs for the conservation of Uruguayan threatened amphibians, and Singh et al. (2021) perceived that the Thai PAs are effective to protect the terrestrial amphibian hotspots but fail to protect the mammalian and bird ones. Moreover, the protection degree of species by PAs can depend not only on their size and their strategic management but also on the structural connection between distinct PAs and natural areas (Le Saout et al. 2013). Similarly, the structure of the PAs network evaluated can also provide different results about the effectiveness of PAs. Sánchez-Fernández and Abellán (2015), verified that whereas European amphibians are mostly underrepresented by the PAs, the Natura 2000 network of PAs still is more effective than the nationally designated PAs.

As for the present, our results suggest that the protection degree of direct-developing anurans of the genus *Ischnocnema* will tend to be maintained in the future. More specifically, our models indicate that whereas important contractions on species distributions are predicted, the proportion of it is ranges covered by PAs will tend to increase. Mi et al. (2023) found a similar pattern, with an increase in the proportion of amphibian and reptile habitats covered by PAs. Nevertheless, the increase in the protection degree provided by PAs is not a real genuine in protection. Instead, it results from the reduction in the total area of distribution of direct-developing anurans and the confinement of such species to these areas. Also, as viewed by Lehikoinen et al. (2019) for birds, PAs can serve as buffers against climatic change, mitigating the impacts of biodiversity loss and providing the opportunities for species to adapt to climatic changes. In this sense, our results suggest that the Atlantic Forest PAs will act as true refuges for many direct-developing anurans in the face of future climate change.

4.3 Conservation perspectives: Overcoming challenges to ensure the survival of direct-developing frogs in the Atlantic Forest

Despite our results providing a good and optimistic perspective for amphibian conservation, they need to be cautiously viewed. It is important to note that the extinction risk is unknown for half of the evaluated species, whereas for the majority of species, the population trend is not defined. Several authors have already predicted that there is a high chance of data-deficient species being at risk of extinction (Bland et al., 2014; González-del-Pliego et al., 2019; Howard and Bickford, 2014). Borgelt et al. (2022) predict that 85% of data-deficient amphibians are facing extinction risk. It is known that the extinction risk of amphibians can be related to the reproductive modes being those with direct development the most prone to population decline and being threatened with extinction (Fontana et al., 2021). Moreover, climate change can cause many other impacts on amphibians in addition to reducing the range of species, such as the increased spread of the chytrid fungus *Bd* and other pathogens, alterations in physiological performance, reproductive phenology, and body size, exposition to UV-radiation (Li et al., 2013; López-Alcaide and Macip-Ríos, 2011). Thus, direct-developing frogs from the Atlantic Forest can be already struggling to persist in these PAs which can become their last refuges.

It is important to note that here we are considering that the number and the cover of PAs will be stable and not suffer modifications. Also, we did not consider the PAs at municipal level. According to SOS Mata Atlântica (2023), the number of PAs and the coverage of these areas in the biome are highly superior to those found in the CNUC, thus indicating that these areas can serve as important tools for protecting the Atlantic Forest. One way to guarantee the future of amphibians in the Atlantic Forest is the creation of new PAs mainly in the gap areas (Lemes and Loyola, 2013; Mi et al., 2023). Nonetheless, if new PAs are implemented, they need to consider not only the current richness pattern of species but also the predictions of shifts in the species distribution for the future (Loyola et al., 2013). On the other hand, an essential tool for the conservation of biodiversity was the fulfillment of Target 11 of Aichi of the Convention on Biological Diversity (CBD) by 2020, which aimed not only to increase the coverage of protected areas around the world but also to guarantee the effective management and equity, ecological representativeness and connectivity between systems of protected areas (CBD, 2010). However, less than ten percent of the world's terrestrial PAs are structurally connected (Ward et al., 2020). Thus, the creation of new efforts and goals, such as the 30x30 conservation target which aims to protect 30% of terrestrial areas by 2030 (CBD, 2020), can help to guarantee biodiversity conservation. If this goal is achieved, we may have a reduction of up to 50% in the risk of species extinction in the future (Hannah et al., 2020).

Other actions can still be taken to improve the effectiveness of PAs and the consequent protection of amphibians. The PAs effectiveness can be further amplified by reinforcing protection measures in less restrictive protected areas, thereby maximizing their conservation outcomes (Mi et al., 2023). Also, according to Loyola et al. (2008), the use of life-history traits in the implementation of conservation strategies, such as the prioritization of new protected areas can be an important strategy to guarantee the survival of species. Thus, associated with the reduction of emission of house green gases the implementation of new PAs, the connection among the current ones, and, mostly, proper maintenance and management of the actual PAs can guarantee the survival of this extraordinary and intriguing group in the Atlantic Forest.

5. Conclusions

Our results revealed important predictions of direct-developing frogs of the genus *Ischnocnema* and the importance of the Atlantic Forest PAs for their protection. Although we predict that all species will experience range reduction in both future scenarios, we also observed that Atlantic Forest PAs are effective for the protection of this species group in the present. Further, our results suggest that the distribution of direct-developing frogs inside the Atlantic Forest PAs will tend to increase in the future. Together, these results reveal not only that Atlantic Forest PAs function as true refuges for this species group but also that they can guarantee the survival of these species in a changing world. We emphasize the importance of the right management of the current PAs, the improvement of the connectivity among these areas, and the implementation of new PAs to ensure the protection of amphibians in the Atlantic Forest. Certainly, these data are extremely important as they provide a new perspective on the conservation and the future of the group in the Atlantic Forest, thus assisting in decision-making for planning projects for the protection of Atlantic Forest direct-developing frogs.

Declaration of competing interest

The authors declare that have no conflicts of interest.

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Supplementary material

Table A1 – Occurrence points of *Ischnocnema* species from Atlantic Forest and conservation status following the IUCN criteria. NE – Not Evaluated. LC – Least Concern. DD – Data Deficient. NT – Near Threatened.

Species	**Status**	**Population Trend**	**Longitude**	**Latitude**	**Source**
I. abdita	NE	Not Evaluated	-45.06999969	-23.43000031	Species Link
			-46.533729	-23.390486	GBIF
			-45.88	-23.39	GBIF
			-46.36638889	-23.37333333	Species Link
			-45.44	-23.37	Species Link
			-44.8	-23.366667	Vasconcelos et al. 2018
			-46.74000168	-23.36000061	Species Link
			-40.42	-20.2639	Vasconcelos et al. 2018
			-43.8014	-20.2533	Species Link
			-44.4211	-20.1967	Species Link
			-40.33333333	-20.16666667	Vancine et al. 2018
I. bolbodactyla	LC	Decreasing	-44.8475	-23.3575	Vancine et al. 2018
			-45.026667	-23.346667	Vasconcelos et al. 2018
			-46.701389	-23.346111	GBIF
			-45.136	-23.345	GBIF
			-42.48333861	-19.75004083	Vancine et al. 2018
			-39.91388889	-16.59916667	Vancine et al. 2018
			-39.78279877	-16.58390045	Species Link
			-39.239053	-16.511452	Vasconcelos et al. 2018
			-39.05944444	-15.16638889	Vancine et al. 2018
			-39.10555556	-14.74222222	Vancine et al. 2018
I. guentheri	LC	Stable	-47.13	-23.3	Vasconcelos et al. 2018
			-46.29055556	-23.29666667	Vancine et al. 2018
			-44.793635	-23.296462	GBIF
			-47	-23.28333333	Vancine et al. 2018
			-46.643257	-23.251392	GBIF
			-45.02222222	-23.25138889	Species Link
			-45.60611111	-23.23944444	Vancine et al. 2018

-46.540643	-23.226966	GBIF
-45.31	-23.22	GBIF
-44.71305556	-23.21805556	GBIF
-46.05384	-23.212596	GBIF
-46.274118	-23.201451	GBIF
-46.88	-23.180278	GBIF
-45.88000107	-23.17000008	Species Link
-44.17222222	-23.1425	Vancine et al. 2018
-46.13527778	-23.13305556	Vancine et al. 2018
-45.30944444	-23.12638889	Vancine et al. 2018
-46.54999924	-23.11000061	Species Link
-44.84102	-23.10174	Vasconcelos et al. 2018
-47.0442	-23.09705	GBIF
-45.5075	-23.09	Vancine et al. 2018
-43.97	-23.07305556	Vancine et al. 2018
-45.931131	-23.071389	GBIF
-44.96	-23.07	Species Link
-44.689339	-23.038078	Vasconcelos et al. 2018
-43.533333	-23.033333	Vasconcelos et al. 2018
-41.116667	-20.516667	Vasconcelos et al. 2018
-41.01666667	-20.51666667	Vancine et al. 2018
-43.96305556	-20.50166667	Vancine et al. 2018
-43.85779953	-20.49970055	Species Link
-43.59305556	-20.47972222	Vancine et al. 2018
-41.01666667	-20.4	Vancine et al. 2018
-40.825694	-20.387167	GBIF
-43.511485	-20.360436	Vasconcelos et al. 2018
-43.797077	-20.344527	GBIF
-40.2925	-20.3297	Vasconcelos et al. 2018
-40.57	-20.326389	GBIF
-40.418661	-20.300464	Vasconcelos et al. 2018
-42.34109879	-20.28389931	Species Link
-43.8014	-20.2533	Species Link
-43.484892	-20.22349	GBIF
-44.4211	-20.1967	Species Link
-40.529722	-20.100556	GBIF
-43.7894	-20.0875	Species Link
-43.4075	-20.0747	Species Link
-42.07611111	-20.07	Vancine et al. 2018
-40.69305556	-20.04277778	Species Link
-43.8467	-19.9856	Species Link
-43.97055556	-19.97611111	Vancine et al. 2018
-40.540447	-19.965183	GBIF
-43.4153	-19.9594	Species Link
-40.406667	-19.9325	Vasconcelos et al. 2018

-40.63356611	-19.91678	Vancine et al. 2018
-43.8067	-19.8864	Species Link
-40.563056	-19.855	GBIF
-40.36970139	-19.83189964	Species Link
-43.3622	-19.8261	Species Link
-40.273333	-19.820278	GBIF
-41.716389	-19.799167	Vasconcelos et al. 2018
-42.1392	-19.7897	Species Link
-41.82194444	-19.73111111	Vancine et al. 2018
-42.7322	-19.7122	Species Link
-39.9325	-19.692222	GBIF
-40.552625	-19.668056	GBIF
-42.56677167	-19.6500875	Vancine et al. 2018
-40.074717	-19.435844	GBIF
-41.38	-19.3597	Species Link
-41.578333	-19.317222	GBIF
-43.425	-19.0372	Species Link
-40.533375	-18.96666667	Vancine et al. 2018
-42.9325	-18.775	Species Link
-40.871003	-18.611125	GBIF
-43.3067	-18.4658	Species Link
-39.844167	-18.355278	GBIF
-39.194473	-17.509932	Vasconcelos et al. 2018
-39.67305556	-17.29194444	Vancine et al. 2018
-39.358645	-17.017059	GBIF
-39.558425	-16.998997	Vasconcelos et al. 2018
-39.095	-16.4754	Vasconcelos et al. 2018
-40.991	-16.346	Vasconcelos et al. 2018
-39.12083333	-16.32444444	Vancine et al. 2018
-39.63583333	-15.92666667	Vancine et al. 2018
-40.52388889	-15.81777778	Vancine et al. 2018
-39.450044	-15.657987	Vasconcelos et al. 2018
-40.42309952	-15.56830025	Species Link
-39.565	-15.392	GBIF
-39.38361111	-15.2275	Vancine et al. 2018
-39.05944444	-15.16638889	Vancine et al. 2018
-39.516667	-15.133333	Vasconcelos et al. 2018
-39.3167	-15.0946	GBIF
-39.047984	-14.795863	Vasconcelos et al. 2018
-39.172348	-14.795545	Vasconcelos et al. 2018
-39.28027778	-14.78583333	Species Link
-39.59601	-14.700156	Vancine et al. 2018
-39.22111111	-14.69833333	Vancine et al. 2018
-39.300794	-14.509523	Vasconcelos et al. 2018
-39.45076	-14.487317	Vancine et al. 2018

-39.06055556	-14.42388889	Vancine et al. 2018
-40.1	-14.416667	Vasconcelos et al. 2018
-39.1704	-14.3535	Vasconcelos et al. 2018
-39.083881	-14.315036	Vasconcelos et al. 2018
-38.99670029	-14.27750015	Species Link
-39.7175	-14.1284	Vasconcelos et al. 2018
-38.9981	-14.1192	Vasconcelos et al. 2018
-39.18222222	-14.01416667	Vancine et al. 2018
-39.45111111	-13.9525	Vancine et al. 2018
-39.104167	-13.945278	Vasconcelos et al. 2018
-40.11025	-13.944722	Vasconcelos et al. 2018
-39.67277778	-13.86444444	Vancine et al. 2018
-39.218963	-13.825858	GBIF
-39.1616	-13.7405	Vasconcelos et al. 2018
-39.637923	-13.723597	Vasconcelos et al. 2018
-39.21027778	-13.64944444	Vancine et al. 2018
-39.716667	-13.583333	Vasconcelos et al. 2018
-38.967636	-13.509878	Vasconcelos et al. 2018
-39.1409	-13.4906	Vasconcelos et al. 2018
-39.090714	-13.359962	Vasconcelos et al. 2018
-41.900697	-13.300652	GBIF
-39.675	-13.2871	Vasconcelos et al. 2018
-39.65944444	-13.12194444	Vancine et al. 2018
-39.3953	-13.0617	Vasconcelos et al. 2018
-38.507	-13.005	GBIF
-38.618928	-12.956735	Vasconcelos et al. 2018
-38.33916667	-12.88388889	Vancine et al. 2018
-39.48166667	-12.84055556	Vancine et al. 2018
-38.8296	-12.839	Vasconcelos et al. 2018
-38.495752	-12.756117	Vasconcelos et al. 2018
-38.331638	-12.69702	Vasconcelos et al. 2018
-38.562636	-12.673064	Vasconcelos et al. 2018
-38.3039	-12.5816	Vasconcelos et al. 2018
-38.03666667	-12.56694444	Vancine et al. 2018
-38.405	-12.45083333	Vancine et al. 2018
-38.1927	-12.4151	Vasconcelos et al. 2018
-38.5808	-12.352	Vasconcelos et al. 2018
-37.59166667	-11.90305556	Vancine et al. 2018
-37.50694	-11.513344	Vasconcelos et al. 2018
-40.52777778	-11.3925	Vancine et al. 2018
-37.207169	-10.99949	Vasconcelos et al. 2018
-37.05833333	-10.54166667	Vancine et al. 2018
-36.37138889	-9.938611111	Vancine et al. 2018
-36.20027778	-9.690833333	Vancine et al. 2018
-35.709014	-9.587067	Vasconcelos et al. 2018

			-35.17167	-8.733611	Vancine et al. 2018
			-34.94722	-8.003611	Vancine et al. 2018
			-34.95806	-7.909167	Vancine et al. 2018
			-35.14472	-6.72425	Vancine et al. 2018
			-38.91083	-4.280556	Vancine et al. 2018
I. henselii	LC	Unknown	-45.948214	-23.028381	GBIF
			-43.3675	-23.0052	Species Link
			-43.92888889	-23.00027778	Vancine et al. 2018
			-44.3	-23	GBIF
			-44.10027778	-22.99138889	Vancine et al. 2018
			-44.67	-22.9631	GBIF
			-43.47239	-22.95753	GBIF
			-45.838829	-22.954712	GBIF
			-43.011662	-22.953132	GBIF
			-43.2333	-22.95	GBIF
			-40.85361111	-16.0275	Vancine et al. 2018
			-39.48166667	-12.84055556	Vancine et al. 2018
			-38.03833333	-12.56638889	Vancine et al. 2018
			-39.3118	-12.5647	Vasconcelos et al. 2018
			-38.29	-12.53	Vasconcelos et al. 2018
			-38.5053	-12.5117	Vasconcelos et al. 2018
			-38.405	-12.45083333	Vancine et al. 2018
			-38.1757	-12.3149	Vasconcelos et al. 2018
			-38.2244	-12.2111	Vasconcelos et al. 2018
			-44.1528	-12.0142	Vasconcelos et al. 2018
			-37.66138889	-11.99861111	Vancine et al. 2018
			-37.09982	-10.926985	GBIF
			-36.456247	-9.321131	Vasconcelos et al. 2018
			-35.939723	-9.30634	Vasconcelos et al. 2018
			-35.454456	-9.265749	Vasconcelos et al. 2018
			-36.42806	-9.229167	Vancine et al. 2018
			-35.878894	-9.219278	GBIF
			-35.18833	-8.721111	Vancine et al. 2018
			-35.859203	-8.696342	GBIF
			-35.20167	-8.038889	Vancine et al. 2018
			-34.947555	-8.007055	Vasconcelos et al. 2018
			-34.8731	-7.94083	Vasconcelos et al. 2018
			-35.165012	-7.923776	GBIF
			-35.00667	-7.841944	Vancine et al. 2018
			-34.859	-7.832	Vasconcelos et al. 2018
			-34.928329	-7.228725	GBIF
			-34.87389	-7.112222	Vancine et al. 2018
			-35.746984	-6.971076	GBIF
			-35.14825	-6.718722	Vancine et al. 2018
			-35.09189987	-6.186669827	Species Link

			-38.9331	-4.26333	Vasconcelos et al. 2018
			-40.91944	-3.825833	Vancine et al. 2018
I. holti	DD	Unknown	-43.3	-22.93333	GBIF
			-43.439999	-22.93	GBIF
			-45.459602	-22.928396	GBIF
			-43.842222	-22.928333	GBIF
			-40.600278	-19.935556	GBIF
			-39.415332	-15.22236	Vasconcelos et al. 2018
			-39.504403	-13.563077	Vasconcelos et al. 2018
I. izecksohni	DD	Unknown	-42.689271	-22.924263	Vasconcelos et al. 2018
			-44.442468	-22.922604	Vasconcelos et al. 2018
			-45.459722	-22.920278	GBIF
			-43.5	-22.9167	GBIF
			-43.35	-22.9167	GBIF
			-43.183333	-22.916667	Vasconcelos et al. 2018
			-45.959622	-22.912142	GBIF
			-46.825	-22.903	GBIF
			-43.8925	-22.90194444	Vancine et al. 2018
			-41.01666667	-20.51666667	Vancine et al. 2018
			-41.86830139	-20.43330002	Species Link
			-41.01666667	-20.4	Vancine et al. 2018
			-40.659361	-20.387167	GBIF
			-43.54777778	-20.38138889	Vancine et al. 2018
			-40.48056	-20.330306	Vasconcelos et al. 2018
I. juipoca	LC	Stable	-43.0925	-22.901944	Vasconcelos et al. 2018
			-43.23333	-22.9	GBIF
			-47.06000137	-22.89999962	Species Link
			-43.896944	-22.899444	GBIF
			-45.966844	-22.893005	GBIF
			-42.68444444	-22.88222222	Vancine et al. 2018
			-46.79000092	-22.87999916	Species Link
			-45.5225	-22.8708	Vasconcelos et al. 2018
			-48.54972222	-22.86527778	Vancine et al. 2018
			-45.419819	-22.861434	GBIF
			-45.86694444	-22.85861111	Vancine et al. 2018
			-45.73	-22.85	GBIF
			-44.207778	-22.839722	Vasconcelos et al. 2018
			-43.50444444	-22.82694444	Vancine et al. 2018
			-41.116667	-20.516667	Vasconcelos et al. 2018
			-41.007778	-20.510833	GBIF
			-43.96305556	-20.50166667	Vancine et al. 2018
			-43.8578	-20.4997	Vasconcelos et al. 2018
			-42.095278	-20.499611	GBIF
			-43.59305556	-20.47972222	Vancine et al. 2018
			-41.8683	-20.4333	Species Link

			-40.695833	-20.411667	Species Link
			-41.190711	-20.41154	GBIF
			-41.01666667	-20.4	Vancine et al. 2018
			-43.54111111	-20.37861111	Vancine et al. 2018
			-43.537194	-20.286745	Vasconcelos et al. 2018
			-40.52194444	-20.28111111	Vasconcelos et al. 2018
			-39.565	-15.39194444	Species Link
			-39.01624	-15.181349	Vasconcelos et al. 2018
			-39.2452	-15.1548	Vasconcelos et al. 2018
			-39.0794	-14.7942	Vasconcelos et al. 2018
			-39.649557	-14.762575	Vancine et al. 2018
			-39.45076	-14.487317	Vancine et al. 2018
			-38.99670029	-14.27750015	Species Link
			-42.475	-14.0694	Species Link
			-39.67277778	-13.86444444	Vancine et al. 2018
			-39.21027778	-13.64944444	Vancine et al. 2018
			-39.65944444	-13.12194444	Vancine et al. 2018
I. manezinho	NT	Decreasing	-46.102506	-22.819018	GBIF
			-43.47447	-22.818949	Vasconcelos et al. 2018
			-45.633	-22.817	Vasconcelos et al. 2018
			-44.03333	-22.81455	GBIF
			-44.369564	-22.806664	GBIF
			-45.287222	-22.803889	GBIF
			-35.046667	-8.235556	Vasconcelos et al. 2018
			-34.87389	-7.138611	Vancine et al. 2018
			-35.749775	-6.967318	GBIF
I. nasuta	LC	Decreasing	-45.46944444	-22.76611111	Vancine et al. 2018
			-46.87916667	-22.76416667	Vancine et al. 2018
			-43.4511	-22.7592	Vasconcelos et al. 2018
			-44.6125	-22.7581	Species Link
			-46.144444	-22.755556	GBIF
			-45.59	-22.73	GBIF
			-40.42	-20.2639	Species Link
			-43.47305556	-20.095	Vancine et al. 2018
			-42.067814	-20.082088	Vasconcelos et al. 2018
			-40.60029984	-19.93560028	Species Link
I. nigriventris	DD	Unknown	-45.474	-22.69	GBIF
			-44.619205	-22.687548	Vasconcelos et al. 2018
			-42.402864	-22.681693	Vasconcelos et al. 2018
			-44.31999969	-22.68000031	Species Link
			-39.05	-16.26	Vasconcelos et al. 2018
			-39.115587	-14.534158	Vancine et al. 2018
			-39.09051	-13.643301	Vasconcelos et al. 2018
			-39.70666667	-13.57861111	Vancine et al. 2018
I. octavioi	LC	Decreasing	-43.049864	-22.670475	Vasconcelos et al. 2018

			-44.43972222	-22.67027778	Species Link
			-45.225	-22.573	GBIF
			-44.75	-22.5667	GBIF
			-43.2129	-22.5634	Vasconcelos et al. 2018
			-42.033333	-22.55	Vasconcelos et al. 2018
			-44.85527778	-22.545	Species Link
			-42.9833	-22.5333	GBIF
			-43.0904	-22.525834	GBIF
			-43.73121	-22.525473	GBIF
			-43.87111111	-20.00111111	Vancine et al. 2018
			-43.97055556	-19.97611111	Vancine et al. 2018
			-40.540447	-19.965183	GBIF
			-43.4153	-19.9594	Species Link
			-40.406667	-19.9325	GBIF
			-40.639281	-19.903331	GBIF
			-40.82416667	-19.9025	Vancine et al. 2018
			-42.971516	-19.871876	GBIF
			-40.2733	-19.8203	Vasconcelos et al. 2018
I. oea	NT	Decreasing	-45.455556	-22.669444	Species Link
			-50.409722	-22.66	Vasconcelos et al. 2018
			-42.405296	-22.656426	Vasconcelos et al. 2018
			-44.58333	-22.63333	GBIF
			-43.4717	-22.6233	Species Link
			-43.891168	-22.621135	Vasconcelos et al. 2018
			-45.16527778	-22.61333333	Species Link
			-43.040278	-22.584722	Vasconcelos et al. 2018
			-43.233333	-22.583333	Vasconcelos et al. 2018
			-40.29222222	-20.32972222	Species Link
			-40.521944	-20.281111	GBIF
			-40.42	-20.263889	GBIF
			-44.4211	-20.1967	Species Link
			-42.0014	-20.1239	Species Link
			-40.746111	-20.040556	Vasconcelos et al. 2018
			-40.5375	-19.98333333	Vancine et al. 2018
I. parva	LC	Decreasing	-43.75444444	-22.5125	Vancine et al. 2018
			-45.14916667	-22.50861111	Vancine et al. 2018
			-43.62	-22.5	Vasconcelos et al. 2018
			-44.56667	-22.5	GBIF
			-43.270713	-22.489228	GBIF
			-42.91666667	-22.48333333	Vancine et al. 2018
			-44.337063	-22.482704	Vasconcelos et al. 2018
			-43.127	-22.482	GBIF
			-44.446667	-22.469167	GBIF
			-42.227093	-22.467723	Vasconcelos et al. 2018
			-42.757	-22.467	GBIF

-43.01944444	-22.45722222	Vancine et al. 2018
-43.839401	-22.456948	GBIF
-43.62333333	-20.49972222	Vancine et al. 2018
-40.638333	-20.455556	GBIF
-41.85197222	-20.42141667	Species Link
-41.016667	-20.4	Vasconcelos et al. 2018
-43.4161	-20.3778	Species Link
-40.283333	-20.333334	Vasconcelos et al. 2018
-40.47694444	-20.28083333	Vancine et al. 2018
-40.933461	-20.164408	GBIF
-44.21833333	-20.12388889	Vancine et al. 2018
-44.5764	-20.0753	Species Link
-43.8042	-19.9672	Species Link
-40.533333	-19.95	GBIF
-43.9378	-19.9208	Species Link
-43.38222222	-19.89361111	Vancine et al. 2018
-40.563056	-19.855	GBIF
-43.310922	-19.826502	Vasconcelos et al. 2018
-42.1392	-19.7897	Species Link
-41.82444444	-19.70916667	Vancine et al. 2018
-42.51676472	-19.66690417	Vancine et al. 2018
-40.072222	-19.391111	Vasconcelos et al. 2018
-41.556944	-19.343333	GBIF
-40.533375	-18.96666667	Vancine et al. 2018
-50.45166667	-18.44833333	Vancine et al. 2018
-40.150556	-18.030278	GBIF
-39.67305556	-17.29194444	Vancine et al. 2018
-39.78279877	-16.58390045	Species Link
-39.250413	-16.495779	Vasconcelos et al. 2018
-40.05638889	-16.41	Vancine et al. 2018
-39.05	-16.26	Vasconcelos et al. 2018
-39.37361111	-15.97361111	Vancine et al. 2018
-39.669242	-15.904579	Vasconcelos et al. 2018
-39.448297	-15.69563	Vasconcelos et al. 2018
-39.56583333	-15.39361111	Vancine et al. 2018
-39.029845	-15.195545	Vasconcelos et al. 2018
-39.345388	-15.182533	GBIF
-39.52694444	-15.15527778	Vancine et al. 2018
-39.05	-15.06667	GBIF
-39.0794	-14.7942	Vasconcelos et al. 2018
-39.649557	-14.762575	Vancine et al. 2018
-39.115587	-14.534158	Vancine et al. 2018
-39.0258	-14.472	Vasconcelos et al. 2018
-40.220384	-14.356761	Vasconcelos et al. 2018
-38.99670029	-14.27750015	Species Link

			-39.14333333	-14.01777778	Vancine et al. 2018
			-40.0836	-13.8575	Species Link
			-39.171114	-13.82156	GBIF
			-39.70666667	-13.57861111	Vancine et al. 2018
			-39.0832	-13.4935	Vasconcelos et al. 2018
			-39.19527778	-13.34222222	Vancine et al. 2018
			-39.675	-13.2871	Vasconcelos et al. 2018
			-39.3953	-13.0617	Vasconcelos et al. 2018
I. penaxavantinho	DD	Unknown	-45.1653	-22.4492	Species Link
			-42.76995	-22.448047	GBIF
			-42.9458	-22.4478	GBIF
			-42.147541	-22.444148	Vasconcelos et al. 2018
			-44.598458	-22.443095	GBIF
I. randorum	DD	Unknown	-42.773907	-22.440482	Vasconcelos et al. 2018
			-42.98333	-22.43333	GBIF
			-41.474083	-19.320167	GBIF
			-39.1019	-16.2331	Vasconcelos et al. 2018
			-39.115587	-14.534158	Vancine et al. 2018
			-39.14333333	-14.01777778	Vancine et al. 2018
I. sambaqui	DD	Unknown	-43.015144	-22.432841	Vasconcelos et al. 2018
			-42.768	-22.432	GBIF
			-38.508542	-13.000761	GBIF
			-38.00111111	-12.57	Vancine et al. 2018
			-37.63972222	-12.005	Vancine et al. 2018
			-35.18889	-8.721944	Vancine et al. 2018
I. verrucosa	DD	Unknown	-48.33027778	-23.42805556	Vancine et al. 2018
			-46.65	-23.41667	Vasconcelos et al. 2018
			-45.07527778	-23.41194444	Vancine et al. 2018
			-46.530755	-23.395566	GBIF
			-42.029999	-22.42	GBIF
			-42.938714	-22.419324	Vasconcelos et al. 2018
			-42.816291	-22.417826	GBIF
			-43.114789	-22.417455	Vasconcelos et al. 2018
			-44.881513	-22.417355	Vasconcelos et al. 2018
			-42.583	-22.417	GBIF
			-42.520556	-20.879167	GBIF
			-41.024167	-20.509444	GBIF
			-40.292222	-20.329722	GBIF
			-45.586944	-20.326111	Vasconcelos et al. 2018
			-40.598772	-20.299647	GBIF
			-43.5081	-20.2875	Species Link
			-40.47694444	-20.28083333	Vancine et al. 2018
			-40.931167	-20.169444	GBIF
			-42.023168	-20.157222	Vasconcelos et al. 2018
			-40.30777778	-20.12861111	Species Link

I. vizottoi	NE	Not Evaluated	-42.07611111	-20.07	Vancine et al. 2018
			-40.746111	-20.040556	GBIF
			-44.615106	-22.414346	GBIF
			-42.7552	-22.4137	GBIF
			-42.608542	-22.413533	Vasconcelos et al. 2018
			-42.965556	-22.412222	GBIF
			-39.345388	-15.182533	GBIF

Table A2 – Models evaluation according to AUC, Somer's D, and TSS.

Species	**GLM**			**MAXENT**			**RF**			**SRE**		
	AUC	**SomersD**	**TSS**	**AUC**	**SomersD**	**TSS**	**AUC**	**SomersD**	**TSS**	**AUC**	**SomersD**	**TSS**
I. abdita	0.93	0.87	0.90	0.88	0.76	0.83	0.84	0.68	0.39	0.86	0.71	0.76
I. bolbodactyla	0.90	0.79	0.82	0.86	0.74	0.77	0.67	0.35	0.24	0.83	0.65	0.64
I. guentheri	0.88	0.77	0.64	0.89	0.79	0.67	0.87	0.75	0.62	0.76	0.52	0.52
I. henselii	0.92	0.84	0.76	0.91	0.83	0.76	0.92	0.85	0.63	0.71	0.42	0.44
I. holti	0.99	0.99	0.99	0.90	0.81	0.89	0.89	0.79	0.29	0.98	0.97	0.90
I. izecksohni	0.95	0.90	0.90	0.93	0.87	0.85	0.93	0.87	0.38	0.88	0.77	0.80
I. juipoca	0.90	0.80	0.76	0.92	0.85	0.80	0.91	0.83	0.58	0.76	0.51	0.53
I. manezinho	0.83	0.66	0.76	0.79	0.57	0.70	0.63	0.26	0	0.71	0.42	0.58
I. nasuta	0.94	0.88	0.90	0.92	0.84	0.86	0.78	0.56	0.19	0.82	0.64	0.71
I. nigriventris	0.82	0.64	0.73	0.72	0.43	0.57	0.72	0.44	0.25	0.70	0.39	0.48
I. octavioi	0.91	0.82	0.82	0.90	0.80	0.80	0.79	0.59	0.09	0.85	0.70	0.71
I. oea	0.89	0.78	0.77	0.87	0.75	0.78	0.80	0.61	0.39	0.81	0.63	0.69
I. parva	0.84	0.69	0.63	0.87	0.75	0.65	0.78	0.57	0.33	0.79	0.59	0.59
I. penaxavantinho	0.97	0.94	0.97	0.98	0.96	0.98	0.93	0.87	0.20	0.94	0.89	0.94
I. randorum	0.95	0.9	0.95	0.81	0.63	0.80	0.55	0.11	0	0.87	0.75	0.82
I. sambaqui	0.87	0.75	0.87	0.87	0.74	0.85	0.80	0.59	0.20	0.75	0.50	0.72
I. verrucosa	0.92	0.84	0.81	0.93	0.87	0.84	0.83	0.66	0.39	0.83	0.66	0.67
I. vizottoi	0.93	0.87	0.93	0.98	0.97	0.98	0.66	0.32	0.30	0.93	0.87	0.88

Table A3 – Variable contribution for the four algorithms to the species distribution model and for the final ensemble of direct-developing frogs of genus *Ischnocnema*. PCurv – profile of curvature. TWI – topographic wetness index. Bio12 – annual precipitation. Bio13 – precipitation of wettest month. Bio18 – precipitation of warmest quarter. Bio19 – precipitation of coldest quarter. Bio02 – mean diurnal range. Bio04 – temperature seasonality. Bio08 – mean temperature of the wettest quarter. Bio09 – mean temperature of the warmest quarter.

Species	**Variable**	**GLM**	**MAXENT**	**RF**	**SRE**	**Ensemble**
I. abdita	PCurv	1.54	1.43	0.87	1.49	1.35
	TWI	1.04	1.13	0.35	1.33	0.98
	Bio12	0.87	0.83	0.51	1.12	0.84
	Bio13	0.89	1.07	1.31	1.09	1.08
	Bio18	0.81	0.98	1.82	0.74	1.06
	Bio19	1.13	0.96	1.34	1.07	1.12
	Bio02	1.27	1.19	2.14	0.48	1.26
	Bio04	1.61	0.83	0.36	1.50	1.11
	Bio08	0.60	0.68	0.85	0.79	0.72
	Bio09	0.49	0.97	1.09	0.62	0.77
I. bolbodactyla	PCurv	0.35	0.41	0.67	0.56	0.47
	TWI	0.52	0.40	0.22	0.23	0.37
	Bio12	0.96	1.44	0.30	1.02	1.02
	Bio13	0.58	0.60	1.03	0.27	0.57
	Bio18	0.67	0.69	5.61	0.26	1.25
	Bio19	0.65	0.61	1.61	0.71	0.79
	Bio02	4.20	4.07	1.59	4.19	3.80
	Bio04	3.03	1.95	0.71	4.12	2.68
	Bio08	0.66	0.83	0.69	0.95	0.79
	Bio09	0.54	0.65	0.33	0.62	0.56
I. guentheri	PCurv	0.50	0.78	0.69	0.49	0.63
	TWI	1.34	0.96	0.86	0.50	0.95
	Bio12	0.74	0.95	0.92	0.56	0.82
	Bio13	0.96	0.92	0.97	0.53	0.87
	Bio18	0.61	0.80	0.88	0.73	0.76
	Bio19	0.80	1.10	1.26	0.54	0.96
	Bio02	2.06	1.35	1.35	1.91	1.64
	Bio04	1.70	1.36	1.57	6.58	2.47
	Bio08	0.88	0.88	0.74	1.02	0.87

	Bio09	0.83	0.97	0.89	0.53	0.83
I. henselii	PCurv	0.45	0.70	0.58	0.56	0.57
	TWI	0.70	0.88	0.54	0.56	0.69
	Bio12	0.67	0.83	0.87	0.42	0.74
	Bio13	0.99	1.01	1.06	0.40	0.93
	Bio18	0.83	1.01	1.21	0.57	0.95
	Bio19	1.40	1.18	1.54	0.84	1.30
	Bio02	1.61	1.37	0.99	3.06	1.57
	Bio04	1.36	1.27	1.54	4.37	1.82
	Bio08	0.72	0.70	0.75	0.74	0.72
	Bio09	1.59	1.15	1.15	0.74	1.22
I. holti	PCurv	1.25	1.40	0.75	1.16	1.15
	TWI	0.81	2.63	3.80	0.76	1.87
	Bio12	1.86	0.69	0.43	1.39	1.15
	Bio13	0.74	0.63	4.98	0.84	1.68
	Bio18	0.71	0.60	0.00	0.92	0.59
	Bio19	0.91	0.64	1.23	1.11	0.97
	Bio02	1.66	1.93	0.87	1.49	1.50
	Bio04	1.63	1.24	0.84	1.43	1.31
	Bio08	0.24	0.47	0.44	0.52	0.41
	Bio09	0.67	0.57	0.07	0.60	0.50
I. izecksohni	PCurv	0.57	0.77	0.65	0.49	0.63
	TWI	1.62	1.55	2.21	1.59	1.75
	Bio12	0.59	0.73	0.55	0.62	0.62
	Bio13	0.66	0.81	0.92	0.59	0.75
	Bio18	0.96	0.97	0.55	0.58	0.77
	Bio19	1.37	1.50	1.21	2.03	1.51
	Bio02	1.36	1.14	0.91	1.28	1.17
	Bio04	1.94	1.33	2.41	2.11	1.94
	Bio08	0.66	0.69	0.89	0.70	0.74
	Bio09	0.68	0.71	0.44	0.67	0.63
I. juipoca	PCurv	0.47	0.77	0.48	0.38	0.54
	TWI	3.98	1.59	1.29	1.15	2.07
	Bio12	0.82	0.82	0.64	1.19	0.83
	Bio13	0.55	0.66	0.67	0.56	0.62
	Bio18	0.71	0.76	0.82	0.75	0.76
	Bio19	0.56	0.93	1.32	1.05	0.96
	Bio02	1.31	1.60	1.20	1.22	1.35
	Bio04	1.62	1.42	2.01	3.56	2.00
	Bio08	0.72	0.94	1.22	0.53	0.89
	Bio09	0.68	0.74	0.70	0.71	0.71
I. manezinho	PCurv	0.58	0.63	0.65	0.37	0.56
	TWI	0.67	0.16	0.00	0.19	0.32
	Bio12	0.56	1.19	2.70	1.27	1.20
	Bio13	2.33	2.92	0.75	1.40	2.09
	Bio18	1.36	1.39	0.70	0.48	1.09
	Bio19	0.37	0.62	4.96	0.11	1.01
	Bio02	1.39	1.47	0.00	5.56	2.14
	Bio04	1.47	1.19	1.78	2.32	1.62
	Bio08	0.66	0.66	1.62	0.89	0.84
	Bio09	1.21	0.67	0.00	0.47	0.72
I. nasuta	PCurv	0.92	1.04	0.56	0.51	0.80
	TWI	1.85	1.58	1.45	1.44	1.61
	Bio12	0.80	0.83	0.40	1.35	0.85
	Bio13	0.91	1.16	0.47	1.13	0.95
	Bio18	0.85	1.10	1.37	0.89	1.03

	Bio19	1.01	0.99	0.73	1.15	0.98
	Bio02	0.98	0.73	0.66	1.17	0.89
	Bio04	1.28	0.75	1.20	1.14	1.08
	Bio08	0.75	0.85	1.84	0.70	0.97
	Bio09	0.84	1.08	1.86	0.70	1.07
I. nigriventris	PCurv	0.77	1.74	0.43	4.13	1.61
	TWI	0.87	0.66	0.51	0.13	0.59
	Bio12	1.35	3.53	0.61	1.10	1.63
	Bio13	0.49	0.64	0.51	0.35	0.50
	Bio18	2.73	0.88	0.70	0.57	1.40
	Bio19	0.88	0.30	0.78	1.36	0.82
	Bio02	1.64	1.89	0.70	0.95	1.34
	Bio04	1.00	0.80	0.43	4.00	1.44
	Bio08	0.26	0.66	30.60	0.00	7.25
	Bio09	0.77	0.31	0.44	0.41	0.52
I. octavioi	PCurv	0.68	0.95	0.32	0.35	0.60
	TWI	0.86	1.24	1.95	0.67	1.14
	Bio12	1.10	0.82	0.55	1.19	0.93
	Bio13	1.27	1.33	0.68	1.18	1.15
	Bio18	1.04	1.17	0.86	0.72	0.96
	Bio19	1.29	1.27	2.05	1.54	1.50
	Bio02	0.71	0.66	0.74	1.11	0.80
	Bio04	2.12	1.09	1.78	1.83	1.70
	Bio08	0.60	0.74	0.64	0.83	0.70
	Bio09	0.67	0.84	1.10	0.90	0.86
I. oea	PCurv	1.01	1.50	0.44	0.48	0.90
	TWI	1.12	1.59	1.26	0.86	1.22
	Bio12	0.73	0.75	0.72	1.18	0.84
	Bio13	0.84	0.99	0.75	1.01	0.90
	Bio18	0.69	0.69	1.03	0.79	0.79
	Bio19	1.72	1.59	1.83	1.48	1.66
	Bio02	1.00	0.72	0.89	1.05	0.91
	Bio04	1.97	1.02	1.17	1.95	1.53
	Bio08	0.59	0.65	0.52	0.62	0.60
	Bio09	0.66	0.75	1.77	0.88	0.98
I. parva	PCurv	0.64	1.06	0.49	0.49	0.70
	TWI	1.39	1.13	1.04	0.52	1.04
	Bio12	0.47	0.72	0.70	0.56	0.61
	Bio13	0.62	0.90	1.12	0.50	0.79
	Bio18	0.60	0.77	0.78	0.68	0.71
	Bio19	0.62	0.90	1.14	0.49	0.78
	Bio02	2.28	1.42	1.13	1.68	1.64
	Bio04	3.84	1.84	2.00	9.71	4.19
	Bio08	0.62	0.71	0.79	0.76	0.71
	Bio09	0.52	0.78	1.07	0.55	0.72
I. penaxavantinho	PCurv	1.93	2.42	1.49	3.29	2.29
	TWI	1.71	2.34	0.20	4.65	2.23
	Bio12	0.53	0.66	0.43	0.52	0.54
	Bio13	0.83	0.75	0.97	0.13	0.67
	Bio18	0.51	0.96	3.10	0.83	1.32
	Bio19	1.33	1.13	3.53	1.70	1.89
	Bio02	0.68	0.57	0.20	0.67	0.54
	Bio04	1.43	0.70	0.67	1.21	1.00
	Bio08	0.81	0.54	0.68	0.03	0.52
	Bio09	0.68	0.69	0.68	0.04	0.53
I. randorum	PCurv	0.67	0.47	0.00	0.63	0.58

	TWI	1.39	0.80	0.00	0.50	0.89
	Bio12	0.84	1.11	0.00	0.78	0.86
	Bio13	0.68	0.73	0.00	1.47	0.91
	Bio18	0.24	0.53	Inf	0.65	Inf
	Bio19	1.22	0.57	0.00	0.62	0.81
	Bio02	1.84	3.38	0.00	1.41	2.03
	Bio04	2.30	2.63	0.00	3.66	2.71
	Bio08	0.91	0.64	0.00	1.08	0.85
	Bio09	0.56	0.57	Inf	0.41	Inf
I. sambaqui	PCurv	0.64	0.60	0.00	1.25	0.60
	TWI	1.22	0.65	1.32	2.10	1.25
	Bio12	0.81	1.44	0.00	0.34	0.71
	Bio13	1.38	1.74	6.98	0.57	2.61
	Bio18	1.09	0.63	0.00	2.04	0.89
	Bio19	0.72	0.61	0.00	0.32	0.44
	Bio02	3.09	2.29	Inf	1.81	Inf
	Bio04	0.69	1.73	0.00	0.54	0.80
	Bio08	0.40	0.52	0.53	0.40	0.46
	Bio09	0.80	0.50	0.00	1.57	0.68
I. verrucosa	PCurv	0.95	1.13	1.21	0.40	0.94
	TWI	1.93	1.12	1.46	1.33	1.47
	Bio12	0.64	0.84	0.88	0.73	0.77
	Bio13	0.88	0.95	0.68	1.32	0.95
	Bio18	0.65	0.84	0.80	0.72	0.75
	Bio19	1.04	1.13	0.85	1.34	1.09
	Bio02	0.81	0.89	0.82	0.61	0.79
	Bio04	1.84	1.31	1.89	1.95	1.72
	Bio08	0.82	0.91	0.98	0.93	0.90
	Bio09	0.80	0.91	0.67	1.03	0.85
I. vizottoi	PCurv	0.69	0.71	0.48	0.54	0.63
	TWI	2.98	4.42	114.66	2.07	15.06
	Bio12	1.29	0.97	0.66	1.03	1.05
	Bio13	0.83	0.38	0.48	0.64	0.59
	Bio18	0.84	0.69	0.48	0.74	0.72
	Bio19	0.41	0.25	0.66	0.74	0.48
	Bio02	1.23	1.12	0.48	0.96	1.04
	Bio04	0.54	1.45	0.48	1.29	1.04
	Bio08	1.19	1.03	0.48	1.54	1.17
	Bio09	0.77	0.68	0.48	0.83	0.73

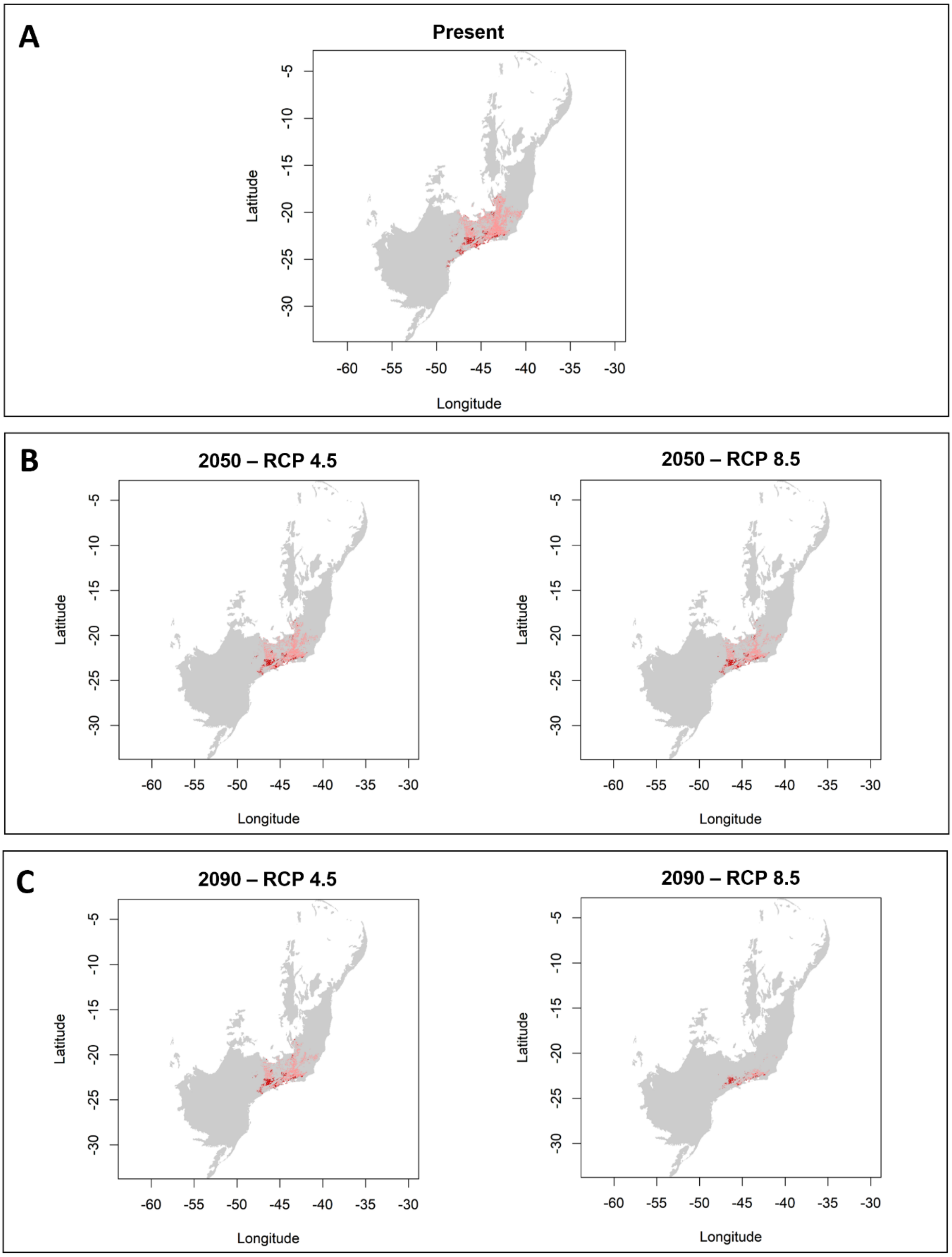

Fig. A1 - Predicted distribution of *I. abdita* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

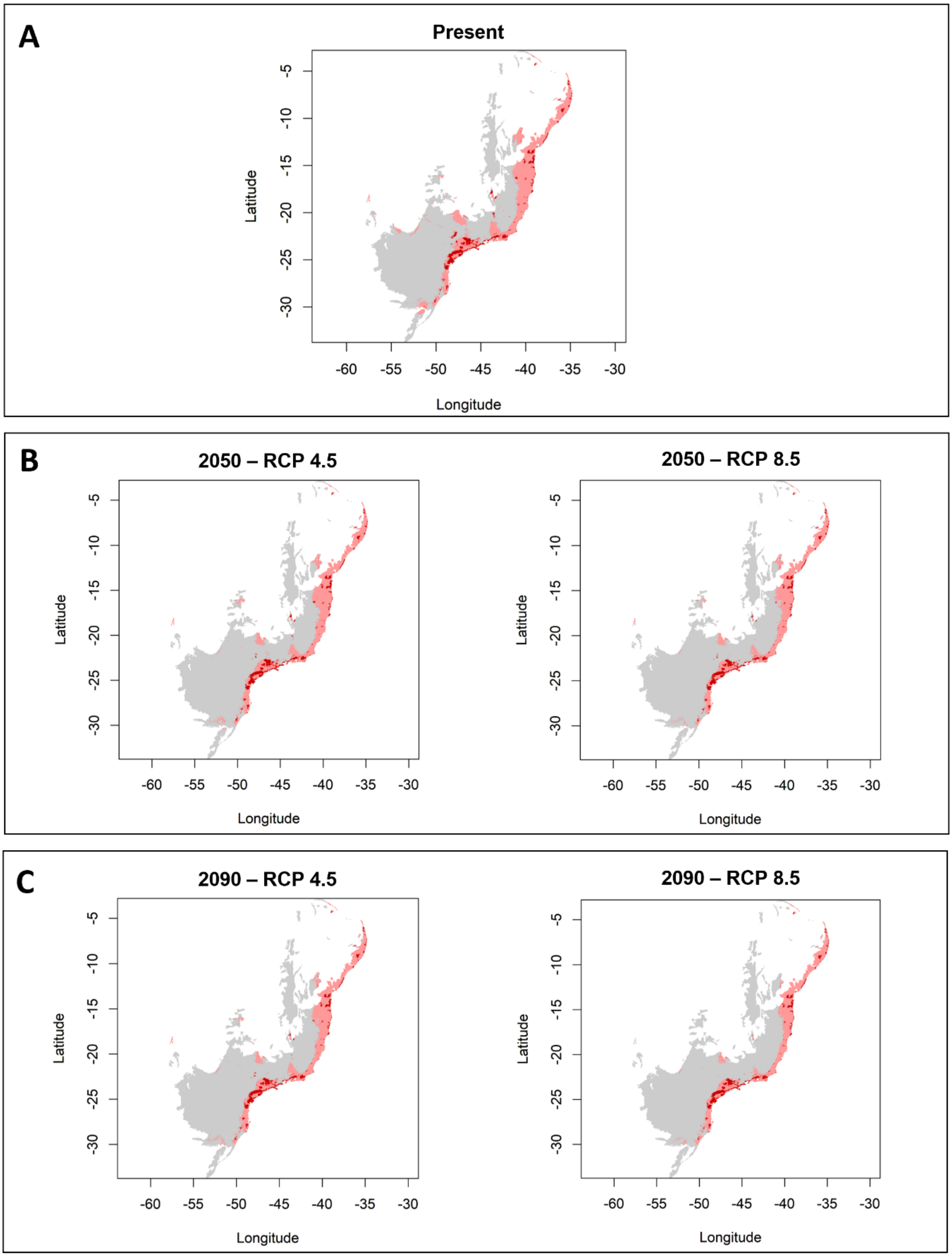

Fig. A2 -Predicted distribution of *I. bolbodactyla* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

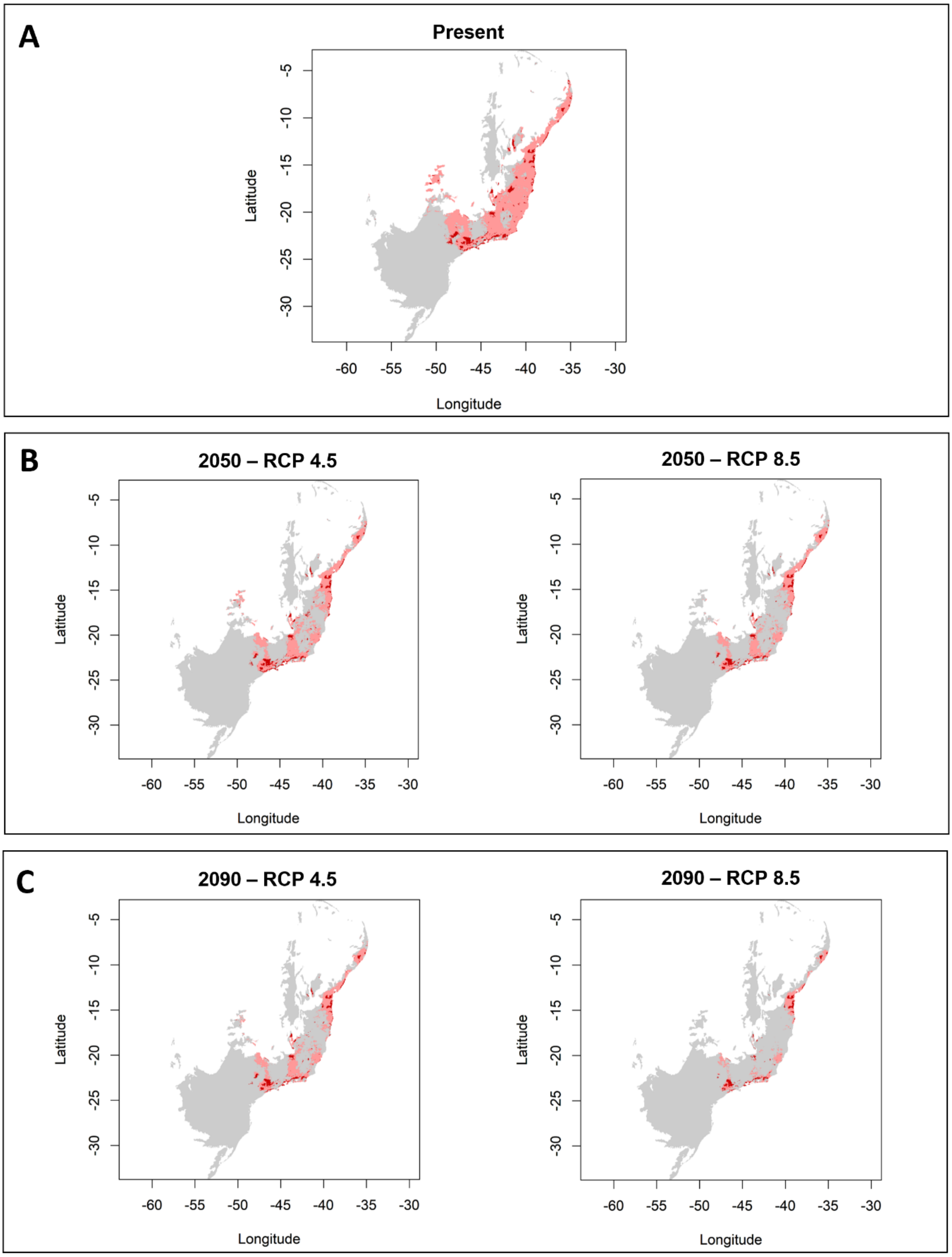

Fig. A3 -Predicted distribution of *I. guentheri* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

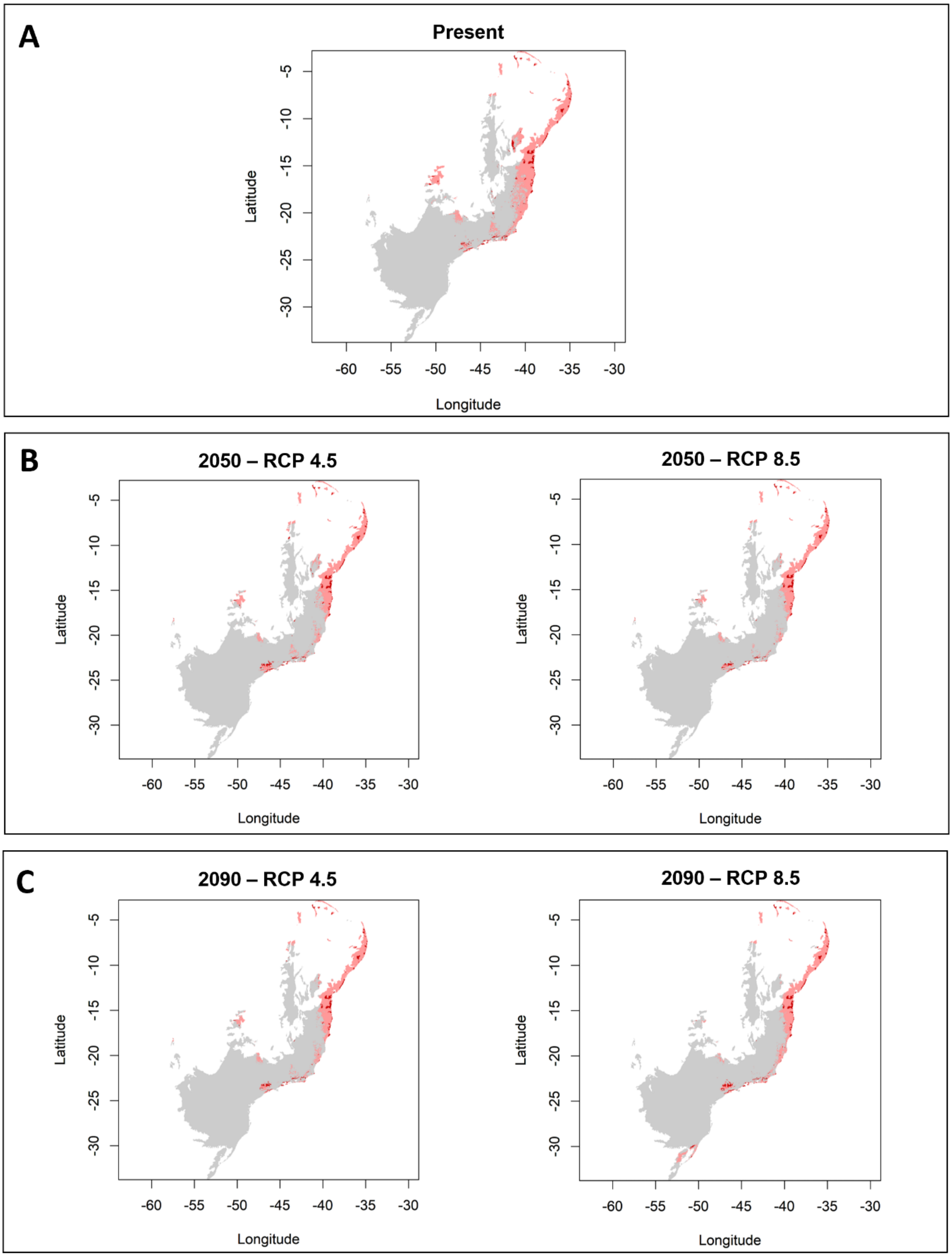

Fig. A4 -Predicted distribution of *I. henselii* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

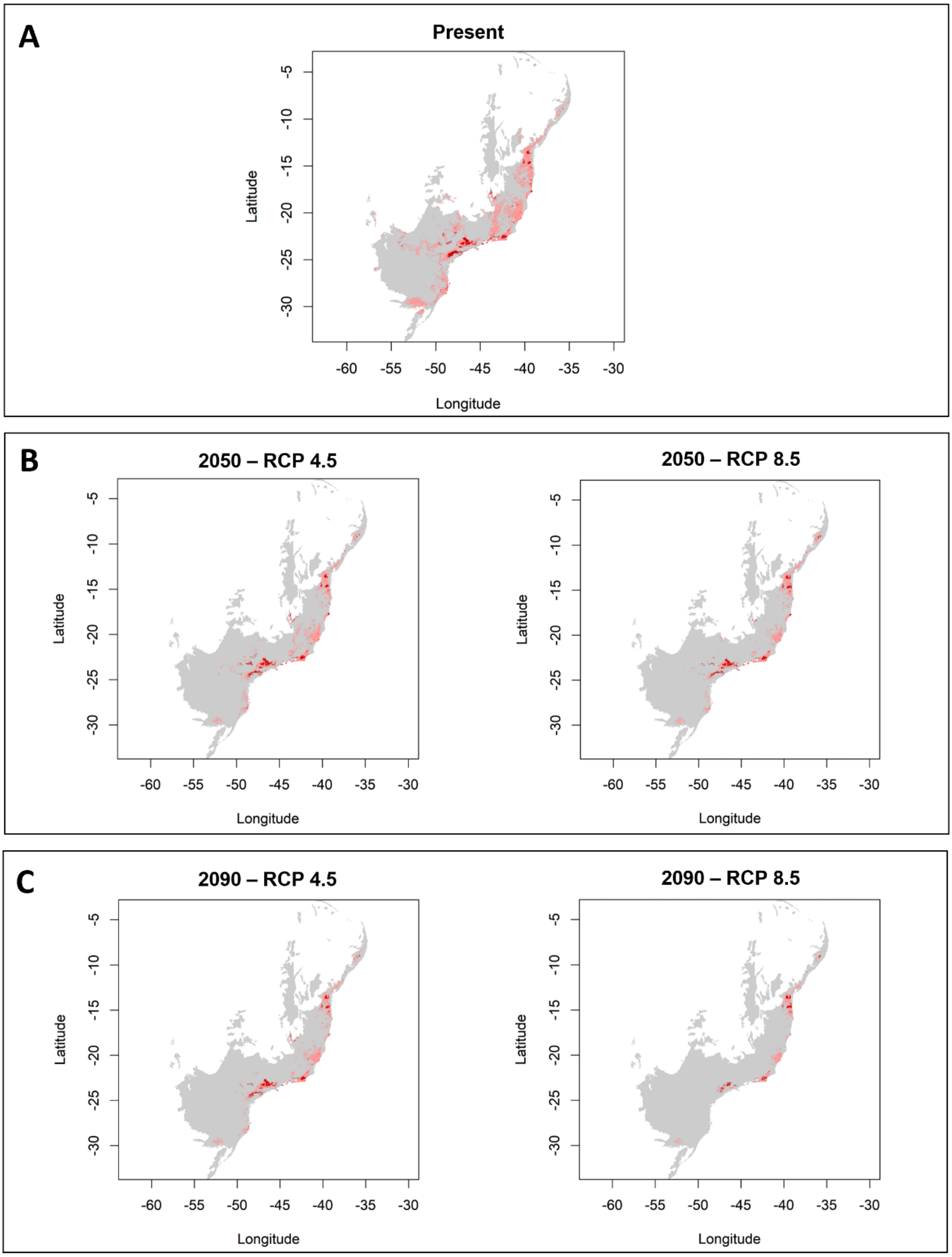

Fig. A5 -Predicted distribution of *I. holti* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

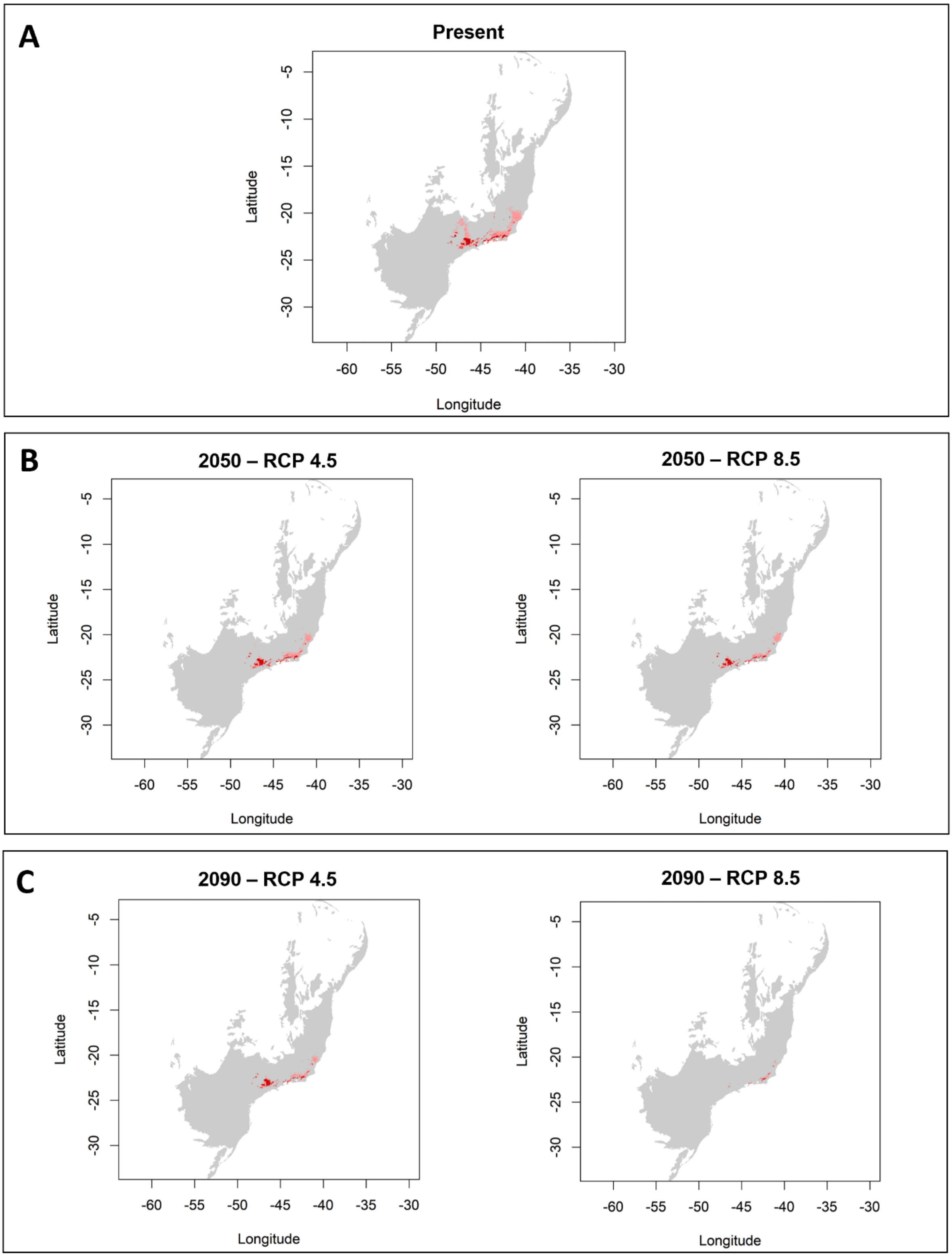

Fig. A6 -Predicted distribution of *I. izecksohni* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

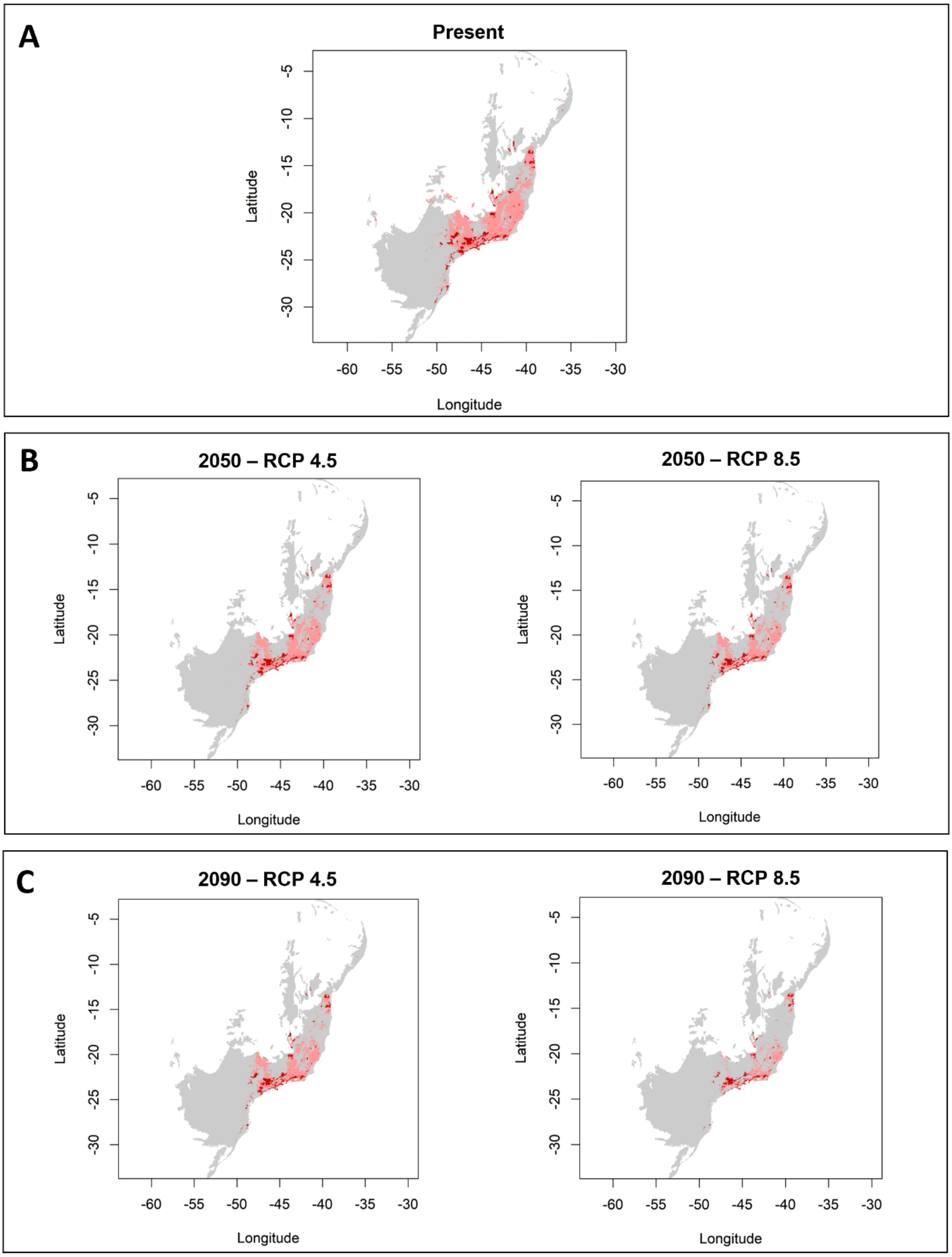

Fig. A7 -Predicted distribution of *I. juipoca* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

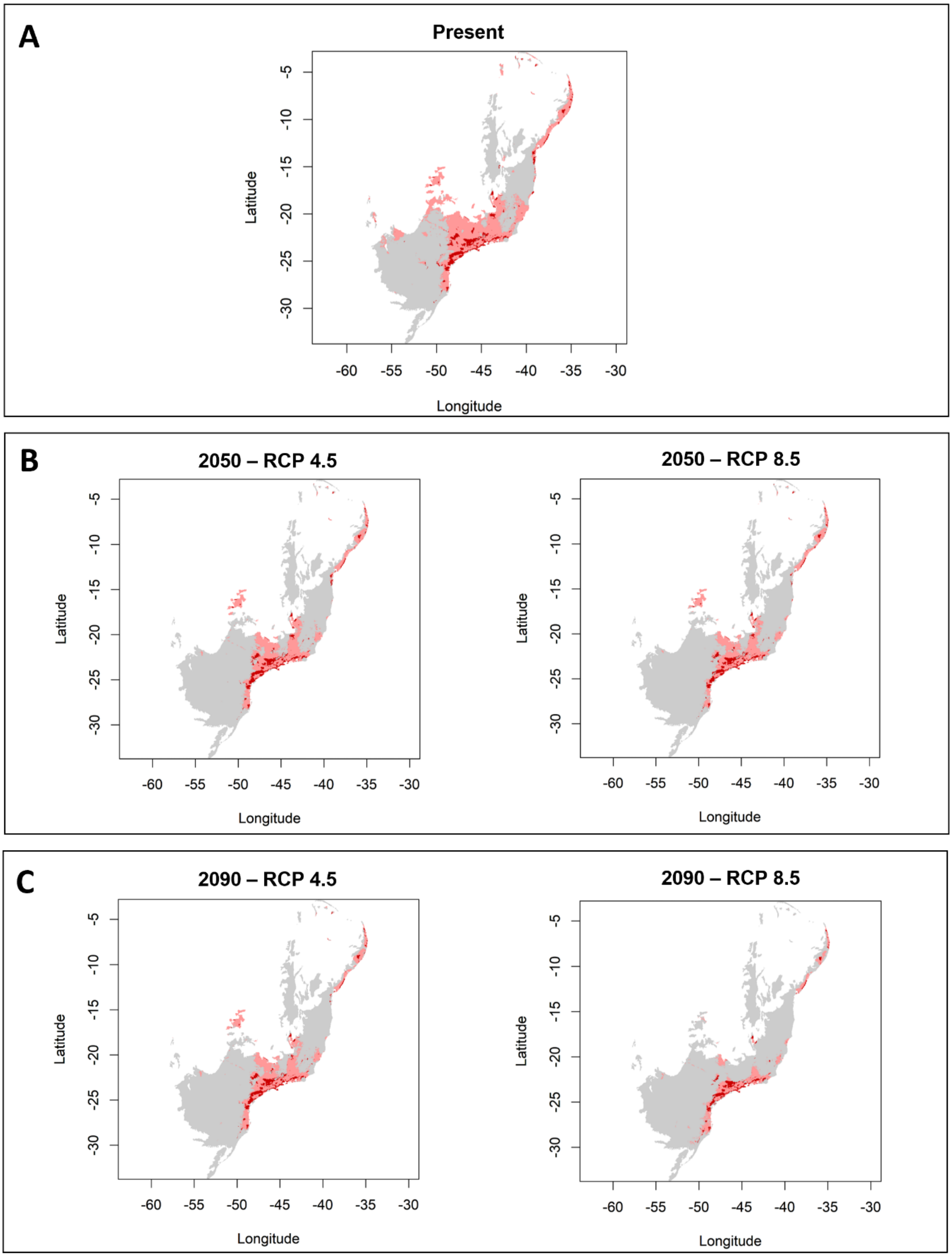

Fig. A8 -Predicted distribution of *I. manezinho* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

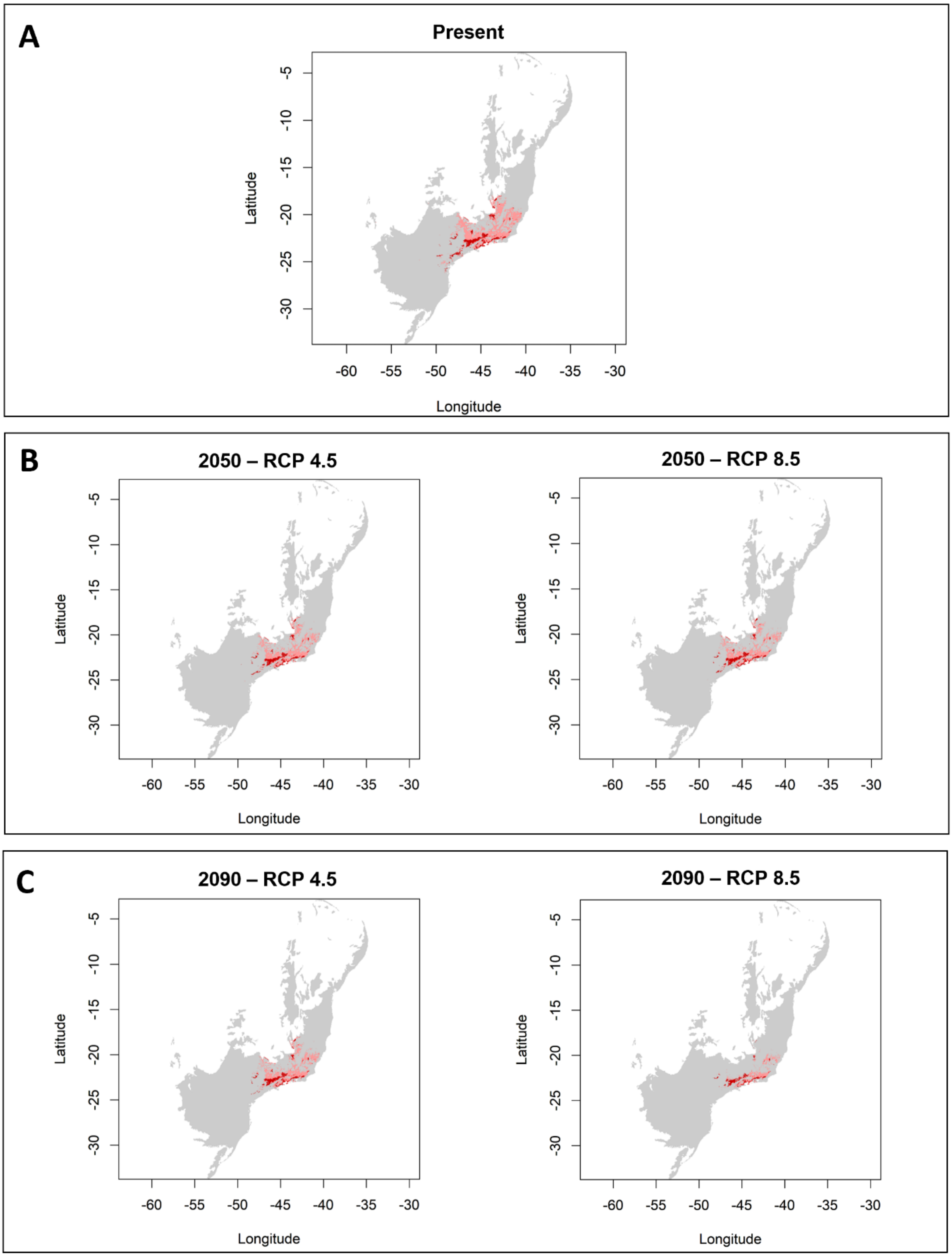

Fig. A9 -Predicted distribution of *I. nasuta* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

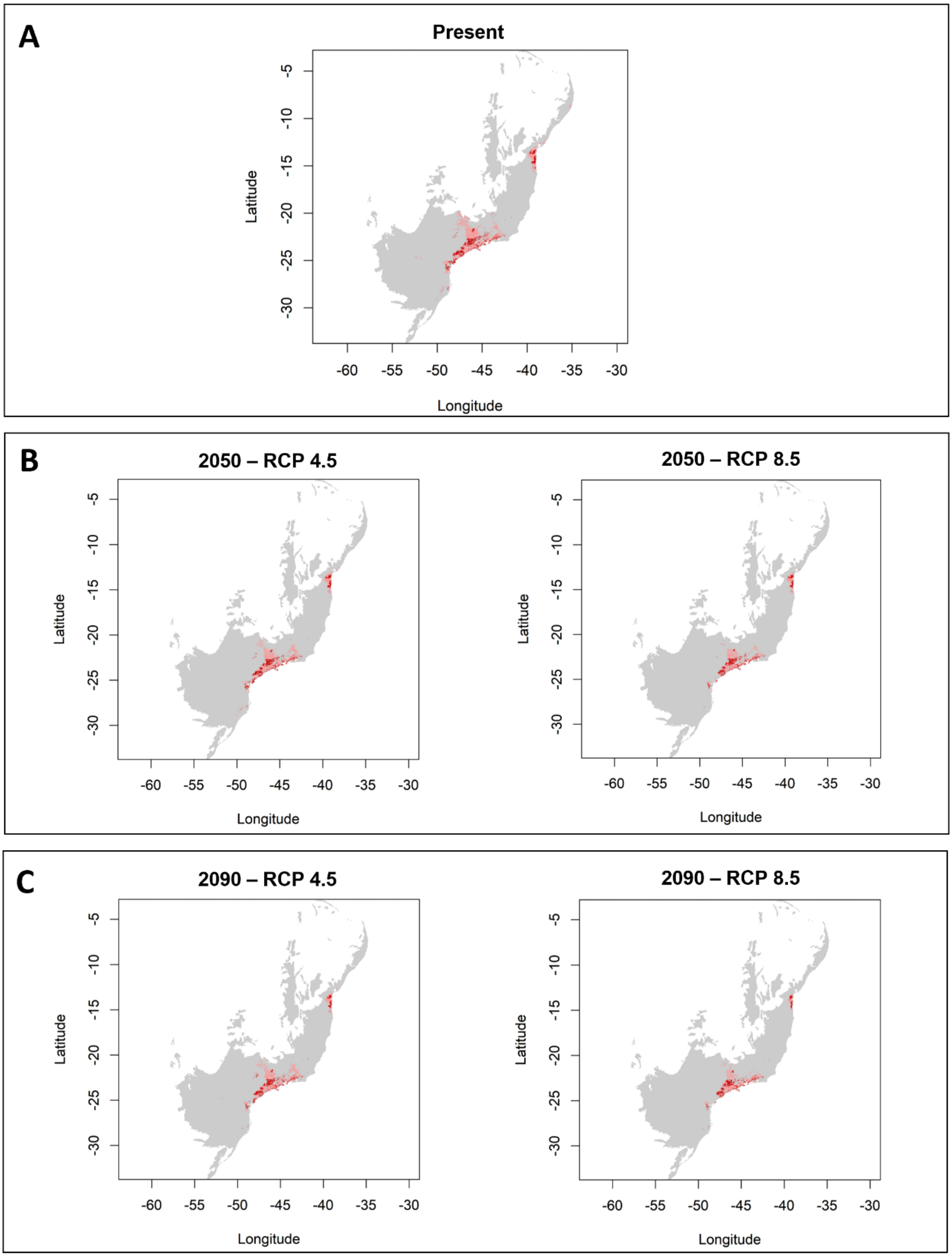

Fig. A10 -Predicted distribution of *I. nigriventris* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

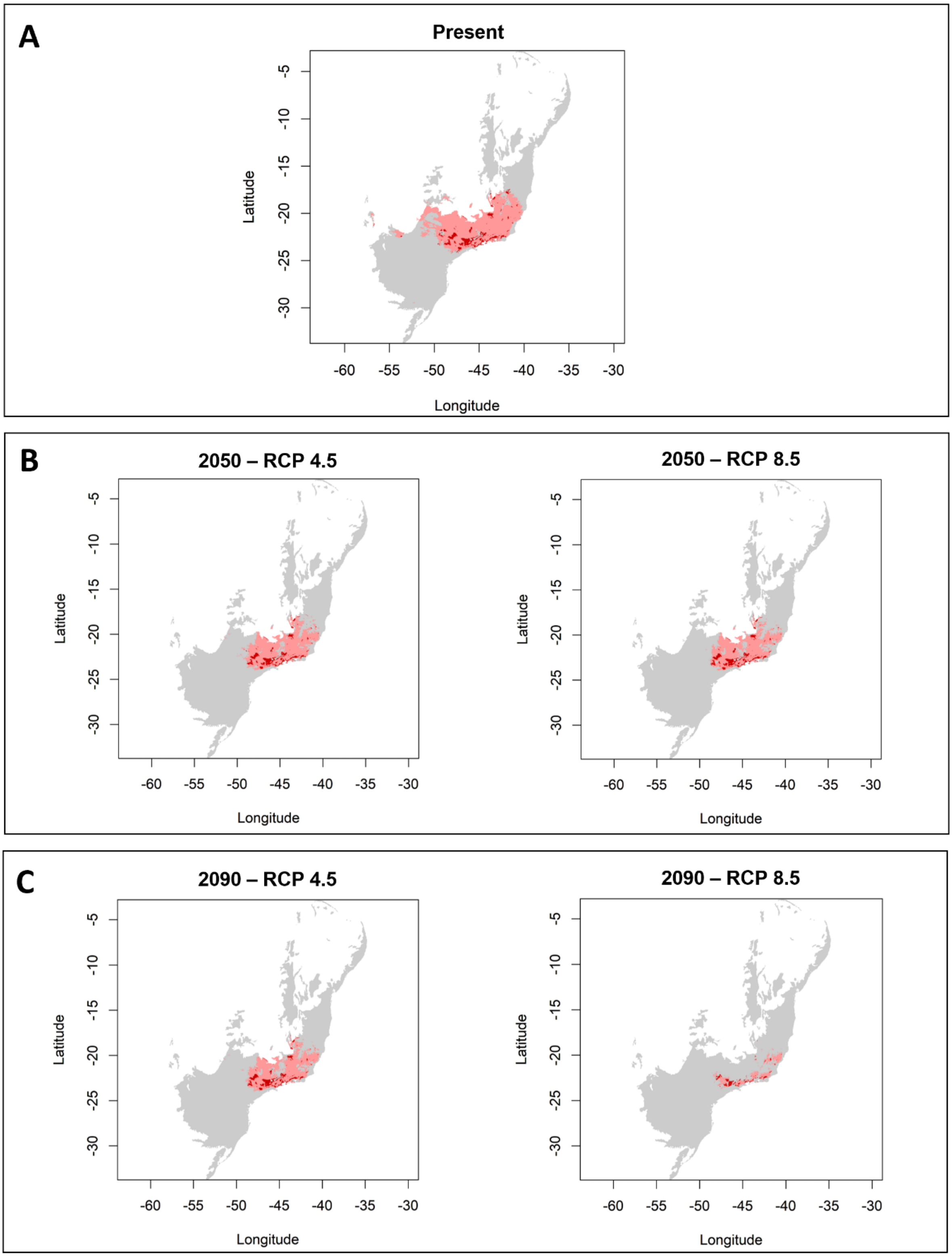

Fig. A11 -Predicted distribution of *I. octavioi* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

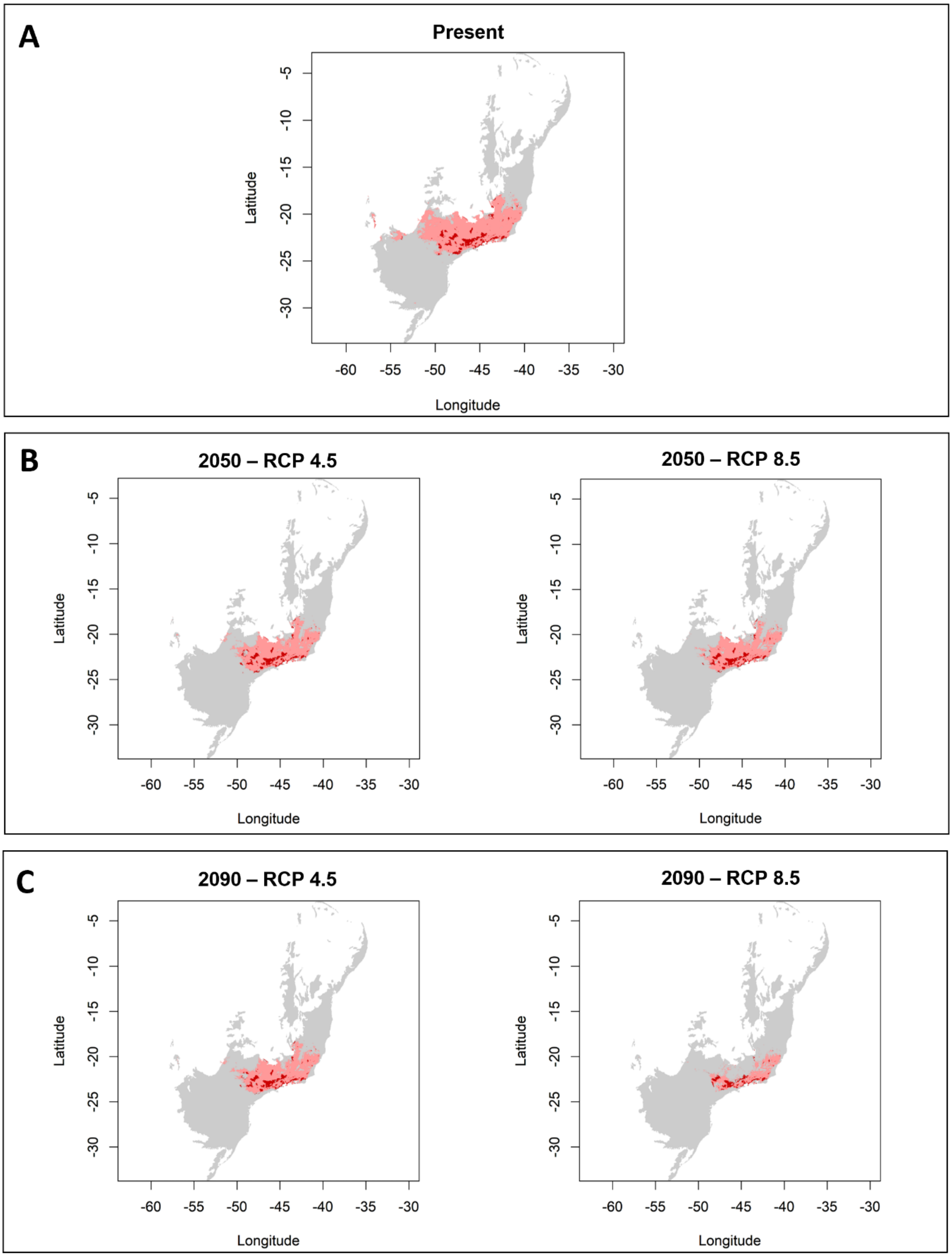

Fig. A12 -Predicted distribution of *I. oea* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

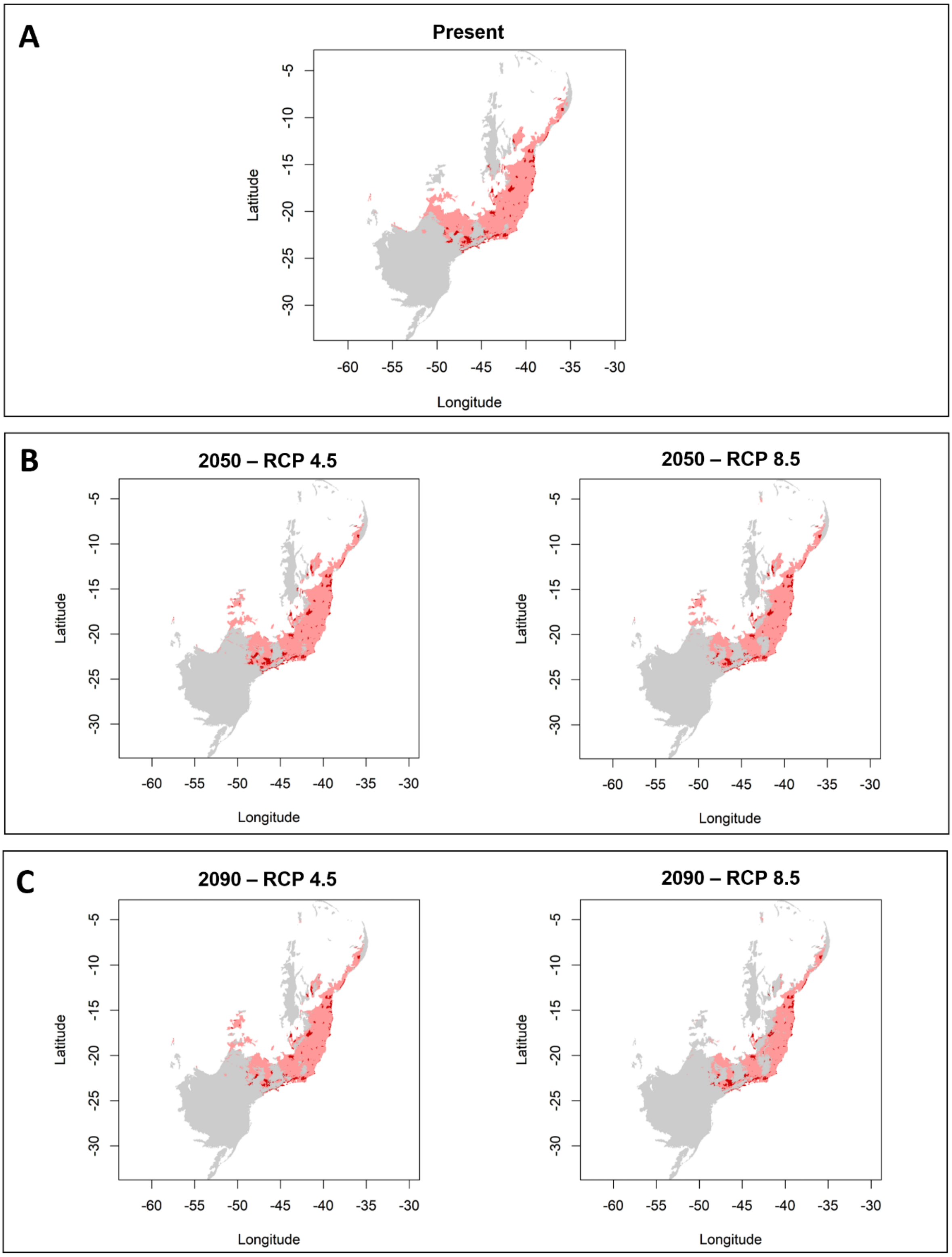

Fig. A13 - Predicted distribution of *I. parva* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

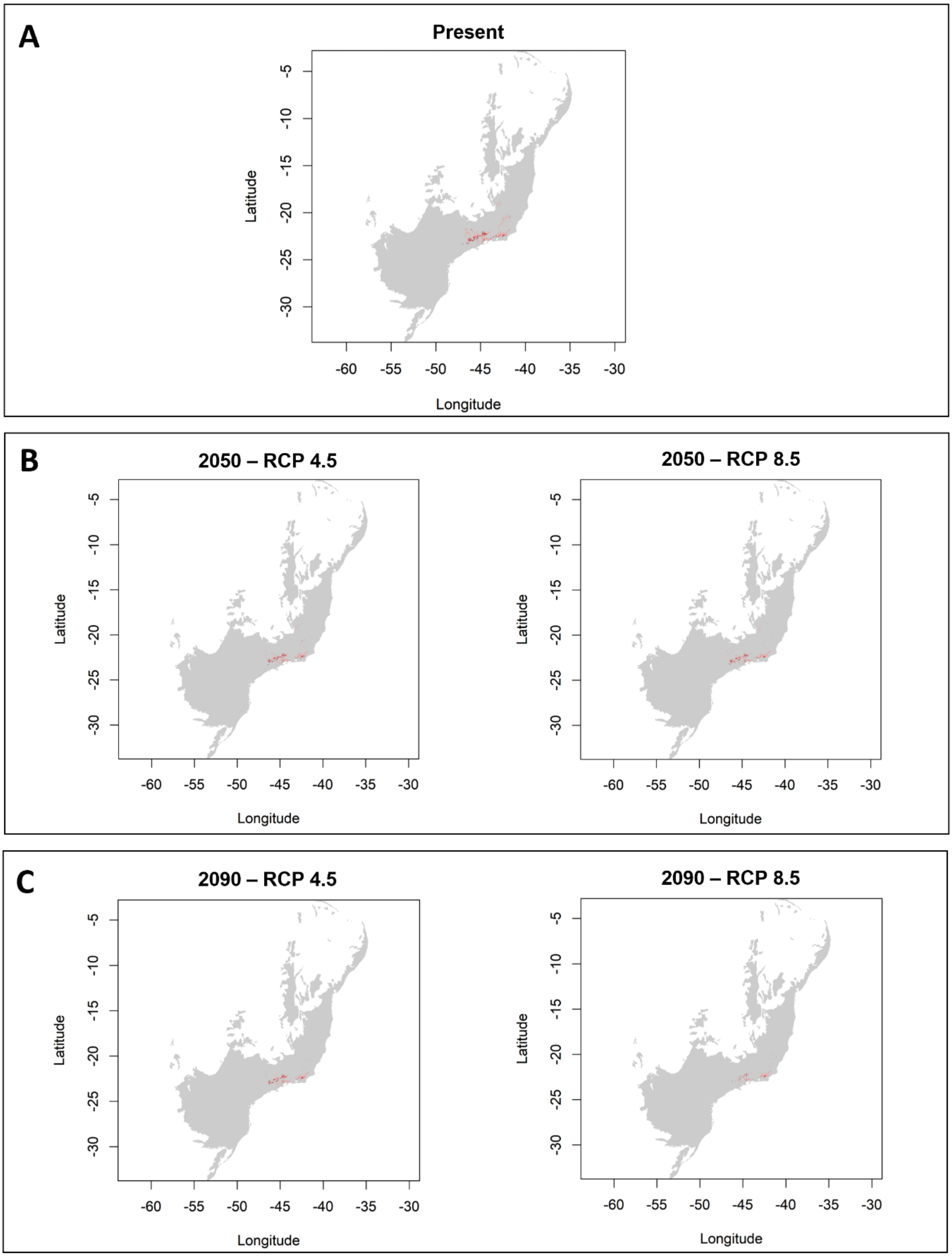

Fig. A14 -Predicted distribution of *I. penaxavantinho* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

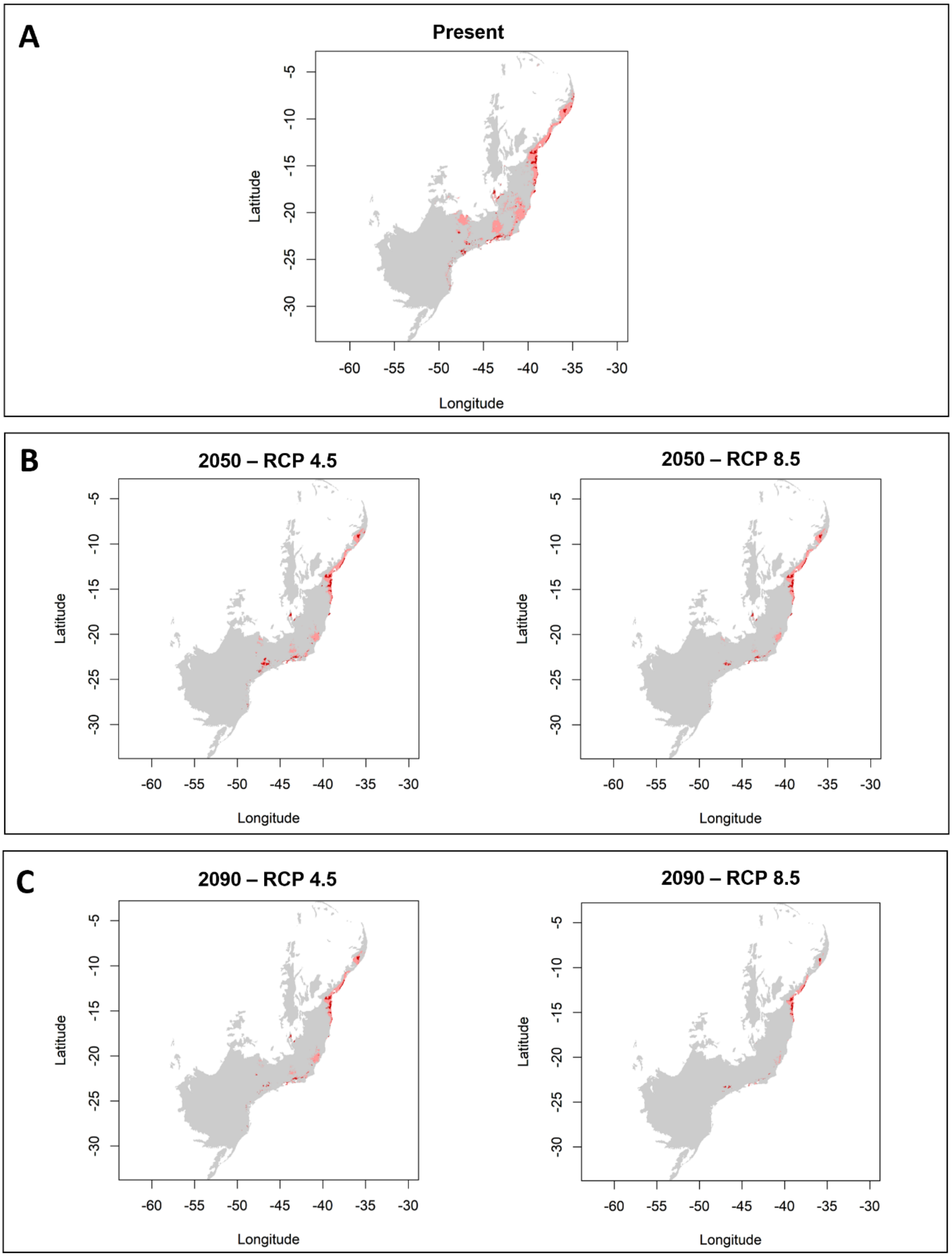

Fig. A15 -Predicted distribution of *I. randorum* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

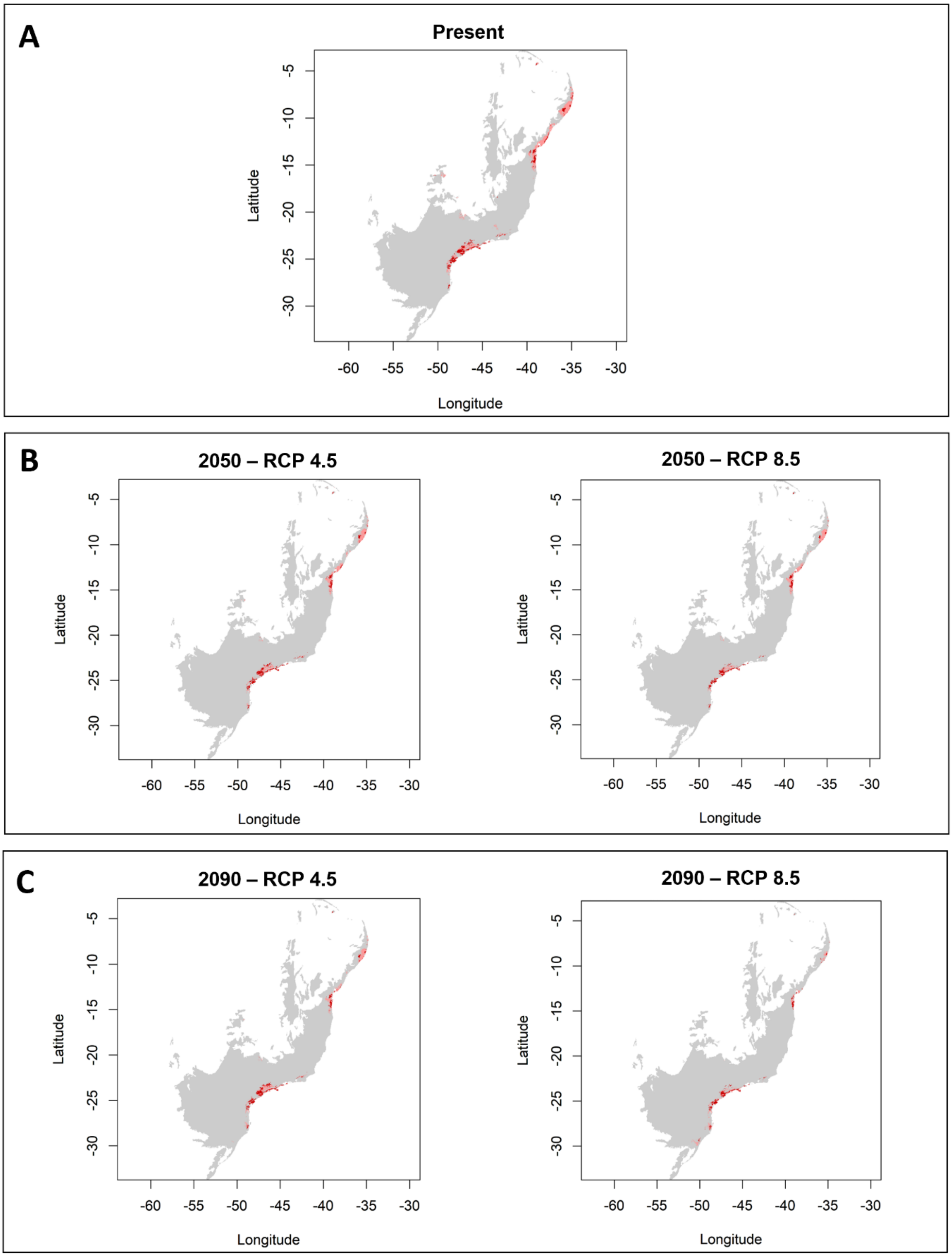

Fig. A16 -Predicted distribution of *I. sambaqui* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Distribution covered by PAs are shown in dark red and outside from PAs are shown in light red.

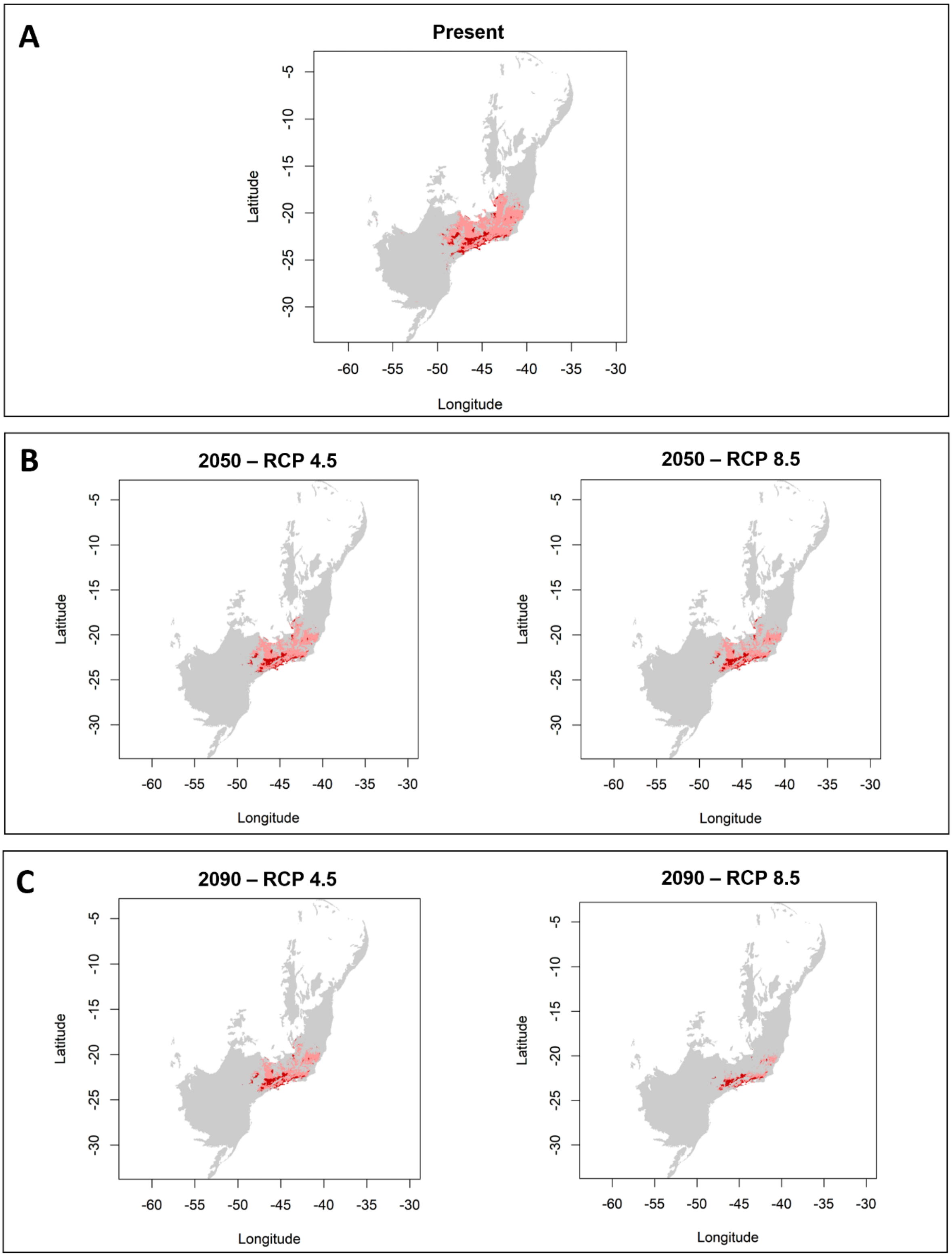

Fig. A17 -Predicted distribution of *I. verrucosa* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

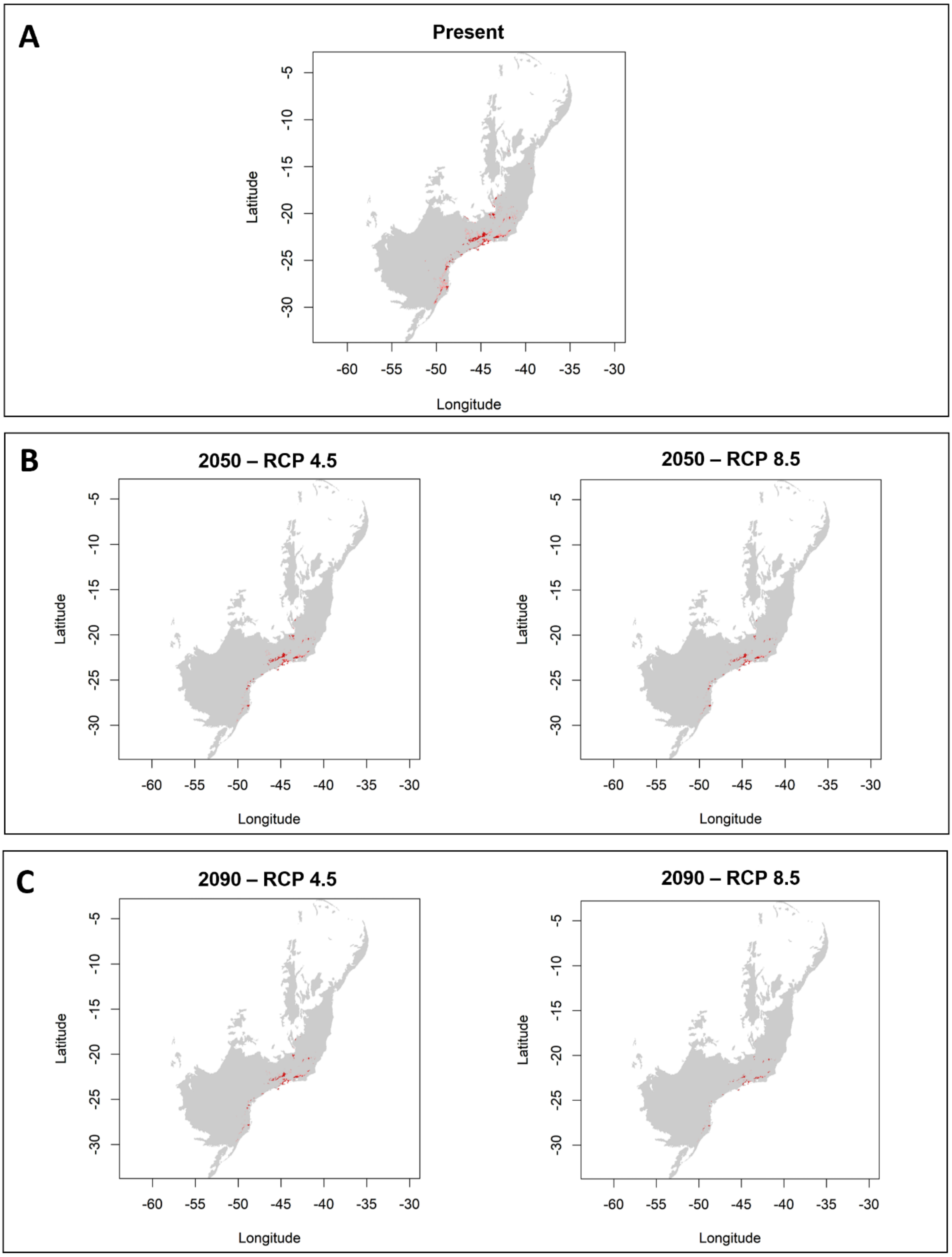

Fig. A18 -Predicted distribution of *I. vizottoi* in the Atlantic Forest. (A) At present. (B) For 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. (C) For 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. The distribution area within the PAs is shown in dark red and outside the PAs in light red.

Table A4 – Mean percentage overlap (MPO) between the distribution of direct-developing frogs of genus *Ischnocnema* and the protected areas of the Atlantic Forest for the present time. N cells – number of cells with occurrences of each species. All values were significantly higher than expected by chance.

Species	**N cells**	**MPO**	**MPOr**
I. abdita	5383	14.68	7.51
I.bolbodactyla	20917	13.75	7.50
I.guentheri	25947	10.07	7.49
I.henselii	14260	9.22	7.50
I.holti	13118	10.46	7.51
I.izecksohni	3204	22.38	7.50
I.juipoca	17892	14.42	7.50
I.manezinho	24955	13.46	7.50
I.nasuta	7290	19.91	7.51
I.nigriventris	4471	29.75	7.51
I.octavioi	20551	9.07	7.50
I.oea	21714	9.94	7.49
I.parva	30660	7.80	7.50
I.penaxavantinho	660	33.11	7.44
I.randorum	7658	13.98	7.49
I.sambaqui	3540	32.81	7.50
I.verrucosa	12982	15.14	7.50
I.vizottoi	1838	43.55	7.52

Table A5 – Mean percentage overlap (MPO) between the distribution of direct-developing frogs of genus *Ischnocnema* and the protected areas of the Atlantic Forest for 2050 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. N cells – number of cells with occurrences of each species. MPOr – MPO random All values were significantly higher than expected by chance.

	RCP 4.5			**RCP 8.5**		
Species	**N cells**	**MPO**	**MPOr**	**N cells**	**MPO**	**MPOr**
I.abdita	3880	17.16	7.47	2887	20.12	7.49
I.bolbodactyla	18196	14.96	7.50	16748	15.50	7.49
I.guentheri	14438	14.41	7.49	10884	15.79	7.50
I.henselii	10535	11.59	7.50	9339	11.83	7.50
I.holti	6556	16.22	7.49	5124	18.22	7.50
I.izecksohni	1865	29.78	7.50	1521	31.21	7.52
I.juipoca	12249	17.30	7.49	9953	18.84	7.49
I.manezinho	15796	17.76	7.49	13891	18.47	7.50
I.nasuta	5397	21.91	7.51	4774	23.70	7.51
I.nigriventris	3572	32.75	7.50	2771	35.61	7.50
I.octavioi	13463	11.73	7.49	11609	13.18	7.50
I.oea	14722	12.32	7.50	12777	13.08	7.50
I.parva	29019	9.01	7.49	24811	8.91	7.50
I.penaxavantinho	422	35.68	7.54	379	36.65	7.50
I.randorum	3849	22.43	7.49	2976	22.91	7.52
I.sambaqui	2407	37.91	7.50	2009	38.51	7.50
I.verrucosa	8922	17.54	7.50	7272	19.83	7.50
I.vizottoi	944	56.79	7.51	695	60.25	7.48

Table A6 – Mean percentage overlap (MPO) between the distribution of direct-developing frogs of genus *Ischnocnema* and the protected areas of the Atlantic Forest for 2090 under the moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. N cells – number of cells with occurrences of each species. MPOr – MPO random. All values were significantly higher than expected by chance.

	RCP 4.5			**RCP 8.5**		
Species	**N cells**	**MPO**	**MPOr**	**N cells**	**MPO**	**MPOr**
I.abdita	3122	19.31	7.50	934	33.92	7.46
I.bolbodactyla	17470	15.23	7.50	15140	16.80	7.50
I.guentheri	11106	15.62	7.51	5297	22.76	7.50
I.henselii	9885	11.49	7.51	9878	12.46	7.50
I.holti	5072	17.94	7.48	2547	18.79	7.50
I.izecksohni	1362	34.36	7.50	230	28.33	7.47
I.juipoca	10276	18.71	7.49	5383	25.11	7.49
I.manezinho	14680	17.65	7.49	8453	23.55	7.49
I.nasuta	5006	22.32	7.50	2343	31.79	7.49
I.nigriventris	3415	32.20	7.48	2343	31.79	7.49
I.octavioi	11477	13.14	7.50	2912	19.88	7.47
I.oea	13423	12.73	7.50	5954	18.93	7.50
I.parva	25908	8.41	7.50	20087	10.41	7.50
I.penaxavantinho	336	38.93	7.42	192	28.92	7.59
I.randorum	2868	21.74	7.50	1385	28.42	7.52
I.sambaqui	2171	42.01	7.51	1357	48.93	7.48
I.verrucosa	6833	20.42	7.49	2847	33.93	7.50
I.vizottoi	704	59.91	7.55	317	64.38	7.47

CONSIDERAÇÕES FINAIS

Da mesma forma que os quatro capítulos que compõem essa tese podem ser vistos como seções isoladas, ao serem combinados, eles se tornam complementares e contam, juntos, uma história eco-evolutiva sobre um dos aspectos mais interessantes da história de vida dos anfíbios, a especialização reprodutiva. Como esperado, essa tese traçou uma linha cronológica sobre o desenvolvimento direto em anuros. No primeiro capítulo defini o estado da arte no contexto do conhecimento ecológico-evolutivo do desenvolvimento direto em anfíbios anuros. Através de uma revisão da literatura, consegui criar um quadro teórico no qual identifiquei e esclareci as principais hipóteses e forças seletivas que guiaram a evolução desse modo reprodutivo. Dentre esses agentes, destaco os papéis de importantes fatores bióticos como a predação e a competição, e de fatores abióticos como as condições ambientais (clima e estrutura ambiental). Da mesma forma, também apontei as lacunas de conhecimento sobre esse assunto, bem como indiquei as futuras direções para o entendimento da evolução do desenvolvimento direto, através da sugestão de estudos que efetivamente testem de forma integrada essas hipóteses com dados reais, em diferentes regiões e em diferentes escalas. Assim, consegui compreender parte do passado, mesmo que de forma ainda limitada, através do conhecimento dos mecanismos evolutivos associados à evolução desse modo reprodutivo.

Nos dois capítulos seguintes, traduzi os resultados do quadro teórico montado no primeiro capítulo em hipóteses que puderam ser efetivamente testadas. No capítulo II, utilizando dados de comunidades locais de anuros da Mata Atlântica, consegui testar essas relações em uma escala espacial fina. Os resultados deste capítulo mostraram que variáveis ambientais, como a umidade e a sazonalidade da precipitação, exercem grande influência sobre a proporção de espécies de desenvolvimento direto nessas comunidades. Além disso, a diversidade funcional também desempenha um papel fundamental na estruturação dessas comunidades. Trabalhando em escala de comunidades nesse capítulo, os resultados permitiram evidenciar relações que podem não ser tão perceptíveis em escalas maiores.

No terceiro capítulo, utilizando uma abordagem macroecológica, expandi a escala e investiguei as relações entre diferentes fatores bióticos (composição filogenética e diversidade funcional) e abióticos (clima e topografia) com o desenvolvimento direto em anuros do Novo Mundo. Os resultados desse capítulo demonstram principalmente a importância da história evolutiva para a ocorrência dessas espécies ao longo de toda a região das Américas. Também, verifiquei que as relações testadas variam conforme o bioma avaliado, sendo o papel do componente biótico (composição filogenética) preponderante nos biomas tropicais, enquanto os fatores abióticos, como temperatura e umidade, estão mais relacionados ao desenvolvimento direto nos biomas temperados. Dessa forma, tanto os resultados do capítulo II quanto do capítulo III forneceram importantes *insights* sobre o passado por meio das relações investigadas, bem como possibilitaram avaliar o presente ao verificar os padrões de distribuição dessas espécies e de estrutura das comunidades de anuros ao longo do Novo Mundo e da Mata Atlântica.

Fechei a tese com o capítulo IV, onde modelei a distribuição atual de 18 espécies anuros de desenvolvimento direto do gênero *Ischnocnema* na Mata Atlântica. Também realizei previsões futuras quanto à distribuição dessas espécies frente a distintos cenários de mudanças climáticas. Além disso, investiguei o papel das áreas protegidas da Mata Atlântica em resguardar tanto a distribuição atual quanto futura dessas espécies. Com os resultados desse capítulo, pude visualizar os centros de riqueza de espécies para esse gênero. Verifiquei, também, que as áreas protegidas se mostram relativamente efetivas em proteger a área de distribuição dessas espécies tanto no presente quanto para o futuro. No entanto, esses resultados também apontam para um panorama preocupante, uma vez que encontrei um forte declínio na área de distribuição futura de muitas espécies. Assim, os resultados desse capítulo me permitiram não somente avaliar o presente dessas espécies, mas também criar predições a respeito do futuro delas.

Saliento que os resultados dessa tese contribuem significativamente com o conhecimento do desenvolvimento direto em anuros. Além disso, o fornecimento das informações (mapas) de distribuição e as previsões futuras para espécies do gênero *Ischnocnema*, podem servir como bases para ações, planos e estratégias de conservação para esse grupo de espécies na Mata Atlântica. Ressalto também a importância fundamental do conhecimento de história natural das espécies, bem como do amplo acesso a esse tipo de informação. Essa tese foi construída inteiramente com dados provenientes de literatura, evidenciando assim que a disponibilidade de tais informações se mostra uma ferramenta essencial e propulsora para a promoção da ciência. Por fim, destaco que ainda há muitas perguntas a serem respondidas acerca da evolução do desenvolvimento direto e da diversificação reprodutiva dos anfíbios. Tais questões podem ser exploradas através da inclusão de outras medidas e aspectos ecológicos, que não foram avaliados aqui. Além disso, futuros trabalhos podem considerar escalas ainda mais amplas (global), ou por meio de experimentos delineados em escalas mais finas (locais).