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Predictive Ecology: A Two-Chapter Analysis of Lizard Invasion and Serpent Potential Invasion using Ecological Niche Models in Brazil

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Ecologia Preditiva: Uma Análise em Dois Capítulos sobre a Invasão de Lagartos e a Potencial Invasão de Serpentes usando Modelos de Nicho Ecológico no Brasil.

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Resumo:

A área da biologia da invasão se torna cada vez mais importante, e conforme os estudos desta área avançam, crescem também os desafios ao se estudar nesta área. A falta de informação sobre as espécies muitas vezes é um obstáculo para que estudos mais aprofundados possam ser realizados, mostrando que a área ainda carece muito da ciência de base. Frente a estes obstáculos, uma ferramenta que pode fornecer muita informação sobre espécies fora de seu habitat endêmico é a modelagem de nicho ecológico (ENM), muitas vezes utilizada dentro do contexto da biologia de paisagem ou conservação vem cada vez sendo mais empregada no contexto da invasão, ou na predição de áreas onde espécies possam se tornar invasoras. Dentro desse contexto a presenta tese busca apresentar duas aplicações distintas dos ENM uma em uma invasão que já ocorreu, tentando buscar a origem de sua invasão, e em outro momento buscando antecipar áreas de risco para serpentes invasoras no Brasil. No primeiro capítulo foi possível encontrar um padrão de distribuição genética de lagartos no Brasil que possivelmente teve influência das zonas de origem deste mesmo lagarto na África, corroborando uma antiga hipótese em que as lagartixas de parede tem sua introdução devido a navios negreiros. No segundo capítulo conseguimos identificar zonas críticas caso ocorra uma possível invasão de *Python* no Brasil, ainda podemos identificar regiões onde possa ocorrer uma competição por nicho mais acirrada, proporcionando prejuízo para as constritoras endêmicas. Por fim, nos dois capítulos foi possível contribuir para o conhecimento sobre espécies invasoras utilizando a ferramenta proposta, com abordagens diferentes em cada um dos capítulos.

Palavras chave: Biologia da invasão; modelagem de nicho ecológico, lagartos, serpentes, invasão, animais exóticos

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Introdução

Existe um grande debate sobre o que define uma espécie invasora. Vários autores tentaram padronizar esse conceito criando frameworks e categorias para cada estágio de invasão (e.g., Blackburn et al. (2011); Pereyra (2016); Kapitza et al. (2019)). Para a presente tese eu adoto o conceito proposto por Blackburn (2011), que define uma espécie como completamente invasiva quando indivíduos podem se dispersar, sobreviver e reproduzir em diversos locais em um maior ou menor espectro de habitats e aumentar sua dispersão. A dispersão de espécies invasoras em ambientes não nativos tem alterado drasticamente a composição de comunidades em escala global, e o declínio das populações nativas frequentemente ocorre simultaneamente com a disseminação de espécies invasoras (Gurevitch e Padilla, 2004), aumentando também a homogeneização dos ambientes (McKinney e Lockwood, 1999). Observa-se que a introdução de espécies invasoras frequentemente é prejudicial ao meio ambiente e pode causar desequilíbrios ecológicos, afetando não apenas diretamente a biodiversidade, mas também, indiretamente, as populações humanas (Rosenzweig, 2001). Também é importante destacar que espécies capazes de expandir sua distribuição geográfica podem se beneficiar da perturbação humana e da homogeneização dos ambientes naturais, acrescentando um problema adicional aos ecossistemas de espécies endêmicas (Newbold et al., 2018).

Espécies invasoras são conhecidas por forçar a extinção local de espécies endêmicas, perturbando o nicho ecológico ao adicionar um competidor adicional ou devido à predação (Dorcas et al., 2012; Simberloff et al., 2013). Um dos principais desafios para entender o processo de invasões biológicas é a ausência de um programa global efetivo de monitoramento (Latombe et al., 2017), tornando os dados disponíveis para o estudo de espécies invasoras muito escassos (Pergl et al., 2020).

Modelos de Nicho Ecológico (ENMs), como uma ferramenta versátil, desempenham um papel crucial em desvendar padrões de distribuição de espécies, aproveitando seus nichos ambientais. Além de sua função primária de estimar a distribuição potencial de uma espécie, essa abordagem de modelagem fornece insights inestimáveis para a tomada de decisões em conservação. Por exemplo, ela auxilia na seleção estratégica de áreas protegidas e no aprimoramento de suas fronteiras para aumentar a eficácia da conservação (Guisan e Thuiller, 2005). Além disso, a modelagem de nicho ecológico prova ser um recurso multifacetado, contribuindo significativamente para a exploração de padrões ecológicos e evolutivos em vários ecossistemas (Gutiérrez et al., 2014). Sua aplicação se estende à identificação de lacunas críticas na conservação, oferecendo orientações essenciais para priorizar esforços de conservação e alocação de recursos (de Novaes e Silva et al., 2014; Lessmann et al., 2014). A versatilidade da modelagem de nicho destaca sua importância como uma ferramenta abrangente e dinâmica com implicações de amplo alcance para a pesquisa e gestão da conservação ecológica.

ENMs também são empregados para prever o potencial de uma espécie introduzida tornar-se invasiva e potencialmente alterar sistemas naturais (por exemplo, Peterson 2001, 2003; Peterson e Robins 2003; Pyron et al. 2008; Ulhanek e Eung 2011). Esses modelos operam sob a suposição de que, em um período de tempo relativamente curto em termos evolutivos, uma espécie mantém conservadoramente seu nicho ambiental. As preferências e tolerâncias das espécies para variáveis climáticas são consideradas preditores confiáveis da distribuição espacial da espécie (Wiens e Graham 2005). Essa abordagem se mostra particularmente eficaz na estimativa da distribuição potencial de uma espécie antes de sua introdução (Peterson e Vieglais 2001; Jeschke e Strayer 2008).

Compreender a distribuição potencial de uma espécie introduzida antes de seu estabelecimento é essencial para medidas proativas de conservação e gestão. Essa abordagem proativa está alinhada com os princípios da conservação preventiva, permitindo a identificação de áreas suscetíveis à invasão e facilitando esforços direcionados para mitigar o impacto de espécies invasoras nos ecossistemas nativos (Javier et al., 2020).

Além disso, a aplicação da modelagem de nicho para prever a potencial invasão contribui para uma compreensão mais ampla da dinâmica ecológica, oferecendo insights sobre as interações entre espécies introduzidas e os componentes bióticos e abióticos existentes em um ecossistema. Ao utilizar modelagem preditiva, pesquisadores e conservacionistas podem aprimorar sua capacidade de enfrentar os desafios impostos por espécies invasoras, promovendo, em última instância, estratégias de conservação mais eficazes e práticas de gestão sustentável (Fordham et al., 2013).

Estudos biogeográficos dependem fortemente da disponibilidade de dados sobre a distribuição das espécies em investigação. A ausência de tais dados constitui um fator limitante para a pesquisa em várias áreas da ecologia aplicada (Beck et al., 2012). Bancos de dados como o Global Biodiversity Information Facility (GBIF) desempenham um papel crucial na compilação de informações sobre a distribuição da biodiversidade a partir de instituições como museus e coleções biológicas. Apesar dos possíveis vieses decorrentes da variação na qualidade dos dados disponíveis, a utilização de tais ferramentas é de valor inestimável para estudos de distribuição (Beck et al., 2014). Além disso, esses bancos de dados frequentemente apresentam uma gama mais extensa de pontos de distribuição em comparação com compilações independentes da literatura (Beck et al., 2013).

A dependência de bancos de dados abrangentes, como o GBIF, destaca a importância de esforços colaborativos na coleta e compartilhamento de dados de biodiversidade. Ao agregar informações de fontes diversas, esses bancos de dados ampliam o alcance e a profundidade das análises biogeográficas, permitindo que pesquisadores explorem padrões e tendências em uma escala mais ampla. Ao reconhecer as potenciais limitações associadas à qualidade dos dados, a utilização desses bancos de dados centralizados representa uma abordagem pragmática para superar os desafios impostos pela escassez de dados (Feng et al., 2019).

No contexto da ecologia aplicada, a integração de dados de fontes como o GBIF facilita uma compreensão mais holística da distribuição das espécies, permitindo que os pesquisadores tomem decisões informadas em áreas que vão desde o planejamento de conservação até a gestão de espécies invasoras. À medida que a tecnologia e as iniciativas colaborativas de compartilhamento de dados continuam a avançar, o papel de bancos de dados abrangentes no apoio à pesquisa biogeográfica tende a se tornar ainda mais fundamental, oferecendo insights valiosos sobre as complexidades dos sistemas ecológicos e auxiliando no desenvolvimento de estratégias de conservação eficazes (Feng et al., 2019).

Compreender os processos que facilitam a introdução de espécies em novos ambientes não deve estar exclusivamente ligado às características das espécies ou do ambiente, mas também às características específicas de como essas invasões ocorreram (Lockwood et al., 2005). Seja intencional ou não, o número de espécies invasoras cresceu ao longo do século XX, proporcionando à comunidade científica amplas evidências de como essas espécies podem causar danos a espécies nativas, ecossistemas e à saúde humana (Simberloff et al., 2013). Dentro dessas características, destaca-se o conceito de pressão de propágulo.

A escassez de informações ecológicas sobre essas espécies destaca a necessidade de pesquisas abrangentes para melhor entender seu comportamento, preferências de habitat e interações com outras espécies (Mahoney et al., 2015). Dada sua presença generalizada e potencial impacto ecológico, obter uma compreensão mais profunda da ecologia de algumas espécies invasoras é crucial para estratégias eficazes de conservação e gestão, especialmente em regiões onde esses répteis coexistem com ecossistemas diversos e paisagens dominadas por atividades humanas.

Este trabalho compreende dois capítulos, cada um formatado como um manuscrito para submissão a periódicos científicos, explorando aspectos distintos da análise ecológica. No primeiro capítulo, o objetivo é fornecer um contexto biogeográfico usando modelagem de nicho. O objetivo principal é investigar as possíveis origens geográficas de diferentes grupos genéticos dentro das populações de *Hemidactylus mabouia*, comumente conhecido como o lagarto-de-parede.

Continuando para o segundo capítulo, as mesmas ferramentas analíticas são empregadas, mas com um objetivo diferente. Em vez de explorar o passado, como visto no primeiro capítulo, o foco muda para uma perspectiva voltada para o futuro. Aqui, exploramos a possibilidade de serpentes invasoras do gênero *Python* estabelecerem populações no território brasileiro e examinamos seu potencial impacto sobre as espécies nativas de serpentes.

O objetivo geral desta tese é destacar as aplicações versáteis de uma única ferramenta analítica em vários cenários. Seja complementando informações em estudos concluídos ou concebendo novos projetos, esses capítulos ressaltam a adaptabilidade e eficácia das ferramentas utilizadas. Um tema crucial entrelaçado nesses trabalhos é o papel significativo do ambiente na formação das distribuições populacionais, não apenas em habitats nativos, mas também em áreas onde as espécies se tornam invasoras. Ao navegar por essas paisagens diversas, a tese busca contribuir com insights nuances ao conhecimento existente e enfatizar a intrincada interação entre fatores ambientais e dinâmicas populacionais. Em essência, este trabalho serve como evidência das aplicações multifacetadas das ferramentas ecológicas, fornecendo insights sobre as dinâmicas passadas, presentes e futuras de espécies diversas em diferentes contextos ecológicos.

Capítulo 1

O objetivo do primeiro capítulo é integrar ferramentas de ENMs adicionando conhecimento a um trabalho já realizado pela equipe de pesquisa, buscando elucidar a hipótese de que a introdução de *H. mabouia* pode ter ocorrido devido a influência de navios negreiros. Além do ENM, foi estudado de forma intensiva um banco de dados sobre navegações negreiras entre 1514 e 1866, de forma a estimar quantos navios negreiros oriundos de zonas de *H. mabouia* aportaram no litoral brasileiro.

Trabalhando com essas duas ferramentas em conjunto, adicionado dos grupos genéticos encontrados pelo trabalho “Biologia da invasão de *Hemidactylus mabouia* no Brasil: análise da estrutura genética populacional” de Pontes e colaboradores, 2017; o trabalho desenvolvido teve como resultado um padrão que corrobore a hipótese original proposta, carecendo de mais informações para afirmações mais robustas.

Ao final da tese, será adicionado um apêndice com os resultados elaborados por mim, já adicionados os resultados obtidos por outros colaboradores. Este documento apresentará formato de manuscrito, que será finalizado e submetido para periódico científico ainda a definir.

Capítulo 2

O segundo capítulo da tese está apresentado em formato de manuscrito, já submetido para a revista *Biological Invasions* – *Springer* e até o momento de elaboração deste texto em processo de revisão (Major Reviews).

Este trabalho busca utilizar os ENMs como forma de predizer áreas dentro do Brasil onde 4 diferentes espécies de *Python* podem se tornar invasoras. Adicionado a este processo, modelos de 4 diferentes gêneros de serpentes constritoras endêmicas foram adicionadas com o intuito de estabelecer regiões em que haverá competição caso uma das *Python* se torne invasora.

Como resultado obtive uma grande área de potencial invasão de *Python*, sendo que algumas espécies, a citar, *P. sebae* e *P. bivittatus,* poderão influenciar de forma deletéria as serpentes nativas. Esses resultados de sobreposição de nicho ainda podem ser pensados como uma forma de proxy, indicando que caso haja uma grande constritora no ambiente, isso pode indicar uma facilitação da invasão de outra serpente. Essa é uma nova forma de se pensar a utlização da sobreposição de nicho, porém deve ser observada de forma cautelosa, carecendo de um estudo mais profundo dos organismos estudados.

O principal resultado deste trabalho é a sobreposição dos modelos das 8 serpentes estudadas, adicionadas de um mapa que soma todo o território modelado para as serpentes brasileiras estudadas, convergindo assim em uma matriz de 29 mapas de fácil observação, auxiliando a leitura dos resultados, identificando áreas críticas para cada uma das espécies estudadas, seja de forma isolada, ou de forma sobreposta.

References

American Pet Products Association (APPA). (2021). Pet industry market size & ownership statistics

Barker, D. G., & Barker, T. M. (1994). Pythons of the world. Volume I: Australia. Advanced Vivarium Systems.

Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., et al. (2013). Online solutions and the “Wallacean shortfall”: What does GBIF contribute to our knowledge of species’ ranges? Diversity and Distributions, 19, 1043–1050.

Beck, J., Ballesteros-Mejia, L., Nagel, P., & Kitching, I. J. (2012). What’s on the horizon for macroecology? Ecography, 35, 673–683.

Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species’ geographic distributions. Ecological Informatics, 19, 10–15.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., … Richardson, D. M. (2011). A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Buchanan, B. W., Fisher, R., Perry, G., et al. (2008). Effects of night lighting on urban reptiles and amphibians. Herpetological Conservation, 3, 239–256.

Cordier, J.M., Loyola, R., Rojas-Soto, O., Nori, J. (2020). Modeling invasive species risk from established populations: Insights for management and conservation. Perspectives in Ecology and Conservation, 18(2), 132-138. https://doi.org/10.1016/j.pecon.2020.06.001

de Novaes e Silva, V., Pressey, R. L., Machado, R. B., et al. (2014). Formulating conservation targets for a gap analysis of endemic lizards in a biodiversity hotspot. Biological Conservation, 180, 1–10.

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., & Mazzotti, F. J. 2012. Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. Proceedings of the National Academy of Sciences, 109(7), 2418-2422.

Feng, X., Park, D.S., Walker, C., et al. (2019). A checklist for maximizing reproducibility of ecological niche models. Nat Ecol Evol, 3, 1382–1395. https://doi.org/10.1038/s41559-019-0972-5

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Keith, D.A., Brook, B.W. (2013). Tools for integrating range change, extinction risk and climate change information into conservation management. Ecography, 36, 956-964. https://doi.org/10.1111/j.1600-0587.2013.00147.x

Fuenmayor, G. R., Ugueto, G., Bauer, A. M., et al. (2005). Expansion and natural history of a successful colonizing gecko in Venezuela (Reptilia: Gekkonidae: *Hemidactylus mabouia*) and the discovery of *H. frenatus* in Venezuela. Herpetological Review, 36, 121–124.

Fujisaki, I., Hart, K.M., Mazzotti, F.J., et al. (2010). Risk assessment of potential invasiveness of exotic reptiles imported to south Florida. Biol Invasions, 12, 2585–2596. https://doi.org/10.1007/s10530-009-9667-1

Greene, H. W. (1997). Snakes: The evolution of mystery in nature. University of California Press.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. Ecology Letters, 8, 993–1009.

Gutiérrez, E. E., Boria, R. A., & Anderson, R. P. (2014). Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums. Ecography, 37, 741–753.

Hoddle, M. S. (2004). Restoring Balance: Using Exotic Species to Control Invasive Exotic Species. Conservation Biology, 18, 38–49.

Howard, K. G., Parmerlee, J. S., & Powell, R. (2001). Natural history of the edificarian geckos *Hemidactylus mabouia*, *Thecadactylus rapicauda, and Sphaerodactylus sputator* on Anguilla. Caribbean Journal of Science, 37, 285–288.

Jeschke, J. M., & Strayer, D. L. (2008). Usefulness of Bioclimatic Models for Studying Climate Change and Invasive Species. Annals of the New York Academy of Sciences, 1134, 1–24.

Kapitza, K., Zimmermann, H., Martin-Lopez, B., von Wehrden, H. (2019). Factors driving social perceptions of invasive species: a systematic literature review. NeoBiota, 43, 47-63. https://doi.org/10.3897/neobiota.43.31619

Latombe, G., P. Pyšek, J. M. Jeschke, T. M. Blackburn, S. Bacher, C. Capinha, M. J. Costello, M. Fernández, R. D. Gregory, D. Hobern, et al. 2017. A vision for global monitoring of biological invasions. Biol. Conserv. 213: 295–308.

Lemke, A, Kowarik, I, von der Lippe, M. How traffic facilitates population expansion of invasive species along roads: The case of common ragweed in Germany. J Appl Ecol. 2019; 56: 413–422. https://doi.org/10.1111/1365-2664.13287

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution, 20, 223–228.

Mahoney, P.J., Beard, K.H., Durso, A.M., Tallian, A.G., Long, A.L., Kindermann, R.J., Nolan, N.E., Kinka, D., Mohn, H.E. (2015). Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. Diversity Distrib., 21, 64-74. https://doi.org/10.1111/ddi.12240

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14: 450–453.

Newbold, T., L. N. Hudson, S. Contu, S. L. L. Hill, J. Beck, Y. Liu, C. Meyer, H. R. P. Phillips, J. P. W. Scharlemann, and A. Purvis. 2018. Widespread winners and narrow-ranged losers: land use homogenizes biodiversity in local assemblages worldwide. PLoS Biol. 16: e2006841.

Pereyra, P. J. (2016). Revisiting the use of the invasive species concept: An empirical approach. Austral Ecology, 41(5), 519–528. https://doi.org/10.1111/aec.12340

Pergl, J., P. Pyšek, F. Essl, J. M. Jeschke, F. Courchamp, J. Geist, M. Hejda, I. Kowarik, A. Mill, C. Musseau, et al. 2020. Need for routine tracking of biological invasions. Conserv. Biol. 34: 1311–1314.

Peterson, A. T. (2001). Predicting species' Geographic distributions based on ecological niche modeling. BioOne, 103, 599–605.

Peterson, A. T. (2003). "Predicting the geography of species" Invasions via ecological niche modeling. The Quarterly Review of Biology, 78, 419–433.

Peterson, A. T., & Robins, C. R. (2003). Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation. Conservation Biology, 17, 1161–1165.

Peterson, A.T. (2005). Predicting potential geographic distributions of invading species. Current Science, 89, 9–10.

Pizzatto, L., Marques, O., & Facure, K. (2009). Food habits of Brazilian boid snakes: overview and new data, with special reference to *Corallus hortulanus*. Amphibia-Reptilia, 30(4), 533-544. https://doi.org/10.1163/156853809789647121

Pyron, R. A., Burbrink, F. T., & Guiher, T. J. (2008). Claims of Potential Expansion throughout the U.S. by Invasive *Python* Species Are Contradicted by Ecological Niche Models. PLos One, 3, 1–7.

Reed, R.N., Willson, J.D., Rodda, G.H., Dorcas, M.E. (2012). Ecological correlates of invasion impact for Burmese pythons in Florida. Integr Zool, 7(3), 254-270. https://doi.org/10.1111/j.1749-4877.2012.00304.x

Riddle, B. R., Dawson, M. N., Hadly, E. A., Hafner, D. J., Hickerson, M. J., Mantooth, S. J., & Yoder, A. D. (2008). The role of molecular genetics in sculpting the future of integrative biogeography. Progress in Physical Geography: Earth and Environment, 32(2), 173-202. https://doi.org/10.1177/0309133308093822

Rocha, C. F. D., & Anjos, L. A. (2007). Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. Brazilian Journal of Biology, 67, 485–91.

Rocha, C. F. D., Anjos, L. A., & Bergallo, H. G. (2011). Conquering Brazil: the invasion by the exotic gekkonid lizard *Hemidactylus mabouia* (Squamata) in Brazilian natural environments. Zoologia, 28, 747–754.

Rosenzweig, M. L. (2001). The four questions: What does the introduction of exotic species do to diversity? Evolutionary Ecology Research, 3, 361–367.

Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M. 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol, 28(1), 58-66. https://doi.org/10.1016/j.tree.2012.07.013.

Simberloff, D., Reed, R.N., Rodda, G.H. (2010). Giant constrictors: biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the *Boa constrictor*. Biol Invasions, 12, 2375–2377. https://doi.org/10.1007/s10530-009-9643-9

Ulhanek, S. T. A. K., & Eung, B. R. L. (2011). Using ecological niche models to predict the abundance and impact of invasive species : application to the common carp. Ecological Applications, 21, 203–213.

Wiens, J. J., & Graham, C. H. (2005). Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Reviews of Ecology, Evolution, and Systematics, 36, 519–539.

Capítulo 1

História da introdução e estrutura genética da lagartixa de parede *Hemidactylus mabouia* (Squamata, Gekkonidae) no Brasil

Fênix Porto Pontes, Fernando Pacheco Rodrigues, Victor Hugo Silva Guimarães, Lilian Gimenes Giugliano.

Resumo

Devido à complexidade de alguns dos métodos empregados no manuscrito encontrando no Apêndice I, esse capítulo busca explicitar com mais detalhes as etapas e processos necessários para categorizar as navegações de navios negreiros, categorizar os portos baseados em regiões biogeográficas, e também detalhes das projeções e sobreposições de mapas e modelos. É percebida que por ser uma abordagem inovadora, o banco de dados se torna de difícil leitura, e sem um maior detalhamento replicar os processos pode se tornar um processo longo, inclusive com maior possibilidade de erros. É notória a necessidade de maior detalhamento do material e métodos empregados na pesquisa, sendo que tal questão será sanada no manuscrito a ser submetido ao final da pesquisa.

Palavras-chave: Metodologia; espécies invasoras; navios negreiros; modelagem de nicho ecológico.

Introduction

Hemidactylus mabouia (Gekkonidae), one of the species known as house gecko, is an excellent model of biological invasion that has been little explored. It originated in Africa and is strongly associated with the presence of human habitation throughout in its current wide distribution (Jesus, Brehm, Pinheiro, & Harris, 2001; C F D Rocha & Anjos, 2007; Short & Petren, 2011c; Townsend & Krysko, 2002; Wagner, Köhler, Schmitz, & Böhme, 2008). Despite this, in Brazil various studies have reported the presence of *H. mabouia* in conserved environments (Anjos & Rocha, 2008; Carlos Frederico D. Rocha & Bergallo, 2011; Telles, Militão, Bergallo, & Rocha, 2015) (Martins, Bruno, & Navegantes, 2012). In addition, several ecological effects associated to *Hemidactylus* invasion have been broadly described. For instance, the arrival of *H. frenatus* on the Mascarene Islands in the Indian Ocean decimated six species of Gekkonidae of the genus Natus (Cole, Jones, & Harris, 2005). It's also well described the competitive displacement of *H. frenatus* over native geckos at the Pacific islands (Petren, Bolger, & Case, 1993). In Florida it was observed that the recent arrival of *H. mabouia* led to a rapid decline of another congeneric and exotic species previously present (*H. garnotii*) in urban areas (Short & Petren, 2011c). Other types of damage caused by invasive *Hemidactylus* have also been reported, such as the association of their distribution with dengue fever incidence (Weterings, Barbetti, & Buckley, 2019) and, even, they there associated to electrical equipment damages in Cuba (Borroto-páez, 2021).

Niche modeling is a tool that can assist in identifying species distribution patterns based on their environmental niches. Often, this information is not only useful for estimating the potential distribution of a species but also provides data for conservation decision-making, such as the selection of protected areas and their more efficient delineation (Guisan and Thuiller 2005). Environmental niche modeling can also be employed in the study of ecological and evolutionary patterns (Gutiérrez et al. 2014), identification of conservation gaps (de Novaes e Silva et al. 2014), optimization of resources for conservation (Lessmann et al. 2014), among various other applications. Niche modeling is also used to predict the potential of an introduced species to become invasive and possibly alter natural systems (Peterson 2001, 2003; Peterson and Robins

2003; Pyron et al. 2008; Ulhanek and Eung 2011). These models operate on the assumption that a species, within a short period, at least in evolutionary terms, conservatively maintains its environmental niche, and that species' preferences and tolerances to climatic variables are good predictors of the species' spatial distribution (Wiens and Graham 2005). This approach proves effective when estimating the potential distribution of a species before its introduction as well (Peterson and Vieglais 2001; Jeschke and Strayer 2008). Such studies are crucial, especially when considering the case of *H. mabouia*, which likely has not reached the limit of its dispersion in the Americas due to its recent introduction (Carranza and Arnold 2006; Rödder et al. 2008).

Biogeography studies heavily rely on the availability of data on the distribution of the studied species; the absence of such data is a limiting factor for work in various fields of applied ecology (Beck et al. 2012). Databases like the Global Biodiversity Information Facility (GBIF 2018) seek to compile information on biodiversity distribution from institutions such as museums and biological collections. Despite potential biases due to the quality of some data, the use of such tools is invaluable for distribution studies (Beck et al. 2014) and provides more distribution points than independent literature compilations (Beck et al. 2013).

Expanding upon the methodology employed in Appendix I of this thesis, the primary objective of this chapter is to offer a more in-depth insight into the intricate process of integrating data pertaining to the trafficking of slave ships with the niche modeling of *H. mabouia*. This comprehensive exploration aims to elucidate the nuanced steps taken to establish meaningful connections between historical records of slave voyages and the ecological niche modeling techniques applied to understand the distribution patterns of *H. mabouia*. By delving into the intricacies of this linkage, the chapter seeks to provide a comprehensive understanding of how the historical context of slave trade can be intertwined with ecological modeling to derive valuable insights into the spatial dynamics of *H. mabouia*.

Material and Methods

Assuming that *H. mabouia* reached South America by transatlantic slave trade, in this work, we evaluated the pattern of vessel origin in each Brazilian port sampled for genetic data. We used environmental niche models to access which regions are potentially able to support the presence of *Hemidactylus mabouia* at Africa. In order to get this information, we obtained georeferenced data of the species in the Global Biodiversity Information Facility (GBIF). with presence in the African continent. To have reliable data, we used only those records that had latitude, longitude, location, country, and were deposited in biological collections with available voucher numbers. Within the records of *H. mabouia*, more than 20 different species can be found, all named as being part of the same species. Only one of these species has been able to become invasive in several regions of the world (Agarwal et al., 2021)

To generate the ecological niche model, we used the maximum entropy algorithm, Maxent 3.4.1 (S. Phillips, Dudík, & Schapire, 2018; S. J. Phillips & Dudík, 2008). This algorithm performed well when compared to other niche modeling methodologies (Elith et al., 2006; Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). To reduce sampling bias and spatial auto-correlation (Boria, Olson, Goodman, & Anderson, 2014), we used the spThin package (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015), from the R software (R Core Team, 2018), using a distance of 10 km and 100 repetitions. We used the repetition that kept the highest number of records.

To select the calibration area of the models, we used the whole continent of Africa. We started using 17 environmental layers, in a resolution of 5 arc second, related to the annual variations of temperature and precipitation obtained in the Worldclim (Fick & Hijmans, 2017). Then we selected only those layers that did not show high correlation with the others ($r > 0.8$), for this step we generated a matrix based on the Pearson correlation coefficient, using the records of the species for analysis. After this step, we kept the layers: Annual Mean Temperature, Mean Diurnal Range, Isothermality, Annual Precipitation, and Precipitation of Driest Month. To transform the logistic models in binary we used the threshold of Maximum training sensitivity plus specificity (Liu et al. 2013) To analyze the performance of the models, we used the boyce index. This index proves to be reliable for analyzing presence-only based predictions (Hirzel el at. 2006).

To represent the number of propagules, records from slave ships obtained from the Slavevoyages website (Slavevoyages Development Team 2018) were used. The criterion used in the search was the primary port of slave acquisition in Africa. When the record provided only a generic description, the first port of slave acquisition in Africa and the primary port of slave disembarkation in the Americas were used. To maintain accurate data records, the following information was kept: year of the voyage, voyage identification (ID), ship name, number of slaves embarked, and number of slaves disembarked.

To define the approximate locations of embarkation and disembarkation ports, current maps of the study regions were overlaid with maps provided by Slavevoyages. The locations were georeferenced using the QGIS 2.18.7 program (QGIS Development Team 2018). To identify regions and find the most suitable points to define locations that have changed names, points found with the assistance of Google Earth Pro 7.3.2 (Google LLC 2018) were used as references.

The flow of vessels was represented by lines generated by linestring geometry in the QGIS 2.18.7 program. The following categories were added to the records of slave ships: species present at the origin port, which could be *H. mabouia* or absent. both, using generated binary models; presence or absent of *H. mabouia* the disembarkation regions, also using binary projections; values of environmental suitability for all ports, obtained with the Raster package of the R program (Hijmans 2018). To extract suitability values, only logistic environmental models generated without the human footprint variable were used, as including it could bias the analysis due to a potential collection bias. To determine from which biogeographic regions the populations of *H. mabouia* potentially originated, we overlapped the binary model of potential distribution generated over the map of biogeographical regionalization and phenogram based on the combined matrix for the African continent (Linder et al. 2012).

To create a correlation between the disembark of vessels in brazilian ports with the genetic groups of *H. mabouia* found in those areas, we used the groups found in the master’s thesis “Biologia da invasão de *Hemidactylus mabouia* no Brasil : análise da estrutura genética populacional” by Pontes et al (2017)

Results

The projection of the model in Africa continent (Fig. 1), added to the ports identified with the use of slaveoyages database showed that almost whole sub-Saharan section of Africa is adequate to the presence of *H. mabouia.* When this result was overlapped with the Matrix proposed by Linden and highlighting this result in parallel with the geolines (Fig.3), it’s clear that two biogeographic regions played a major role as possible origins of *H. mabouia* in Brazil. Congolian and Zanbezian (Fig. 2). To this step we identified 24613 travels between continents.

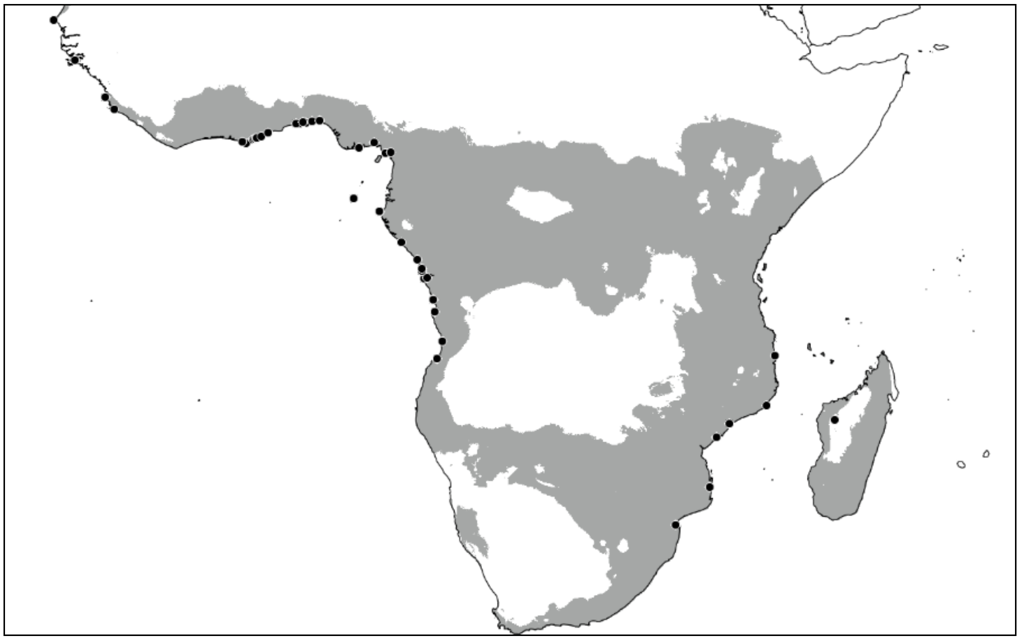

Figure 2 - Projection of the Hemidactylus mabouia *model on Africa, added to the ports where slave ships had their origin, coming to Brazil*

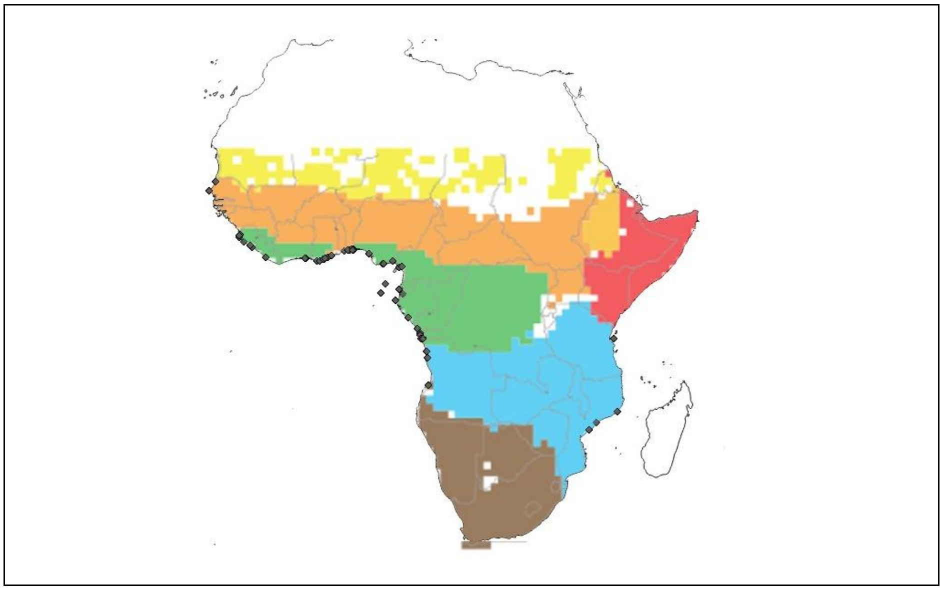

Figure 3- Biogeographic Regions (Linder et al. 2012) with the points of the ports categorized as adequate to Hemidactylus mabouia*. Yellow: Saharian; Orange: Sudanian; Green: Congolian; Blue: Zambezian; Red: Somalian; Brown: Southern*

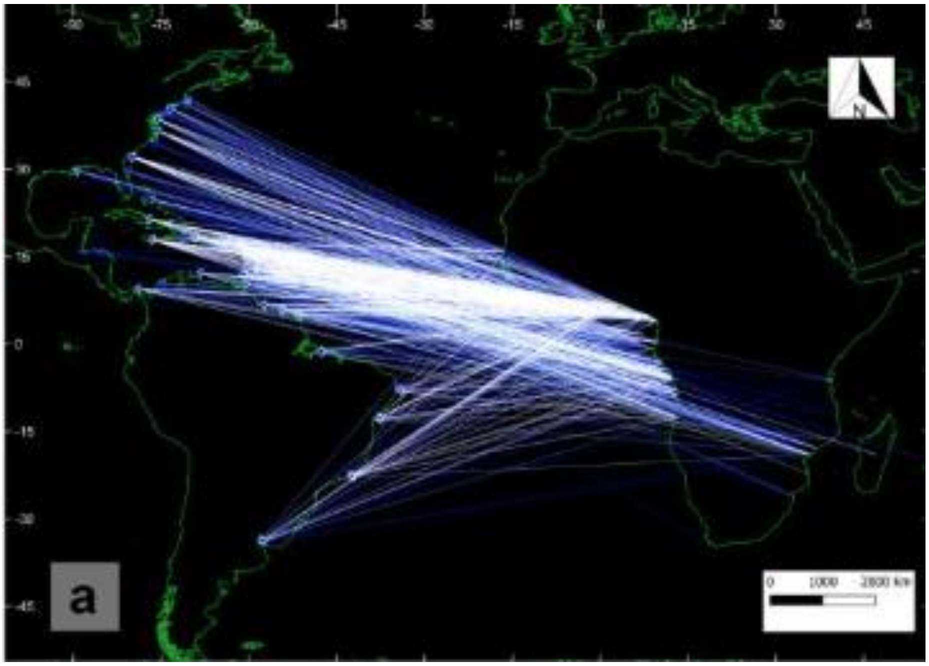

Figure 3- Geolines that shows the flow of slave ships from Africa to America. The areas with a white tones indicate a stronger flow of that route

Previous studies indicate that *H. mabouia* samples from Brazil showed great genetic similarity with the Africans samples, which strongly indicates the recent arrival of this species in the South American continent (Carranza & Arnold, 2006). Since during a long period of time (about three centuries of slave trade cruel system) a great number of vessels from several locations in Africa arrived in Brazil, so many authors consider that *H. mabouia* went accidentally on these ships (Albuquerque et al., 2013; Augusto et al., 2010; Iturriaga & Marrero, 2013; Mageski et al., 2017; C F D Rocha & Anjos, 2007; Vanzolini, 1968), but this hypothesis has never been directly evaluated.

Based on microsatellites data, indicated two genetically distinct clusters These clusters present a geographical distribution pattern in which the group represented in black is mainly in the north (northeast group) and the group represented in gray is predominantly in the southernmost regions (southeast group) When analyzing the results obtained for Rio de Janeiro, Recife and Salvador (former ports of entry for slave ships) we noticed that the first is composed exclusively of individuals assigned to the southeast cluster while the last two regions are composed almost exclusively of individuals assigned to the northeast group. As we obtained a clear genetic differentiation between northeast and southeast ports we decided to evaluate if there were any differences in the origin of the ships. In this way, we could observe (Fig. 4B) that the two northeast ports received practically only vessels from the Congolian biogeographical region (Linder et al., 2012). However, Rio de Janeiro received a large amount, of about one quarter of the vessels, from two other biogeographic regions (Fig. 4B): Southern African and Zambezian regions (Linder et al., 2012). This coincidence provides the first direct evidence in favor to the slave vessels as transportation of *H. mabouia* to Brazil, but, evidently other sources of data and evidences should be analyzed to get a more robust conclusion.

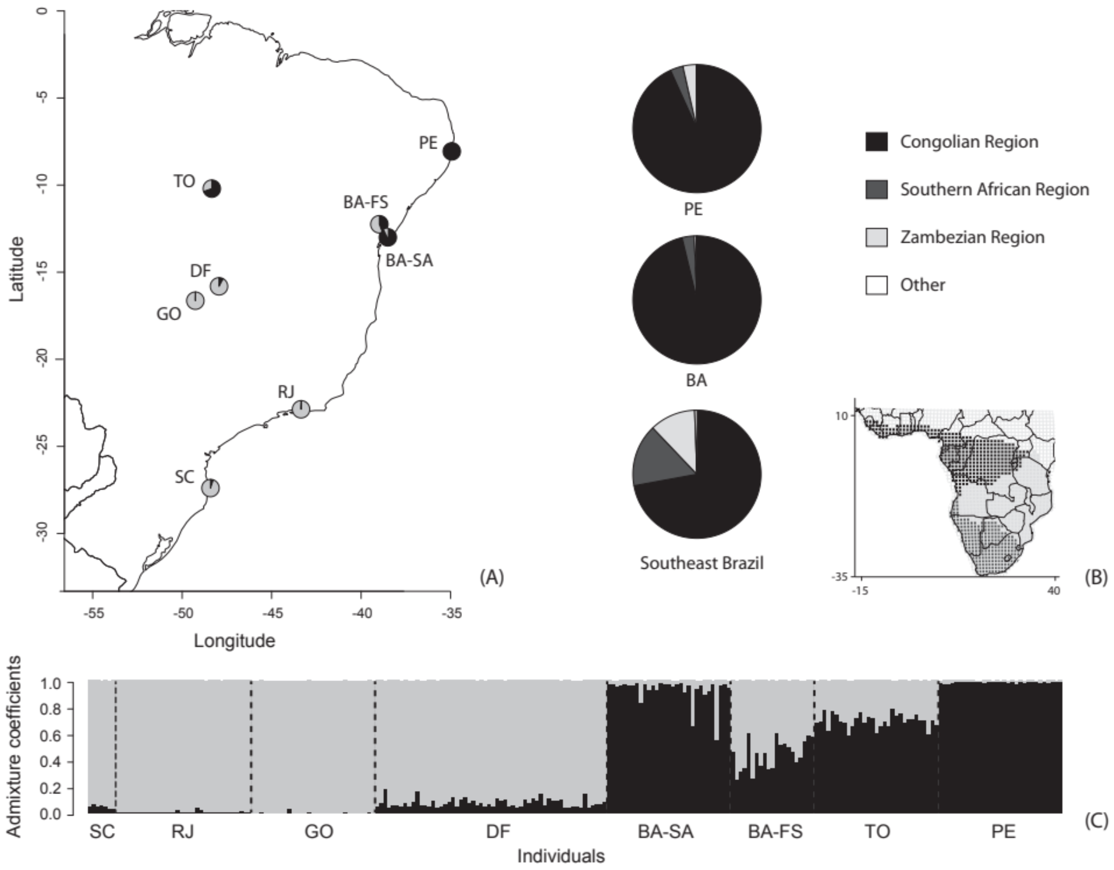

Figure 4. (A) Pie graphics illustrating the geographical distribution the proportion of individuals assigned to each genetic clusters inferred by Structure algorithm. (B) Pie graphics illustrating the proportion of vessels that originated in each biogeographic region in Africa that reached each of the three main arrival ports in Brazil. (C) The clusters obtained from the STRUCTURE 2.2 analyses of 244 individuals of the Hemidactylus mabouia *whereby each column represents an individual and the assignment probability to belong each genetic group.*

It is also interesting to highlight that all the regions sampled that did not receive slave ships (where *H. mabouia* supposedly arrived later from the entry ports) have a large proportion of individuals assigned southeast group (Fig. 4). Brazilian southeast estates that include São Paulo, Rio de Janeiro, Minas Gerais and Espirito Santo is also de most industrialized and urbanized region where most of the products that are distributed to the remaining states of the country originate (IBGE, 2020). This pattern corroborates the results found in Florida which indicates that human activities should be allowing more gene flow at regional scale probably due to cargo transport (Short & Petren, 2011b).

Discussion

In the context of methodological integration, it becomes evident that Ecological Niche Models (ENMs) offer versatility across diverse applications, thereby contributing a novel layer of understanding—an overarching theme within this chapter. This extended exposition serves to illuminate the intricacies of the methodology and unveil detailed results that would be impractical to present comprehensively in a more constrained manuscript focused on a different theme. The findings pertaining to genetic clusters are meticulously detailed in Appendix I, where a manuscript-style presentation is employed to delve into the intricacies of the research, simultaneously addressing additional dimensions of the study.

From the outcomes elucidated in Chapter 1, it becomes apparent that the evidence supports, or semantically, does not refute the original hypothesis positing the introduction of *H. mabouia* predominantly through the transportation of slave ships from Africa to America. Subsequent investigations, especially those delineating the genetic groups originating in Africa, have the potential to shed further light on our discoveries, consequently reinforcing the validity of the initial hypothesis.

References

Agarwal, I., Ceríaco, L. M. P., Metallinou, M., Jackman, T. R., & Bauer, A. M. (2021). How the African house gecko (*Hemidactylus mabouia*) conquered the world. Royal Society Open Science, 8(8). https://doi.org/10.1098/rsos.210749

Albuquerque, N. R. De, Soares, M. P., & Alves, L. S. (2013). Diet of two sit-and-wait lizards*, Phyllopezus pollicaris* (Spix, 1825) (Phyllodactylidae) and *Hemidactylus* *mabouia* (Moreau de Jonnès, 1818) (Gekkonidae) in a perianthropic area of Mato Grosso do Sul, western Brazil. Biota Neotropica, 13(4), 376–381.

Anjos, L. A. dos, & Rocha, C. F. D. (2008). A Lagartixa *Hemidactylus mabouia* Moreau de Jonnes, 1818 (Gekkonidae): uma espécie exótica e invasora amplamente estabelecida no Brasil. Natureza & Conservação, 6(1), 78–89.

Augusto, P., Sousa, G. De, Maria, E., & Freire, X. (2010). Communal nests of *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Squamata: Gekkonidae) in a remnant of Atlantic Forest in northeastern Brazil. Biotemas, 23(3), 231–234.

Carranza, S., & Arnold, E. N. (2006). Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution, 38(2), 531–545. https://doi.org/10.1016/j.ympev.2005.07.012

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302-4315.

Google LLC (2018) Google Earth Pro 7.3.2.5491

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling, 199(2), 142-152.

IBGE. (2020). Demografia das empresas e estatísticas de empreendedorismo: 2018.

Iturriaga, M., & Marrero, R. (2013). Feeding ecology of the Tropical House Gecko *Hemidactylus mabouia* (Sauria : Gekkonidae) during the dry season in Havana, Cuba. 6(January), 11–17.

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography, 40(4), 778-789.

Linder, H. P., de Klerk, H. M., Born, J., Burgess, N. D., Fjeldså, J., & Rahbek, C. (2012). The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. Journal of Biogeography, 39(7), 1189–1205. https://doi.org/10.1111/j.1365-2699.2012.02728.x

Mageski, M., Jesus, P. R., & Ferreira, P. D. (2017). Continued dispersal of the Wood Slave Gecko, *Hemidactylus mabouia*, in natural environments of Brazil. North-Western Journal of Zoology, 13(2), 363–364.

Phillips SJ, Dudík M (2008) Modeling of species distribution with Maxent: new extensions and a comprehensive evalutation. Ecography 31:161–175

Phillips SJ, Dudík M, Schapire RE (2018) Maxent software for modeling species niches and distributions (Version 3.4.1)

PONTES, Fênix Porto. Biologia da invasão de *Hemidactylus mabouia* no Brasil: análise da estrutura genética populacional. 2017. iv, 51 f., il. Dissertação (Mestrado em Zoologia)—Universidade de Brasília, Brasília, 2017.

Hijmans RJ (2018) raster: Geographic Data Analysis and Modeling. R package version 2.8-4

Short, K. H., & Petren, K. (2008). Isolation and characterization of 12 polymorphic microsatellite markers in the tropical house gecko (*Hemidactylus mabouia*). Molecular Ecology Resources, 8(6), 1319–1321. https://doi.org/10.1111/j.1755-0998.2008.02270.x

Capítulo 2

Potential impacts of invasive Pythons in Brazil

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Abstract

The global pet trade's demand has led to the introduction of large constrictor snakes into new environments, either intentionally or accidentally. Brazil boasts the third-highest reptile species diversity globally, with snakes representing the predominant reptilian group, including 12 constrictor species. The potential for competition and predation between invasive and native snakes underscores the need for a comprehensive assessment of risks faced by endemic herpetofauna. This study aims to identify potential areas for invasive python establishment and assess their impact on native constrictors in Brazil. Environmental Niche Models were employed to predict suitable habitats for both invasive pythons and four endemic Brazilian snake species. By overlapping *Python spp*. records with those of endemic serpents, the study sought to understand resource availability for potential invasive species and the vulnerability of native species to python invasion. The results highlight *Python sebae* and *Python bivittatus* as potential invasive species posing a threat to native constrictors. Conversely, *Eunectes murinus*, with its semi-aquatic behavior, exhibited lower vulnerability. Endemic serpents, including *Boa constrictor*, *Corallus hortulanus*, and *Epicrates cenchria*, were identified as highly susceptible to potential competition from invasive pythons. These findings emphasize the importance of understanding the potential ecological impacts of the introduction of invasive species on native ecosystems.

Keywords: Constrictors; competition; snakes; ecological niche models; invasive species

Potenciais impactos de Pythons invasoras no Brasil

Victor Hugo S. Guimarães, Ricardo B. Machado, Lilian G. Giugliano

Resumo

A demanda global pelo comércio de animais de estimação levou à introdução de grandes serpentes constritoras em novos ambientes, seja intencionalmente ou acidentalmente. O Brasil apresenta a terceira maior diversidade de espécies de répteis globalmente, com as serpentes representando sendo o grupo predominante, dentre essas inclusas 12 espécies constritoras. O potencial para competição e predação entre serpentes invasoras e nativas destaca a necessidade de uma avaliação abrangente dos riscos enfrentados pela herpetofauna endêmica. O presente estudo teve como objetivo identificar áreas potenciais para o estabelecimento de pítons invasoras e avaliar seu impacto em constritoras nativas no Brasil. Modelos de Nicho Ambiental foram utilizados para prever habitats adequados tanto para pítons invasoras quanto para quatro espécies endêmicas de serpentes brasileiras. Ao sobrepor registros de *Python spp*. com aqueles de serpentes endêmicas, o estudo buscou entender a disponibilidade de recursos para espécies invasoras potenciais e a vulnerabilidade de espécies nativas à invasão por pítons. Os resultados destacam *Python sebae* e *Python bivittatus* como espécies invasoras potenciais que representam uma ameaça para as constritoras nativas. Por outro lado, *Eunectes murinus*, com seu comportamento semi-aquático, apresentou menor vulnerabilidade. Serpentes endêmicas, incluindo *Boa constrictor*, *Corallus hortulanus* e *Epicrates cenchria*, foram identificadas como altamente suscetíveis à competição potencial com pítons invasoras. Essas descobertas enfatizam a importância de compreender os impactos ecológicos potenciais da introdução de espécies invasoras nos ecossistemas nativos.

Palavras-chave: Constritoras; competição; serpentes; modelagem de nicho ecológico; espécies invasoras

Introduction

Biological invasions are considered one of the greatest threats to global biodiversity, ranking as the third most important threat to reptiles species in the world (IUCN 2023). When introduced into new ecosystems, non-native or alien species can disrupt ecological processes, displace native species, and alter ecosystem structures and functions (Simberloff et al., 2013). The invasion of non-native species poses a significant challenge for preserving ecosystems and biodiversity. Among these invaders, pythons (*Python spp.*) have gained considerable attention owing to their potential to disrupt local wildlife communities (Reed et al., 2012).

The incursion of exotic and invasive animal species has resulted in significant economic losses across diverse sectors, compelling attention to its far-reaching implications. Exotic animals, such as the zebra mussel (*Dreissena polymorpha*), cause immense financial strain by clogging water intake structures and fouling industrial equipment, leading to direct costs amounting to billions of dollars (Leung et al., 2002). Additionally, invasive animals such as the brown tree snakes (*Boiga irregularis*) have wreaked havoc on island ecosystems, jeopardizing native bird populations and causing agricultural losses by preying on domestic poultry (Savidge, 1987). These economic burdens underscore the importance of proactive management strategies to mitigate the detrimental impacts of exotic and invasive animal species and safeguard economic stability and ecological integrity.

The impact of the pet trade on the successful establishment and spread of invasive pythons has been a significant contributing factor. The global demand for exotic pets, including large constrictor snakes, has led to their intentional introduction or accidental escape into new environments (Dorcas et al., 2012). The pet trade provides a pathway for the introduction of invasive pythons, allowing them to establish populations in regions where they would not naturally occur. For example, the Burmese python (*Python bivittatus*), one of the most widespread invasive python species, has been linked to the pet trade as a primary source of introductions (Dorcas et al., 2012). Similarly, the African rock python (*Python sebae*) has been introduced and established in various locations due to the exotic pet trade (Reed et al., 2019). These introductions highlight the role of the pet trade in facilitating the expansion of invasive python populations, leading to ecological disruptions and threats to native wildlife.

The proliferation of invasive python species has emerged as a pressing ecological concern across the globe. One notable example is the Burmese python (*Python bivittatus*), which has established itself as a formidable predator in the Florida Everglades, United States. The introduction of this non-native constrictor has led to significant disruptions in the local ecosystem, resulting in a decline in mammalian populations and alteration of natural food web dynamics (Dorcas et al., 2012). These invasions are characterized by their ability to outcompete native species, leading to cascading effects on biodiversity and ecosystem stability (Willson, 2017). Urgent conservation measures are needed to manage and mitigate the spread of invasive pythons, underscoring the importance of understanding their ecological impacts and implementing effective control strategies to curb their detrimental influence on delicate ecosystems worldwide.

Brazil is ranked as the third richest country in reptile species and, unlike the global pattern it has most species of snakes than other reptiles (Costa et al. 2021). Among the snakes, 12 constrictor species compose the Brazilian diversity. These snakes play vital roles as apex predators and regulate prey populations within their habitats (Cabral et al., 2019). Some of these species have adapted to specific habitats and have evolved in isolation, making them particularly vulnerable to the introduction of invasive species (Stewart-Koster et al., 2015). The potential for interspecific competition and predation between invasive and native snakes necessitates an in-depth assessment of the risks faced by endemic herpetofauna (Piquet, & López-Darias, 2021). Understanding these threats is vital for implementing conservation measures to protect Brazil's unique constrictor snake fauna.

Understanding the potential impact of invasive pythons on Brazilian territory, with a focus on the threat to endemic constrictor snakes, it is crucial for implementing effective management strategies to conserve the unique biodiversity of the country. By studying the ecological interactions between invasive pythons and endemic constrictor snakes, we can identify potential threats, such as the extinction of small and medium-sized mammals, which can affect the entire trophic chain of an environment (Pitt et al, 2018), and devise appropriate measures to mitigate their negative impacts. This research contributes to the broader field of biological invasions and emphasizes the importance of preserving the delicate balance of ecosystems in the face of increasing invasive species introductions.

The primary aim of this study is to identify areas of potential establishment of invasive pythons and to assess the potential impacts on native constrictor species in Brazil. We expected that large native species, especially those form *Eunectes* genus, would be particularly impacted by the introduction of python species due to their ecological and niche requirements similarities. Beyond the conventional ecological niche models that rely on abiotic variables, this research endeavors to offer a fresh perspective. Furthermore, it has the potential to shed light on the intricate dynamics of competition between python snakes and the indigenous constrictor species under examination. It is important to emphasize that the present study aims to anticipate data on a possible invasion, as populations of pythons have not yet been found in natural environments. However, the snake is commonly seized as a pet by operations of the main Brazilian environmental agency, IBAMA. (IBAMA, 2018, 2019, 2020a, 2020b)

Materials and Methods

To determine regions with potential to support the presence of invasive Pythons, we employed Environmental Niche Models. The species chosen to represent this group were *P. sebae*, *P. molurus*, *P. regius*, and *P. bivittatus*. Georeferenced data for these species were obtained from the Global Biodiversity Information Facility (GBIF), which included *Python spp*. presence records in Africa and Asia. To ensure reliable data, we selected records that contained latitude, longitude, location, country, and were deposited in biological collections with available voucher numbers (GBIF, n.d.). The main factor guiding the selection of these four species was data availability, as they share similar dietary characteristics and constrictor behavior.

We projected the ENMs of pythons within Brazil to predict suitable areas where these serpents could potentially establish themselves. Additionally, we generated another set of models using four endemic Brazilian serpents from different genera, namely *Boa constrictor*, *Eunectes murinus*, *Epicrates cenchria*, and *Corallus hortulanus*. This selection aimed to cover a larger area of Brazilian territory, encompassing phylogenetic diversity and considering data availability.

For climate data, we utilized 19 layers of temperature and precipitation from Worldclim (Hijmans et al., 2005). To mitigate potential collinearity among the climate layers, we performed Pearson correlation analysis using the locations of the species for calibration. The climate data were divided into two groups: temperature (bio1 to bio11) and precipitation (bio12 to bio19). Layers exhibiting a correlation equal to or greater than 0.7 were removed to address collinearity concerns (Dormann et al., 2013)

To generate the ecological niche models, we employed the maximum entropy algorithm, Maxent 3.4.1 (Phillips and Dudík 2008; Phillips et al., 2018). This algorithm has shown favorable performance compared with other niche modeling methodologies (Ferrier et al., 2006; Hernandez et al., 2006; Wisz et al., 2008). To reduce sampling bias and spatial autocorrelation (Boria et al., 2014), we utilized the spThin package (Aiello-Lammens et al., 2015) in the R software (R Core Team, 2018), with 50 km and 100 repetitions. We selected the repetition with the highest number of records. The calibration area of the models was determined by constructing a minimum convex polygon using a 0.5° decimal degree buffer. We used 17 environmental layers, with a resolution of 5 arcseconds, representing annual variations in temperature and precipitation obtained from WorldClim (Fick and Hijmans, 2017).

To transform the logistic models into binary models indicating the presence or absence of species, we employed the maximum similarity specificity threshold (MaxSS). Values close to 0 indicate lower environmental suitability, while values close to 1 indicate higher suitability (Liu, White & Newell, 2013). Furthermore, we subtracted the multivariate environmental similarity surfaces (MESS) values from the model area to identify areas where model projections were not possible due to differences between the values of the layers used in model training and projection.

To evaluate model suitability, we employed the Boyce index, which ranges from -1 to 1. Positive values indicate accurate predictions of points from the testing database, values close to 0 suggest the model is not significantly different from a randomly generated model, and negative values indicate mispredictions where the model indicates presence, but no test points are observed (Hirzel et al., 2006).

After generating the models, we overlapped the *Python spp*. records with those of the endemic serpents for two reasons: first, as a biological indicator of resource availability, such as food and nesting sites, for potential invasive species; and second, to predict which endemic species would be more vulnerable if pythons were to become invasive, considering their similar behaviors and close phylogenetic relationships until recently. By overlapping all possible combinations of species and determining the number of overlapping pixels with the model, we gained insights into the most sensitive species and areas that are most at risk. A map containing all four endemic snake genera was also generated to elucidate the potential suitability of the Brazilian territory for the established invasive *Python spp*.. Each pixel of the utilized resolution corresponds to approximately 85 km², providing an estimated value for the threatened areas. All spatial projections, map creation, and GIS manipulations were performed using QGIS 2.18.7 software (QGIS Development Team, 2018).

Results

All Boyce index values were above 0.8, indicating that the generated models were satisfactory for subsequent stages. Among the endemic species, *Eunectes murinus* had the smallest environmental suitability area among the generated models, with only 5921 pixels. This value is much lower than, for example, *Epicrates cenchria*, which had a total of 37087 pixels within the territory. This type of result is expected because of the specificities of *Eunectes* sp., a large semi-aquatic snake.

Among the studied *Python* species, *P. molurus* had the smallest projected niche, with a total of 4786 pixels (Table 1), while *P. sebae* had a total of 43255 pixels, surpassing the values of all endemic species. This represents approximately 3.6 million km^2, a significant value considering the 8.5 million km^2 of the Brazilian territory.

Table 1 - Suitability Assessment of Generated Models: *MaxSS Values, Binary Model Metrics, and Geographic Coverage. MaxSS column represents the Maximum Training Sensitivity Plus Specificity (MaxSS) values, which were instrumental in crafting the binary models. Columns 'Area (pixels) and 'Area (km^2)' correspond to the area covered by each individual model.*

Boyce index	MaxSS	Area (pixels)	Area (km²)
0.836	0.441	27907	2372095
0.877	0.465	24161	2053685
0.848	0.415	37087	3152395
0.867	0.508	5921	503285
0.871	0.111	33583	2854555
0.921	0.093	16628	1413380
0.875	0.328	43255	3676675
0.938	0.177	4786	406810

We systematically constructed a set of 29 distinct Ecological Niche Models (ENMs) and subsequently projected these models onto a comprehensive map of Brazil (see Figure 1). Among these, four models were derived from *Python* serpent species, while an additional four emanated from endemic constrictor snakes. Within the category of endemic snakes, a consolidated model labeled as 'Brazil' was developed. This model serves to delineate geographic areas where the presence of at least one endemic snake species under study is anticipated. This proactive approach aims to establish the extent of regions in which potentially invasive snake species could encounter suitable ecological conditions, encompassing factors such as food availability and suitable shelters. This rationale stems from the parallel behaviors exhibited by various snake constrictor species, highlighting their comparable ecological preferences.

The remaining 20 models represented the spatial overlap between a *Python* species ENM from the initial column and all ENMs of endemic serpents from the initial row. This intersecting framework elucidates the specific species that may face heightened vulnerability due to competitive interactions. Moreover, it offers insights into *Python* serpent species that possess the greatest potential to engage in competitive interactions, posing a substantial threat to the native endemic constrictor snakes inhabiting Brazil. This comprehensive methodology not only sheds light on the potential impacts of invasive species on the native ecosystem but also aids in prioritizing conservation efforts to mitigate potential threats posed by the invasion of non-native snake species.

When overlapping the invasive niches, our results showed that among the studied Pythons, *P. sebae* is the one that demonstrated the greatest potential to become an invader and compete for niche with endemic species, with its projected niche occupying over 52% of *Epicrates* sp.'s niche, 43% of *Boa* sp.'s niche, and 55% of *Corallus* sp.'s niche. From Table 2, we can infer that among the studied species, *P. bivittatus* had the lowest potential to become a competitor, presenting low niche overlap values for all four endemic species. All the models projected on maps are shown in Figure 1, as well as the overlaps of endemic species with potentially invasive species.

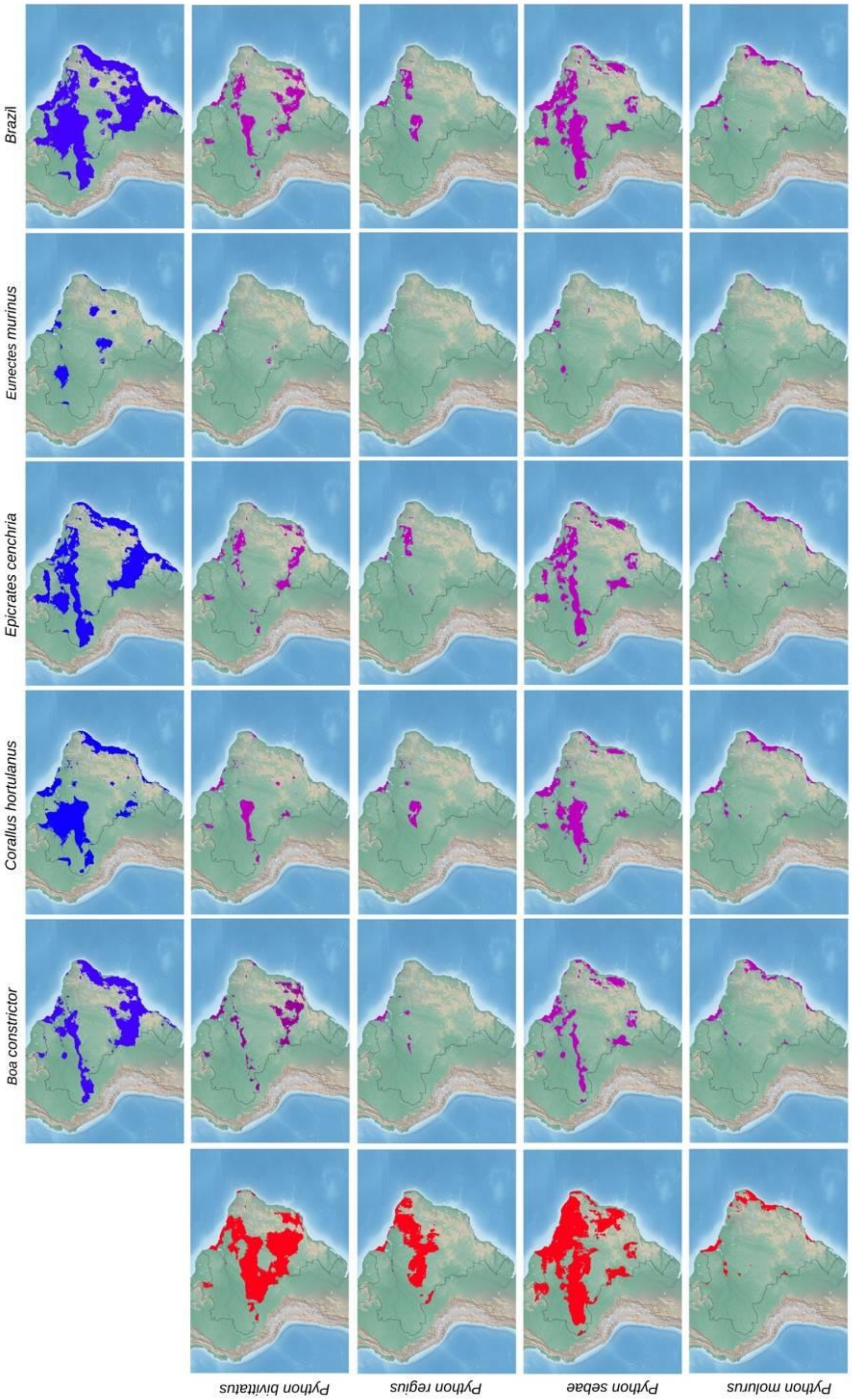

Figure 1 Overlapping Habitat Maps: Invasive Python Species and Brazilian Endemic Constrictor Snakes *- Matrix of potential distribution maps of the studied species. The first column is composed of potentially invasive species of the Python genus, the first row is composed of endemic constrictor snake species from Brazil, and the remaining maps show the overlap of columns with rows. The map named Brazil represents the sum of the four models of endemic species, indicating that at least one of the snakes could be found according to the generated models.*

Table 2 - Overlapping Area Size and Percentage Relative to Total Range: Impact on Endemic Species Distribution *- This table provides insights into the extent of overlapping areas between the studied species and the percentage these areas constitute in relation to the overall spatial distribution of the observed endemic species in the study. The aggregation of the four models was employed to define the "Brazil" column, effectively depicting locations where a minimum of one species could potentially be located.*

Area (km²)	*Boa constrictor*	*Corallus hortulanus*	*Epicrates cenchria*	*Eunectes murinus*	Brazil
P. bivittatus	804610	444975	683740	64430	1261740
P. regius	98855	242420	210120	27030	402390
P. sebae	1023060	1147245	1647130	105485	2166225
P. molurus	273955	319175	234940	49470	339830
Overlapped area (%)					
P. bivittatus	33.91980507	21.66714954	21.68954081	12.80189157	
P. regius	4.167413194	11.80414718	6.665408364	5.370714406	
P. sebae	43.12896406	55.86275403	52.2501146	20.95929742	
P. molurus	11.54907371	15.54157527	7.452746245	9.829420706	

Another species that we identified as potentially competitive in the case of establishment within a territory was *P. bivittatus*. In three out of the four species, the overlap value was above 20%, reaching approximately 34% when overlapped with *Boa constrictor*.

When examining the potential invasion scope of python serpents, it was imperative to gauge the expansiveness of these territories in the context of encompassing the ecological niches of all four native genera (Table 2). Specifically, *P. bivittatus* and *P. sebae* exhibited considerable ranges, spanning 1,261,740 km² and 2,166,225 km², respectively. Except for *Eunectes murinus*, the remaining endemic serpent species faced the prospect of intense competition from *P. bivittatus* and *P. sebae*, with instances of overlapping models exceeding 50 percent. Furthermore, although *P. molurus* and *P. regius* exhibited comparatively lower values in terms of overlap and total area, a significant portion of their suitable habitat was concentrated.

Addressing Table 2 further, *Eunectes murinus* exhibited minimal convergence in its range with that of *Python* species. It is pertinent to acknowledge the inherent limitations associated with the generated models, as skewed data could potentially lead to a reduction in the overall estimated range of species. Despite these constraints, *E. murinus* was the least vulnerable among the examined serpents. Visualization of these models on geographical maps emphasizes the diminutive and dispersed nature of vulnerable regions.

Discussion

Given these results, it can be inferred that incorporating additional approaches along with ENMs can provide enhanced support for the study of invasive species. The primary focus of this approach is to delineate zones where competition with invasive species might transpire. However, employing biotic data can offer a fresh perspective on how a potential invader might behave in an invading environment. As indicated by these findings, *P. bivittatus* and *P. sebae* have demonstrated the greatest potential for becoming invaders, both in terms of the available area within Brazilian territory and in their overlap with other species. *P. bivittatus*, often traded as a pet, introduces an added concern regarding potential invasion. The perpetual inadvertent introduction of a species, even if accidental, increases the risk due to propagule pressure (Lockwood et al., 2007). The manifestation of both biotic and abiotic suitability within the areas for these two species underscores the necessity for vigilant monitoring of these species. Conversely, adopting a contrary viewpoint and examining the extent of overlapping percentages provided a comprehensive understanding of the indigenous species that might be imperiled should such an invasion materialize.

Among the native snakes, only *E. murinus* presented a minimal risk of competition from an invasive snake among evaluate, one of the hypothesis that can be studies is that the semi-aquatic behaviors exhibited by this snake contributed to a lesser degree of overlap with the pythons studied. The other three genera exhibited a substantial overlap between their niche areas and those of the invasive serpents, further intensifying invasion concerns. While the coexistence of Pythons and Boas was observed, as evident from their invasions in Florida, it is important to note that in environments where they both occur, they are exotic species (Hanslowe, 2018). The impact of introducing a new serpent into a region where one is endemic remains unpredictable in terms of its effects on native constrictor populations.

It is crucial to emphasize that the models might lead to underestimated areas due to insufficient data collection in regions of limited scientific exploration or non-submission of collection data by certain organizations or countries (Phillips, 2008). These factors could potentially result in larger areas of invasion and competition. In the case of *E. murinus*, a re-evaluation of its niche size using models with increased training data is advisable. Additionally, the inclusion of a semi-aquatic constrictor, such as *Python reticulatus*, could yield more insights and competition possibilities, warranting future investigations.

The instances involving *P. molurus* and *P. regius* may wrongly imply that these species pose no threat. However, it is crucial to emphasize that the majority of the projected ENMs were clustered in the same localized regions, often within contiguous areas. This concentration of suitable areas suggests the possibility of localized invasion points, indicating that despite their comparatively limited overall suitable habitat, the propensity for species establishment could be significantly bolstered by the existence of such concentrated, favorable zones.

This study seeks to propose supplementary approaches for detecting invasive species risks and, through such approaches, strives to attain a more nuanced understanding of potential occurrences. Moreover, within the obtained results, it is paramount to emphasize that two of the studied species exhibited substantial invasive potential, prompting contemplation of the implications of such work on a larger scale.

Further studies with expanded datasets and incorporation of novel methodologies to assess the invasive potential of the highlighted species are essential. New avenues could involve the incorporation of additional abiotic layers, such as land use data or ENMs of species more susceptible to becoming recurring prey for these animals. In this context, emphasis is primarily on the potential for invasion rather than competition with native species.

Moreover, there is the prospect of conducting these analyses on a broader scale, providing decision-makers with comprehensive insights into the issue. Such an approach could pinpoint high-risk invasion zones and highlight species that require heightened monitoring. The application of such large-scale assessments could significantly aid in the formulation of effective management strategies and resource allocation.

To enhance the predictive power of these models, holistic integration of biotic and abiotic factors is imperative. By incorporating aspects such as interspecific interactions, prey availability, and habitat characteristics, a more nuanced understanding of invasive species dynamics can emerge. Additionally, experimental validation through field studies would validate the model's predictions, enhancing their practical utility in real-world scenarios.

In conclusion, although this study presents valuable insights into the invasive potential of certain species, its scope prompts the need for further research and the application of innovative methodologies. Robust data integration coupled with comprehensive analysis is vital for a well-rounded comprehension of invasion risks and effective conservation strategies.

References

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38(5), 541-545. https://doi.org/10.1111/ecog.01927

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling, 275, 73-77.

Cabral, S. de O., Freitas, I. da S., Morlanes, V., Katzenberger, M., & Calabuig, C. (2019). Potential seed dispersers: a new facet of the ecological role of *Boa constrictor constrictor* Linnaeus 1758. Biota Neotropica, 19(4). https://doi.org/10.1590/1676-0611-bn-2018-0626

Costa, H.C., Guedes, T.B., Bérnils, R.S. (2021). Lista de répteis do Brasil. Herpetologia Brasileira, 10(3): 1-171. Available at https://sbherpetologia.org.br/sociedade-brasileira-de-herpetologia.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., ... & Mazzotti, F. J. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. Proceedings of the National Academy of Sciences, 109(7), 2418-2422.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2006). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions, 12(2), 125-137.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302-4315.

GBIF (Global Biodiversity Information Facility). (n.d.). Retrieved from http://www.gbif.org/

Hanslowe, E. B., Duquesnel, J. G., Snow, R. W., Falk, B. G., Adams, A. A. Y., Metzger, E. F. III, Collier, M. A. M., & Reed, R. N. (2018). Exotic predators may threaten another island ecosystem: A comprehensive assessment of python and boa reports from the Florida Keys. Management of Biological Invasions, 9(3), 369–377. https://doi.org/10.3391/mbi.2018.9.3.18

Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography, 29(5), 773-785.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling, 199(2), 142-152.

IBAMA (2018). IBAMA identifica 1277 animais à venda em redes sociais e realiza operação em 15 estados. Biological Invasions. Retrieved from https://www.gov.br/ibama/pt-br/assuntos/noticias/copy_of_noticias/noticias-2018/ibama-identifica-1277-animais-a-venda-em-redes-sociais-e-realiza-operacao-em-15-estados. Accessed on 26th September 2023.

IBAMA (2019). IBAMA e PM Ambiental apreendem 193 animais silvestres em SP. Biological Invasions. Retrieved from https://www.gov.br/ibama/pt-br/assuntos/noticias/copy_of_noticias/noticias-2019/ibama-e-pm-ambiental-apreendem-193-animais-silvestres-em-sp. Accessed on 26th September 2023.

IBAMA (2020a). Em sete dias, 32 serpentes são resgatadas pelo IBAMA no DF. Biological Invasions. Retrieved from https://www.gov.br/ibama/pt-br/assuntos/noticias/2020/em-sete-dias-32-serpentes-sao-resgatadas-pelo-ibama-no-df. Accessed on 26th September 2023.

IBAMA (2020b). IBAMA e PF apreendem 22 animais silvestres em Aracaju, SE. Biological Invasions. Retrieved from https://www.gov.br/ibama/pt-br/assuntos/noticias/2020/ibama-e-pf-apreendem-22-animais-silvestres-em-aracaju-se. Accessed on 26th September 2023.

IUCN. 2023. The IUCN Red List of Threatened Species. Version 2022-2. Available at https://www.iucnredlist.org. Accessed in 22nd September, 2023.

Leung, B., Lodge, D. M., Finnoff, D., Shogren, J. F., Lewis, M. A., & Lamberti, G. (2002). An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1508), 2407-2413.

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography, 40(4), 778-789.

Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2007). Invasion Ecology. John Wiley & Sons.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31(2), 161-175.

Phillips, S.J. (2008), Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography, 31: 272-278. https://doi.org/10.1111/j.0906-7590.2008.5378.x

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2018). Opening the black box: an open-source release of Maxent. Ecography, 40(7), 887-893.

Piquet, J.C., & López-Darias, M. (2021). Invasive snake causes massive reduction of all endemic herpetofauna on Gran Canaria. Proceedings of the Royal Society B: Biological Sciences, 288(1964). https://doi.org/10.1098/rspb.2021.1939

Pitt, W. C., Beasley, J., & Witmer, G. W. (Eds.). (2018). Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States (pp. 140-143). CRC Press.

QGIS Development Team. (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Reed RN, Willson JD, Rodda GH, Dorcas ME. Ecological correlates of invasion impact for Burmese pythons in Florida. Integr Zool. 2012 Sep;7(3):254-270. https://doi.org/10.1111/j.1749-4877.2012.00304.x. PMID: 22938523.

Savidge, J. A. (1987). The ecological and economic impacts of an introduced snake on Guam and its threat to other Pacific islands. Ples, 3, 29–34.

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M. (2013). Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol, 28(1), 58-66. https://doi.org/10.1016/j.tree.2012.07.013.

Stewart-Koster, B., Olden, J. D., & Johnson, P. T. J. (2015). Integrating landscape connectivity and habitat suitability to guide offensive and defensive invasive species management. Journal of Applied Ecology, 52(2), 366–378. https://doi.org/10.1111/1365-2664.12395

Considerações Finais

A presente tese teve como intuito utilizar os Modelos de Nicho Ecológico (ENM) dentro do contexto da biologia da invasão, área que busco ter como enfoque durante minha carreira acadêmica, futuramente não me atendo apenas ao grupo Squamata.

Dentre os resultados encontrados, no capítulo 1, foi obtido um resultado relevante, principalmente na história da invasão de uma espécie de lagarto, mostrando que no contexto da biologia da invasão ainda existem vários campos e hipóteses a serem exploradas, mesmo aquelas que de já vem se consolidando por décadas. É importante ressaltar a necessidade do esforço científico de incorporar diversos, e muitas vezes divergentes conhecimentos. Tornar os estudos multidisciplinares e integrados creio que seja um diferencial no trabalho desenvolvido.

No segundo capítulo foi possível trabalhar com o foco em prevenção de eventos futuros, dentro da biologia da invasão, mas também dentro da conservação de áreas e paisagens. As limitações das ferramentas empregadas mostram ser um desafio, principalmente no que diz respeito a escassez de alguns dados. No entanto, em um contexto global, creio que a criação de modelos de todas as espécies, de forma a que possamos mapear, calcular, sobrepor e analisar espécies sobre diferentes aspectos, dentro e fora da biologia da invasão, se tornará um elemento essencial para a conservação da biodiversidade a nível global.

Muito ainda há de ser feito e discutido dentro dos contextos abordados nesta tese, no entanto há valor no trabalho realizado até aqui, e que este trabalho possa continuar a ser desenvolvido por mim, outros pesquisadores e futuros pós graduandos que busquem atuar nessa área.

APÊNDICE I

Chapter 1

Introduction history and genetic structure of the house gecko *Hemidactylus mabouia* (Squamata, Gekkonidae) in Brazil

Fênix Porto Pontes, Fernando Pacheco Rodrigues, Victor Hugo Silva Guimarães, Lilian Gimenes Giugliano.

Abstract

This study investigates the genetic structure of *Hemidactylus mabouia* in Brazil, exploring its colonization dynamics with a focus on potential connections to the transatlantic slave trade. Leveraging 12 microsatellite loci, we analyzed 244 individuals through interregional and intraregional assessments. Significant regional variations in allele richness and inbreeding coefficients emerged, supporting genetic differentiation. Our findings revealed two distinct genetic clusters associated with geographic locations, pointing to a possible correlation between genetic patterns and historical slave trade routes. This suggests a historical link between genetic structure and slave trade origins. In conclusion, our research provides comprehensive insights into the genetic structure of *H. mabouia*, offering valuable perspectives on how historical events, particularly the transatlantic slave trade, may have influenced its colonization dynamics in Brazil.

Keywords: Invasive species, geckos, human introduction, slave ships

Introduction

Despite the global number of scientific publications about invasive species has grown exponentially since the 90s, few of those studies have been conducted in Brazil (Lowry et al., 2012). The growing interest in the area is associated to their great economic (Oliveira, Auad, Mendes, & Frizzas, 2013; Pimentel, Zuniga, & Morrison, 2005)(Roy et al., 2014) and ecological impacts (Fagúndez, 2013; Hoffmann et al., 2010; Sala et al., 2000; Tylianakis, Didham, Bascompte, & Wardle, 2008; Wardle, Bardgett, Callaway, & Van Der Putten, 2011). Invasion events also provide an excellent opportunity and even a natural experiment to address issues on ecology and evolution (Sax et al., 2007). In this way, population genetic structure studies and analyses based on molecular data are powerful tools for understanding the processes of establishment and expansion in a new environment (Lee, 2002), measuring the loss of genetic variability (Meimberg et al., 2005; Tsutsui, Suarez, Holway, & Case, 2000), estimating the number of introduction events (Betancur-R. et al., 2011; Cameron, Bayne, & Coltman, 2008), detecting hybridization events (Johannesen, Keyghobadi, Schuler, Stauffer, & Vogt, 2013) and testing expansion models (Ramakrishnan, Musial, & Cruzan, 2010).

Hemidactylus mabouia (Gekkonidae), one of the species known as house gecko, is an excellent model of biological invasion that has been little explored. It originated in Africa and is strongly associated with the presence of human habitation throughout in its current wide distribution (Jesus, Brehm, Pinheiro, & Harris, 2001; C F D Rocha & Anjos, 2007; Short & Petren, 2011c; Townsend & Krysko, 2002; Wagner, Köhler, Schmitz, & Böhme, 2008). Despite this, in Brazil various studies have reported the presence of *H. mabouia* in conserved environments (Anjos & Rocha, 2008; Carlos Frederico D. Rocha & Bergallo, 2011; Telles, Militão, Bergallo, & Rocha, 2015) (Martins, Bruno, & Navegantes, 2012). In addition, several ecological effects associated to *Hemidactylus* invasion have been broadly described. For instance, the arrival of *H. frenatus* on the Mascarene Islands in the Indian Ocean decimated six species of Gekkonidae of the genus Natus (Cole, Jones, & Harris, 2005). It's also well described the competitive displacement of *H. frenatus* over native geckos at the Pacific islands (Petren, Bolger, &

Case, 1993). In Florida it was observed that the recent arrival of *H. mabouia* led to a rapid decline of another congeneric and exotic species previously present (*H. garnotii*) in urban areas (Short & Petren, 2011c). Other types of damage caused by invasive *Hemidactylus* have also been reported, such as the association of their distribution with dengue fever incidence (Weterings, Barbetti, & Buckley, 2019) and, even, they there associated to electrical equipment damages in Cuba (Borroto-páez, 2021).

Although the first biogeographic study focusing on *Hemidactylus* in the New World argued for a natural transatlantic colonization for *H. mabouia* (Kluge, 1969), it is almost a consensus among the present authors that the species arrived in the Americas through human action due it recent origin in America (Anjos & Rocha, 2008; Carranza & Arnold, 2006; Decker et al., 2016; Rödder, Solé, & Böhme, 2008). Molecular studies have indicated that the species is likely a protagonist in an extreme story among recent large-expansion reptiles. Analysis of mtDNA sequences from widely distributed specimens (including several localities in Brazil, the West Indies, southeastern USA, and Africa) found very low genetic divergence (less than 1%) with most of the 30 individuals analyzed having the same haplotype (Carranza & Arnold, 2006). Based on these data and on previous studies (S. Rocha, Carretero, & Harris, 2005; Vences et al., 2004), it is concluded that the original distribution of the species would probably be restricted to a small island in eastern Africa (Mayotte) where the highest intra-population genetic diversity of the species was found (2% divergence and six haplotypes). In this context, a subset of this diversity would have colonized the continent and spread to most of sub-Saharan Africa, and in a second dispersal event (mediated by human transport) would have reached the Americas (Carranza & Arnold, 2006). Due to the African origin, many authors associate transatlantic transport with slave traffic (Albuquerque, Soares, & Alves, 2013; Augusto, Sousa, Maria, & Freire, 2010; Iturriaga & Marrero, 2013; Mageski, Jesus, & Ferreira, 2017; C F D Rocha & Anjos, 2007; Vanzolini, 1968), but no study has directly evaluated this hypothesis.

Since previous studies have found low genetic variability in the mtDNA of *H. mabouia* (Carranza & Arnold, 2006), the use of highly polymorphic markers is recommended for studies of population genetic structure in this species. Thus, the availability of microsatellite primers developed for *H. mabouia* facilitates it population genetic analyses (Short & Petren, 2008). Since the development of this tool, only two studies have been conducted, both in Florida (Short & Petren, 2011b, 2011a). Based on microsatellites, (Short & Petren, 2011b) detected a significant genetic structure at local and global scale, but a low genetic structure at regional scale. Based on this pattern the authors concluded that human activities should be allowing more gene flow at regional scale probably due to cargo transport, however local and global transport should be rare. In a fine scale study, differences on the genetic pattern were found associated with colonization time were areas of older colonization showed higher genetic variability but less genetic structure than areas of more recent colonization (Short & Petren, 2011a).

In this context, we evaluated the genetic structure of *H. mabouia* and its possible association with the slave trade that sadly occurred in Brazil between the 16th and 18th centuries. We used microsatellites, slave trade data and biogeographical analysis to address the forward questions. (1) Is there any association between genetic clustering and the origin of slave ships at the main arrival points of these vessels in Brazil? (2) Would the nuclear genetic marker present a low genetic variability likewise it was found in mtDNA previous analysis indicating a foundation effect during the invasion process in Brazil? (3) Do the genetic diversity and structure differ between localities were slave vessels have landed and others localities in Brazil where *H. mabouia* supposedly arrived later?

Materials and Methods

Sampling, DNA extraction and genotyping

We collected 244 individuals from eight Brazilian urban regions: (Table 1) Distrito Federal (DF), Goiânia (GO), Palmas (TO), Rio de Janeiro (RJ), Feira de Santana (BAFS), Salvador (BASA), Recife (PE), Florianópolis (SC). Three of those regions (RJ, PE and BASA) received great amount of slave ships from Africa mainly during XVII and XVIII and they were probable regions of *H. mabouia* entry into Brazil. In each region individuals were collected in at least 3 localities (except Florianópolis which had only one locality) to allow the fine genetic structure analysis. All animal and tissue collection for this study was approved by SISBIO (no 49427) and by CEUA (Comissão de Ética no Uso Animal, no UnBDoc 46108/2014) from Universidade de Brasília.

Whole genomic DNA was extracted from liver using DNA Wizard Genomic DNA Purification (Promega) following the manufacturer’s instructions. We amplified 12 microsatellite loci previously developed for *H. mabouia* (Short & Petren, 2008). One primer of each pair was tagged using a M13 universal sequence (5’- TGT AAA ACG ACG GCC AGT-3’) on its 5’ end to apply an economic dye-labeling method (Schuelke, 2000). PCR reactions were performed in a final concentration of 1X de Colorless GoTaq® Flexi buffer, 1 mM MgCl2, 2 mM of dNTPs, 0,16 µM of fluorescent M13 primer (FAM, HEX or NED fluorophores) a, 0,16 µM of the reverse primer, 0,04 µM of forward primer, 4 ng/µl of template DNA and 0.5 u/µl de GoTaq® Hot Start (Promega). Thermocycle conditions were: (i) 94°C for 5 min, (ii) 30 cycles of 94°C for 30 s, 50-52°C for 45 s and 72°C for 48 s, (iii) 8 cycles a 94°C for 30 s, 53°C for 45 s e 72°C for 45 s e (iv) 72°C for 10 min. Fragment analyses were conducted on an ABI 3130XL DNA analyzer with ROX 500TM size standard. Allele calls were verified by eye in Microsatellite Plugin 1.4.0. on GENEIOUS 6.0.6.

Microsatellites data analysis

Null allele frequencies were estimated using FreeNA (Chapuis & Estoup, 2007) and tests for linkage equilibrium were conducted in GENEPOP 4.5 (Rousset, 2008). In order to avoid results bias, loci with high values of estimated null alleles frequency (>20%, (Chapuis & Estoup, 2007)) were eliminated from analysis. When there was significant evidence of linkage disequilibrium, we also eliminate one of the involved locus (the one with greater estimated null allele frequency).

For each locus within localities the exact tests for Hardy-Weinberg equilibrium were done in pegas package (Paradis, 2010) from R 3.4.4 (R Core Team, 2018). Basic population genetic parameters presented in Table 1 were estimates using the diveRsity package (Keenan, Mcginnity, Cross, Crozier, & Prodöhl, 2013) from R 3.4.4. Allelic richness (AR) was calculated using rarefaction to account for differences in sample size among locations and regions. Pairwise Fst were calculated for interregional (among regions) and intraregional (among localities of the same region) levels using diveRsity package from R 3.4.4. Confidence intervals on Fst were calculated by bootstrapping (1000 replicates) across loci and α was adjusted according to B-Y FDR method (Narum, 2006) for multiple tests. The Mantel test was performed in the GenAlEx 6.5 program (Peakall & Smouse, 2012) with 1,000 replicates and a 95% confidence interval. Significance of inbreeding coefficient (FIS) was determined by bootstrap with 999 replicates. To evaluate the difference in genetic diversity (Ar) and in intraregional Fst between regions that were arrival ports of *H. mabouia* (BASA, PE, RJ) and regions of secondary colonization (DF, GO, TO, BAFS, SC) we used the comparison of sample groups implemented at FSTAT 2.9.3.2 (Goudet, 2001). To evaluate the possible effect on Fst value of the geographic distance among sites within region, we also plotted the Fst values with the interregional geographic distance.

Table 1. Summary table of the genetic characteristic of all sampled localities within each region.

Regions/Localities	Latitude	Longitude	N	A_R	H_e	F_{IS}	Wp
Distrito Federal (DF)			**58**	**4.804**	**0.791**	**0.043**	**1.000**
DF1	-15.761°	-47.837°	11	4.154	0.703	-0.037	
DF2	-15.896°	-47.945°	18	3.772	0.683	-0.070	
DF3	-15.798°	-48.101°	14	4.134	0.709	0.007	
DF4	-15.761°	-47.860°	15	4.106	0.658	0.046	
Goiânia (GO)			**31**	**3.958**	**0.620**	**0.027**	**0.984**
GO1	-16.690°	-49.264°	12	3.694	0.674	0.051	
GO2	-16.604°	-49.261°	11	3.196	0.569	-0.087*	
GO3	-16.603°	-49.263°	8	3.524	0.563	-0.065*	
Palmas (TO)			**31**	**4.115**	**0.630**	**0.181***	**0.920**
TO1	-10.203°	-48.349°	12	3.462	0.646	0.069	

TO2	-10.210°	-48.325°	11	3.708	0.638	0.227*	
TO3	-10.191°	-48.361°	8	3.434	0.557	0.132*	
Rio de Janeiro (RJ)			**34**	**3.892**	**0.628**	**0.057**	**0.920**
RJ1	-22.910°	-43.236°	13	3.297	0.588	0.002	
RJ2	-22.912°	-43.234°	12	3.431	0.627	-0.030	
RJ3	-22.762°	-43.690°	9	3.599	0.623	-0.046	
F. de Santana (BA)			**21**	**4.377**	**0.674**	**0.025**	**0.993**
BAFS1	-12.264°	-38.930°	10	3.919	0.703	-0.088*	
BAFS2	-12.199°	-38.968°	5	3.600	0.631	-0.071*	
BAFS3	-12.266°	-39.199°	6	3.530	0.610	0.059	
Salvador (BA)			**31**	**4.603**	**0.644**	**0.088**	**0.999**
BASA1	-13.001°	-38.508°	9	3.790	0.632	0.090	
BASA2	-12.999°	-38.507°	10	3.847	0.635	-0.041	
BASA3	-13.000°	-38.510°	12	4.240	0.669	0.081	
Recife (PE)			**31**	**3.978**	**0.650**	**0.050**	**0.722**
PE1	-8.049°	-34.900°	10	3.568	0.662	-0.030	
PE2	-8.051°	-34.949°	10	3.524	0.622	0.142	
PE3	-8.088°	-34.951°	11	3.215	0.600	-0.122*	
Florianópolis (SC)	**-27.394°**	**-48.417**	**7**	**2.887**	**0.555**	**-0.095***	**0.213**

We tested for recent bottlenecks each region using BOTTLENECK v.1. (Cornuet & Luikart, 1996; Piry, Luikart, & Cornuet, 1999). We conducted simulations assuming the TPM model of microsatellite mutation with 95% stepwise mutations. We reported results of the two-tailed Wilcoxon sign-rank test because it is the most powerful test that is suitable for fewer than 20 loci (Piry et al., 1999).

We used the program STRUCTURE v.2.3.4 (Pritchard, Stephens, & Donnelly, 2000) to characterize the population genetic structure within (intraegional) and among regions (interregional). We used the admixture model and correlated allele frequencies to conduct simulations with burn-in of 50,000, followed by 500,000 iterations of Markov Chain Monte Carlo, and 10 simulations at each K ranging from 1 to 7 for the interregional analyses. For the intraregional analysis K ranged from 1 to the maximum number of sampled localities at each region. The optimal K score were inferred by Evanno method (Evanno, Regnaut, & Goudet, 2005) using CLUMPAK (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015). The results were represented graphically using the package LEA (François, 2016) from R 3.4.4 (R Core Team, 2018).

To evaluate possible sex-bias dispersion we compared mAIc, vAIC, FIS and FST parameters between sexes (Jérôme Goudet, Perrin, & Waser, 2002). Statistical significance for these indices was determined by 1000 randomizations as implemented in hierfstat package (Jérôme Goudet, 2005) from R 4.1.1 (R Core Team, 2022).

Slave trade and biogeographic analysis

Assuming that *H. mabouia* reached South America by transatlantic slave trade, in this work, we evaluated the pattern of vessel origin in each Brazilian port sampled for genetic data. We used environmental niche models to access which regions are potentially able to support the presence of *Hemidactylus mabouia* at Africa. In order to get this information, we obtained georeferenced data of the species in the Global Biodiversity Information Facility (GBIF). with presence in the African continent. To have reliable data, we used only those records that had latitude, longitude, location, country, and were deposited in biological collections with available voucher numbers. Within the records of *H. mabouia*, more than 20 different species can be found, all named as being part of the same species. Only one of these species has been able to become invasive in several regions of the world (Agarwal et al., 2021)

To generate the ecological niche model, we used the maximum entropy algorithm, Maxent 3.4.1 (S. Phillips, Dudík, & Schapire, 2018; S. J. Phillips & Dudík, 2008). This algorithm performed well when compared to other niche modeling methodologies (Elith et al., 2006; Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). To reduce sampling bias and spatial auto-correlation (Boria, Olson, Goodman, & Anderson, 2014), we used the spThin package (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015), from the R software (R Core Team, 2018), using a distance of 10 km and 100 repetitions. We used the repetition that kept the highest number of records.

To select the calibration area of the models, we used the whole continent of Africa. We started using 17 environmental layers, in a resolution of 5 arc second, related to the annual variations of temperature and precipitation obtained in the Worldclim (Fick & Hijmans, 2017). Then we selected only those layers that did not show high correlation with the others (r > 0.8), for this step we generated a matrix based on the Pearson correlation coefficient, using the records of the species for analysis. After this step, we kept the layers: Annual Mean Temperature, Mean Diurnal Range, Isothermality, Annual Precipitation, and Precipitation of Driest Month. To transform the logistic models in binary we used the threshold of Maximum training sensitivity plus specificity (Liu et al. 2013) To analyze the performance of the models, we used the boyce index. This index proves to be reliable for analyzing presence-only based predictions (Hirzel el at. 2006).

To identify the origin and destination of slave ships, and to verify if they correspond to the potential presence of *H. mabouia*, we use data from the Slavevoyages database (Slavevoyages Development Team 2018). The criterion used was the first port of obtaining slaves, if this information was not sufficient; we also used the main port of slave purchase. We filtered those records that had the disembarkation of slaves in Brazil and we also excluded those records where the port of origin was outside the area of potential distribution of *H. mabouia*. To define the approximate locations of the ports of embarkation and disembarkation, we projected the current maps of the study regions on the maps available by Slavevoyages. We georeferenced the locations using the QGIS 2.18.7 program (QGIS Development Team 2018). To find regions and search for the most appropriate points to define locations that have changed their names we used as reference the points found with Google Earth Pro 7.3.2 (Google LLC 2018). To determine from which biogeographic regions the populations of *H. mabouia* potentially originated, we overlapped the binary model of potential distribution generated over the map of biogeographical regionalization and phenogram based on the combined matrix for the African continent (Linder et al. 2012).

Results

Interregional analysis

All 12 loci were successfully amplified for the 244 individuals. The linkage disequilibrium tests suggested a significant association between Hm 56 and Hm 122 loci (α=0.05). We also detected an estimated high value of null alleles frequency (r ≥ 0.20) for Hm 136. Based on these estimates, we eliminated Hm 56 and HM 136 from further analysis to avoid possible biases.

The mean number of alleles per locus for the total sample was 14.9 and the rarefied mean allele richness (Ar) ranged from 2.887 at Florianopolis (SC) to 4.804 at Distrito Federal. We found significant inbreeding coefficient (F_{IS}) values for Palmas (TO) and Florianopolis. The comparison of sample groups implemented at FSTAT 2.9.3.2 didn't indicate a significant difference on the allele richness between regions that were arrival ports of *H. mabouia* (BASA, PE, RJ) and regions of secondary colonization (DF, GO, TO, BAFS, SC). Based on Wilcoxon sign-rank test no sign of recent population decrease were found among the sampled regions (Table 1). Interregional F_{ST} estimates resulted in significant values (α = 0.013, B-Y FDR correction) in all pairwise comparisons (Table 2). Further, pairwise relatedness among regions was associated with the geographic distance between them (Mantel test: R =; p =) corroborating the isolation by distance model.

Table 2. Pairwise Fst (lower diagonal) and geographic distance (upper diagonal) among regions.

Regions	DF	GO	TO	RJ	BAFS	BASA	PE	SC
DF	-	165.89	622.64	915.63	1041.22	1065.68	1656.96	1282.83
GO	0.029*	-	718.29	924.15	1024.12	1225.04	1822.58	1195.07
TO	0.066*	0.126*	-	1497.11	1038.69	1116.39	1492.89	1903.22
RJ	0.066*	0.036*	0.157*	-	1264.91	1027.41	1870.72	713.41
BAFS	0.043*	0.086*	0.066*	0.109*	-	92.65	643.92	1943.95
BASA	0.112*	0.169*	0.110*	0.176*	0.095*	-	671.80	1898.37
PE	0.106*	0.149*	0.102*	0.132*	0.108*	0.122*	-	2568.60

SC	0.106*	0.165*	0.123*	0.197*	0.098*	0.157*	0.149*	-

* Significant for α = 0,013, B-Y FDR correction.

Analysis of ΔK estimated by STRUCTURE and CLUMPAK indicated two genetically distinct clusters (ΔK = 56.43 Fig. 1A and 1C). In general, groups are associated with geographic locations: group I (Fig. 1A, gray) is mainly located at mid-west and southeast Brazil, and group II (Fig. 1A, black) is mainly located at north and northeast Brazil. Most analyzed regions all individuals were assigned to only one genetic group, only TO and BA-FS presented highly admixture individuals.

Slave trade and biogeographic analysis

After the applied methodology, to *H. mabouia* complex we obtained a Boyce index of 0.831, the maximum training sensitivity plus specificity was 0,393 resulting in a total of 8433 slaves ships in the analysis. To *H. mabouia sensu strictu* the values obtained was 0,918 and 0,270, respectively, resulting in a total of 8107 ships. The Boyce index for both environmental niche models shows that the generated models are efficient in predicting the distribution of the species.

Figure 1B shows the proportion of vessels that originated from each African biogeographic region (including only those ports where *H. mabouia* occurrence was predicted) that arrived at each Brazilian port. Comparing this result with the genetic clusters, we can observe a biogeographical coincidence. The ports of Salvador (BA-SA) and Recife (PE), where the individuals belong to genetic cluster II, received almost all ships from the Congolese region. On the other hand, the ports of southeastern Brazil, where Rio de Janeiro (RJ) and genetic cluster I are located, received a quarter of the ships from the South African and Zambezian biogeographic region.

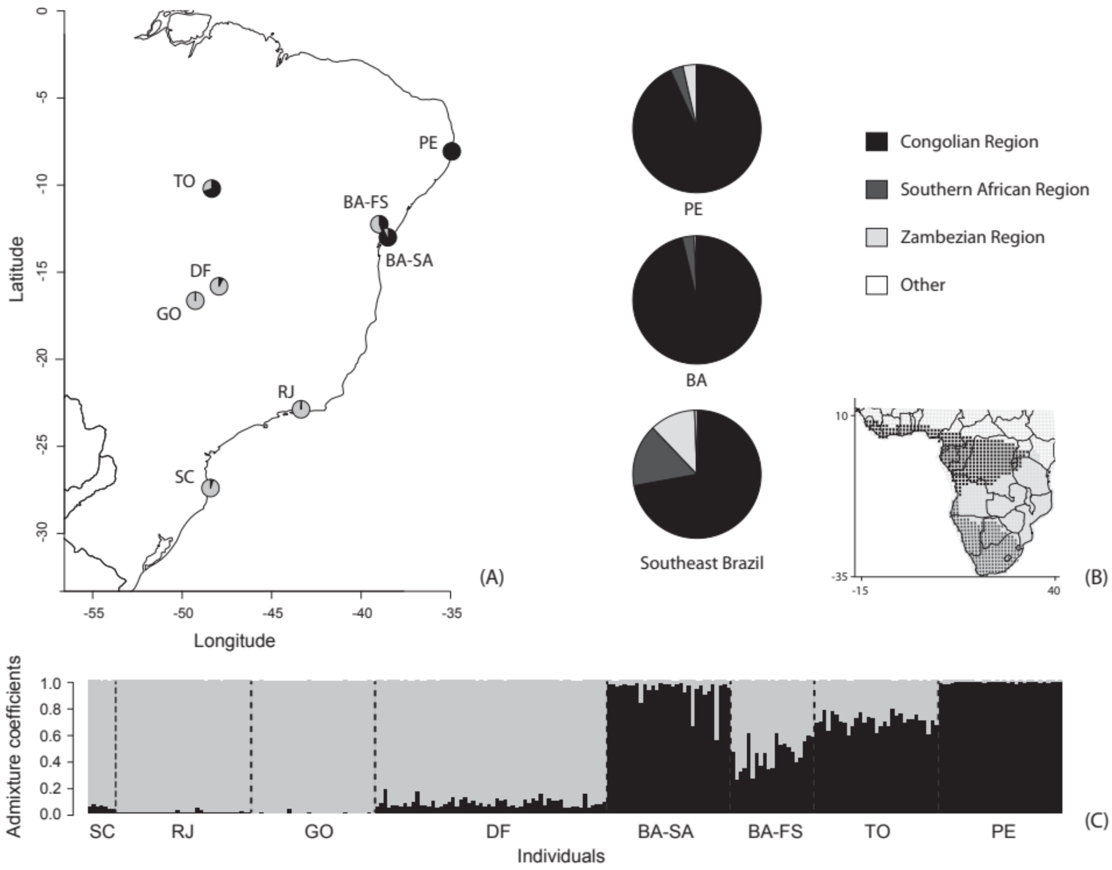

Figure 1. (A) Pie graphics illustrating the geographical distribution the proportion of individuals assigned to each genetic clusters inferred by Structure algorithm. (B) Pie graphics illustrating the proportion of vessels that originated in each biogeographic region in Africa that reached each of the three main arrival ports in Brazil. (C) The clusters obtained from the STRUCTURE 2.2 analyses of 244 individuals of the Hemidactylus mabouia whereby each column represents an individual and the assignment probability to belong each genetic group.

Intraregional analysis

Within localities, the allele richness (AR) ranged from 2.887 at Florianópolis and 4.240 at BASA3 and the expected heterozigozity (He) ranged from 0.563 at GO3 and 0.709 at DF3 (Table 1). Significant inbreeding coefficients (FIS) were found at localities of Goiânia, Palmas, Feira de Santana and Recife (Table 1).

Significant intraregional Fst values between localities were found at all regions except Salvador (BASA) and Palmas (TO) (Table 3). The comparison of sample sets implemented at FSTAT 2.9.3.2 didn’t indicate a significant difference on Fst ($p = 0.99$), but we detected a significant on allele richness ($p = 0.03$) between regions that were arrival ports of *H. mabouia* (BASA, PE, RJ) and regions of secondary colonization (DF, GO, TO, BAFS, SC) indication an increase on genetic diversity during the colonization process. Figure 2 details the comparison of Fst between the set of primary and secondary colonization regions taking into account the geographical distance between the collection localities within each region. Black squares represents regions of former colonization (BASA, PE, RJ) and gray circles represents regions of recent colonization, and there isn’t any clear tendency of higher values of Fst (above linear regression model) at recent colonization regions.

Except for Salvador (k=3), the analysis of intraregional genetic clusters resulted in maximum delta K for K=2 groups for all other regions (Fig. 3). Excluding DF, in none of the cases there was a correspondence between the genetic group and the locality; furthermore all the individuals were admixed with a similar probability of belonging to any genetic group. Is also known that the Evanno method is unable to return a value of K = 1 in the absence of structure in the data (Evanno et al., 2005). Thus, in general, no signs of strong intraregional genetic structuring were observed in the sampled regions regardless of the colonization time. Furthermore, no sign of recent population decrease were found among the sampled localities.

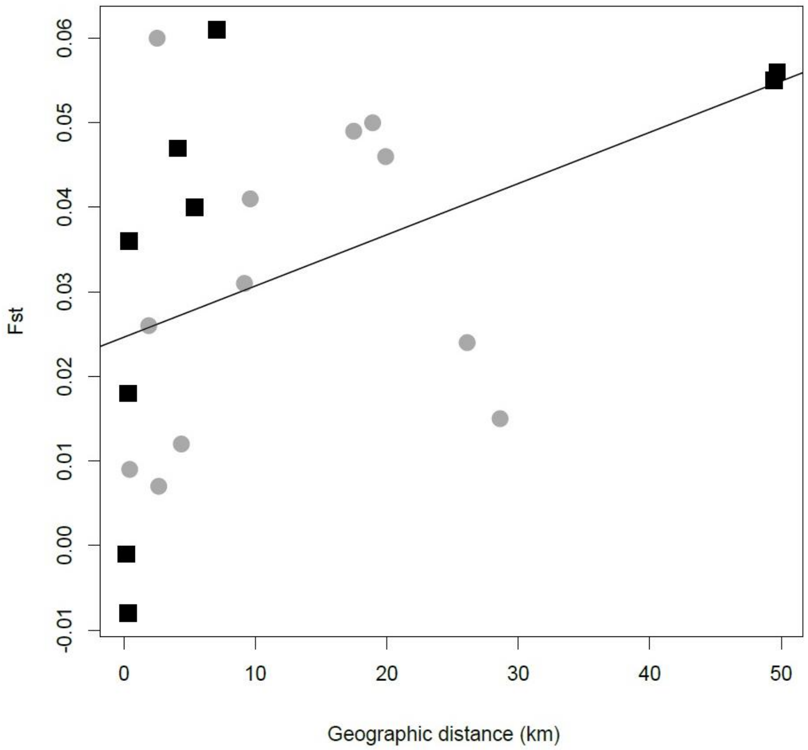

Figure 2. Plot of the Fst values and the geographic distance between intraregional localities. Black squares represent regions that were main arrival ports of slave vessels between the 16th and 18th centuries and gray circles represents others regions in Brazil where H. mabouia supposedly arrived later.

Table 3. Pairwise Fst (lower diagonal) and geographic distance (upper diagonal) among localities within regions.

Locality	**PE1**	**PE2**	**PE3**	
PE1	-	5.37	7.05	
PE2	0.040*	-	4.10	
PE3	0.061*	0.047*	-	
	BAUF	**BASA1**	**BASA2**	
BASA1	-	0.31	0.20	
BASA2	-0.008	-	0.38	
BASA3	-0.001	0.036	-	
	RJ1	**RJ2**	**RJ3**	
RJ1	-	0.31	49.43	
RJ2	0.018	-	49.69	
RJ3	0.055*	0.056*	-	
	BAFS1	**BAFS2**	**BAFS3**	
BAFS1	-	8.30	29.25	
BAFS2	0.006	-	26.16	
BAFS3	0.052*	0.019	-	
	GO1	**GO2**	**GO3**	
GO1	-	9.17	9.61	
GO2	0.031*	-	0.44	
GO3	0.041*	0.009	-	
	DF1	**DF2**	**DF3**	**DF4**
DF1	-	18.92	28.61	2.53
DF2	0.050*	-	19.91	17.48
DF3	0.015	0.046*	-	26.11
DF4	0.060*	0.049*	0.024*	-
	TO1	**TO2**	**TO3**	
TO1	-	2.65	1.89	
TO2	0.007	-	4.37	
TO3	0.026	0.012	-	

Discussion

Is there any association between genetic clustering and the origin of slave ships at the main arrival points of these vessels in Brazil?

Previous studies indicate that *H. mabouia* samples from Brazil showed great genetic similarity with the Africans samples, which strongly indicates the recent arrival of this species in the South American continent (Carranza & Arnold, 2006). Since during a long period of time (about three centuries of slave trade cruel system) a great number of vessels from several locations in Africa arrived in Brazil, so many authors consider that *H. mabouia* went accidentally on these ships (Albuquerque et al., 2013; Augusto et al., 2010; Iturriaga & Marrero, 2013; Mageski et al., 2017; C F D Rocha & Anjos, 2007; Vanzolini, 1968), but this hypothesis has never been directly evaluated.

Based on microsatellites data, analysis of ΔK estimated by STRUCTURE and CLUMPAK indicated two genetically distinct clusters (ΔK=_ Fig. 1C). These clusters present a geographical distribution pattern in which the group represented in black is mainly in the north (northeast group) and the group represented in gray is predominantly in the southernmost regions (southeast group) (Fig. 1A). When analyzing the results obtained for Rio de Janeiro, Recife and Salvador (former ports of entry for slave ships) we noticed that the first is composed exclusively of individuals assigned to the southeast cluster while the last two regions are composed almost exclusively of individuals assigned to the northeast group. As we obtained a clear genetic differentiation between northeast and southeast ports we decided to evaluate if there were any differences in the origin of the ships. In this way, we could observe (Fig. 1B) that the two northeast ports received practically only vessels from the Congolian biogeographical region (Linder et al., 2012). However, Rio de Janeiro received a large amount, of about one quarter of the vessels, from two other biogeographic regions (Fig. 1B): Southern African and Zambezian regions (Linder et al., 2012). This coincidence provides the first direct evidence in favor to the slave vessels as transportation of *H. mabouia* to Brazil, but, evidently other sources of data and evidences should be analyzed to get a more robust conclusion.

It is also interesting to highlight that all the regions sampled that did not receive slave ships (where *H. mabouia* supposedly arrived later from the entry ports) have a large proportion of individuals assigned southeast group (Fig. 1). Brazilian southeast estates that include São Paulo, Rio de Janeiro, Minas Gerais and Espirito Santo is also de most industrialized and urbanized region where most of the products that are distributed to the remaining states of the country originate (IBGE, 2020). This pattern corroborates the results found in Florida which indicates that human activities should be allowing more gene flow at regional scale probably due to cargo transport (Short & Petren, 2011b).

Would the nuclear genetic marker present a low genetic variability likewise it was found in mtDNA previous analysis indicating a foundation effect during the invasion process in Brazil?

Although previous studies based on mitochondrial DNA indicated low genetic variability in almost the entire range of *H. mabouia* (Agarwal et al., 2021; Carranza & Arnold, 2006), our microsatellite nuclear data didn't show indications of an especially low variability compared with others studies with lizards. Furthermore, our data didn't show any signal of recent bottleneck based on nuclear markers.

We also investigate a possible sex biased dispersion (Johansson et al., 2008; Qi, Yang, Lu, & Fu, 2013; Ujvari, Dowton, & Madsen, 2008; Urquhart et al., 2009), but we didn't find any significative signal on local or regional scale indicating no preference or differences on survival based on sex during *H. mabouia* expansion in Brazil. However, our data can't tell about a possible sex bias associates to the arrival of *H. mabouia* to South America, since it might have a higher mortality of females (mainly pregnant ones) during the long travel. Therefore, it would be interesting to future studies analyze South American and African samples together based on nuclear and mitochondrial molecular data to explore deeper into this issue.

References

Agarwal, I., Ceríaco, L. M. P., Metallinou, M., Jackman, T. R., & Bauer, A. M. (2021). How the African house gecko (*Hemidactylus mabouia*) conquered the world. Royal Society Open Science, 8(8). https://doi.org/10.1098/rsos.210749

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38(5), 541–545. https://doi.org/10.1111/ecog.01132

Albuquerque, N. R. De, Soares, M. P., & Alves, L. S. (2013). Diet of two sit-and-wait lizards, Phyllopezus pollicaris (Spix, 1825) (Phyllodactylidae) and *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Gekkonidae) in a perianthropic area of Mato Grosso do Sul, western Brazil. Biota Neotropica, 13(4), 376–381.

Anjos, L. A. dos, & Rocha, C. F. D. (2008). A Lagartixa *Hemidactylus mabouia* Moreau de Jonnes, 1818 (Gekkonidae): uma espécie exótica e invasora amplamente estabelecida no Brasil. Natureza & Conservação, 6(1), 78–89.

Augusto, P., Sousa, G. De, Maria, E., & Freire, X. (2010). Communal nests of *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Squamata: Gekkonidae) in a remnant of Atlantic Forest in northeastern Brazil. Biotemas, 23(3), 231–234.

Barnett, L. K., Phillips, B. L., Heath, A. C. G., Coates, A., & Hoskin, C. J. (2018). The impact of parasites during range expansion of an invasive gecko. Parasitology, 145(11), 1400–1409. https://doi.org/10.1017/S003118201800015X

Betancur-R., R., Hines, A., Acero P., A., Ortí, G., Wilbur, A. E., & Freshwater, D. W. (2011). Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. Journal of Biogeography, 38(7), 1281–1293. https://doi.org/10.1111/j.1365-2699.2011.02496.x

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling, 275, 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012

Borroto-páez, R. (2021). REPTILES & AMPHIBIANS Equipment : New Evidence of Damage to Televisions and Other Electrical Risks. (May).

Cameron, E. K., Bayne, E. M., & Coltman, D. W. (2008). Genetic structure of invasive earthworms *Dendrobaena octaedra* in the boreal forest of Alberta: insights into introduction mechanisms. Molecular Ecology, 17(5), 1189–1197. https://doi.org/10.1111/j.1365-294X.2007.03603.x

Carranza, S., & Arnold, E. N. (2006). Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution, 38(2), 531–545. https://doi.org/10.1016/j.ympev.2005.07.012

Chapuis, M.-P., & Estoup, A. (2007). Microsatellite null alleles and estimation of population differentiation. Molecular Biology and Evolution, 24(3), 621–631. https://doi.org/10.1093/molbev/msl191

Cole, N. C., Jones, C. G., & Harris, S. (2005). The need for enemy-free space: The impact of an invasive gecko on island endemics. Biological Conservation, 125(4), 467–474. https://doi.org/10.1016/j.biocon.2005.04.017

Cornuet, J. M., & Luikart, G. (1996). Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics, 144(4), 2001–2014. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1207747&tool=pmcentrez&rendertype=abstract

Decker, P., Reip, H., Insectenfaune, K. R. Der, Rica, C., Islands, C., Vincent, S., … Na-, M. (2016). Antropogenic effect or niche preference ? contributions to the knowledge of *Hemidactylus mabouia* invasion in South America. North-Western Journal Fo Zoology, 12(2), 389–392.

Elith, J., Graham, C. H., Anderson, R. P., Dudı´k, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. ECOGRAPHY, 29, 129–151. https://doi.org/10.1111/j.1432-1033.1987.tb13499.x

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology, 14(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier, L., Foll, M., & Petit, R. J. (2009). Genetic consequences of range expansions. Annual Review of Ecology, Evolution, and Systematics, 40, 481–501. https://doi.org/10.1146/annurev.ecolsys.39.110707.173414

Fagúndez, J. (2013). Heathlands confronting global change: Drivers of biodiversity loss from past to future scenarios. Annals of Botany, 111(2), 151–172. https://doi.org/10.1093/aob/mcs257

Ferchaud, A. L., Eudeline, R., Arnal, V., Cheylan, M., Pottier, G., Leblois, R., & Crochet, P. A. (2015). Congruent signals of population history but radically different patterns of genetic diversity between mitochondrial and nuclear markers in a mountain lizard. Molecular Ecology, 24(1), 192–207. https://doi.org/10.1111/mec.13011

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302–4315. https://doi.org/10.1002/joc.5086

François, O. (2016). Running Structure-like Population Genetic Analyses with R (pp. 1–9). pp. 1–9. U. Grenoble-Alpes.

Goudet, J. (2001). FSTAT, a program to estimate and test gene diversities and fixation indices. Lausanne, Switzerland: Lausanne University.

Goudet, Jérôme, Perrin, N., & Waser, P. (2002). Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Molecular Ecology, 11(6), 1103–1114. https://doi.org/10.1046/j.1365-294X.2002.01496.x

Goudet, Jérôme. (2005). HIERFSTAT, a package for R to compute and test hierarchical F-statistics. Molecular Ecology Notes, 5(1), 184–186. https://doi.org/10.1111/j.1471-8286.2004.00828.x

Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography, 29, 773–785. https://doi.org/10.1021/jp048527b

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., … Stuart, S. N. (2010). The impact of conservation on the status of the world’s vertebrates. Science, 330(6010), 1503–1509. https://doi.org/10.1126/science.1194442

IBGE. (2020). Demografia das empresas e estatísticas de empreendedorismo: 2018.

Iturriaga, M., & Marrero, R. (2013). Feeding ecology of the Tropical House Gecko *Hemidactylus mabouia* (Sauria : Gekkonidae) during the dry season in Havana , Cuba. 6(January), 11–17.

Jesus, J., Brehm, A., Pinheiro, M., & Harris, D. J. (2001). Relationships of *Hemidactylus* (Reptilia: Gekkonidae) from Cape Verde Islands: what mitochondrial DNA data indicates. Journal of Herpetology, 35(4), 672–675.

Johannesen, J., Keyghobadi, N., Schuler, H., Stauffer, C., & Vogt, H. (2013). Invasion genetics of American cherry fruit fly in Europe and signals of hybridization with the European cherry fruit fly. Entomologia Experimentalis et Applicata, 147(1), 61–72. https://doi.org/10.1111/eea.12041

Johansson, H., Surget-Groba, Y., & Thorpe, R. S. (2008). Microsatellite data show evidence for male-biased dispersal in the Caribbean lizard Anolis roquet. Molecular Ecology, 17(20), 4425–4432. https://doi.org/10.1111/j.1365-294X.2008.03923.x

Keenan, K., Mcginnity, P., Cross, T. F., Crozier, W. W., & Prodöhl, P. A. (2013). DiveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. Methods in Ecology and Evolution, 4(8), 782–788. https://doi.org/10.1111/2041-210X.12067

Kluge, A. G. (1969). The evolution and geographical origin of the New World *Hemidactylus mabouia-brookii* complex (Gekkonidae, Sauria). Miscellaneous Publications Museum of Zoology, University of Michigan, 138, 1–78.

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. Molecular Ecology Resources, 15(5), 1179–1191. https://doi.org/10.1111/1755-0998.12387

Lee, C. E. (2002). Evolutionary genetics of invasive species. Trends in Ecology & Evolution, 17(8), 386–391. https://doi.org/10.1016/S0169-5347(02)02554-5

Linder, H. P., de Klerk, H. M., Born, J., Burgess, N. D., Fjeldså, J., & Rahbek, C. (2012). The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. Journal of Biogeography, 39(7), 1189–1205. https://doi.org/10.1111/j.1365-2699.2012.02728.x

Lowry, E., Rollinson, E. J., Laybourn, A. J., Scott, T. E., Aiello-Lammens, M. E., Gray, S. M., … Gurevitch, J. (2012). Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution, 3(1), 182–196. https://doi.org/10.1002/ece3.431

Mageski, M., Jesus, P. R., & Ferreira, P. D. (2017). Continued dispersal of the Wood Slave Gecko, *Hemidactylus mabouia*, in natural environments of Brazil. North-Western Journal of Zoology, 13(2), 363–364.

Martins, A. R., Bruno, S. F., & Navegantes, A. Q. (2012). Herpetofauna of Núcleo Experimental de Iguaba Grande, Rio de Janeiro state, Brazil. Braz. J. Biol, 72(3), 553–562. Retrieved from http://www.scielo.br/pdf/bjb/v72n3/18.pdf

Meimberg, H., Hammond, J. I., Jorgensen, C. M., Park, T. W., Gerlach, J. D., Rice, K. J., & McKay, J. K. (2005). Molecular Evidence for an Extreme Genetic Bottleneck During Introduction of an Invading Grass to California. Biological Invasions, 8(6), 1355–1366. https://doi.org/10.1007/s10530-005-2463-7

Narum, S. R. (2006). Beyond Bonferroni: Less conservative analyses for conservation genetics. Conservation Genetics, 7(5), 783–787. https://doi.org/10.1007/s10592-005-9056-y

Oliveira, C. M., Auad, a. M., Mendes, S. M., & Frizzas, M. R. (2013). Economic impact of exotic insect pests in Brazilian agriculture. Journal of Applied Entomology, 137(1–2), 1–15. https://doi.org/10.1111/jen.12018

Paradis, E. (2010). Pegas: An R package for population genetics with an integrated-modular approach. Bioinformatics, 26(3), 419–420. https://doi.org/10.1093/bioinformatics/btp696

Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research--an update. Bioinformatics (Oxford, England), 28(19), 2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Petren, K., Bolger, D. T., & Case, T. J. (1993). Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science, 259(5093), 354–358. https://doi.org/10.1126/science.259.5093.354

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31, 161–175. https://doi.org/10.1111/j.2007.0906-7590.05203.x

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics, 52(3), 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Piry, S., Luikart, G., & Cornuet, J.-M. (1999). BOTTLENECK: a computer program for detecting recent reductions in the effective population size using allele frequency data. 90(4), 499–503.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics, 155, 945–959. https://doi.org/10.1111/j.1471-8286.2007.01758.x

Prugnolle, F., & de Meeus, T. (2002). Inferring sex-biased dispersal from population genetic tools: a review. Heredity, 88, 161–165.

Qi, Y., Yang, W., Lu, B., & Fu, J. (2013). Genetic evidence for male-biased dispersal in the Qinghai toad-headed agamid Phrynocephalus vlangalii and its potential link to individual social interactions. Ecology and Evolution, 3(5), 1219–1230. https://doi.org/10.1002/ece3.532

R Core Team. (2018). R: A language and environment for statistical computing. Retrieved from https://www.r-project.org/

Ramakrishnan, A. P., Musial, T., & Cruzan, M. B. (2010). Shifting dispersal modes at an expanding species' range margin. Molecular Ecology, 19(6), 1134–1146. https://doi.org/10.1111/j.1365-294X.2010.04543.x

Rato, C., Carranza, S., Perera, A., Carretero, M. A., & Harris, D. J. (2010). Conflicting patterns of nucleotide diversity between mtDNA and nDNA in the Moorish gecko, Tarentola mauritanica. Molecular Phylogenetics and Evolution, 56(3), 962–971. https://doi.org/10.1016/j.ympev.2010.04.033

Rocha, C F D, & Anjos, L. a. (2007). Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. Brazilian Journal of Biology = Revista Brasleira de Biologia, 67(3), 485–491. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/18094831

Rocha, Carlos Frederico D., & Bergallo, H. G. (2011). Occurrence and distribution of the exotic lizard *Hemidactylus mabouia* Moreau de Jonnès, 1818 in Ilha Grande, RJ, Brazil. Brazilian Journal of Biology, 71(2), 447–450.

Rödder, D., Solé, M., & Böhme, W. (2008). Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). North-Western Journal of Zoology, 4(2), 236–246.

Rousset, F. (2008). GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources, 8(1), 103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x

Roy, B. A., Alexander, H. M., Davidson, J., Campbell, F. T., Burdon, J. J., Sniezko, R., & Brasier, C. (2014). Increasing forest loss worldwide from invasive pests requires new trade regulations. Frontiers in Ecology and the Environment, 12(8), 457–465. https://doi.org/10.1890/130240

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., … Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. Science, 287(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., … Rice, W. R. (2007). Ecological and evolutionary insights from species invasions. Trends in Ecology & Evolution, 22(9), 465–471. https://doi.org/10.1016/j.tree.2007.06.009

Schuelke, M. (2000). An economic method for the fluorescent labeling of PCR fragments. Nature Biotechnology, 18(February), 233–234.

Short, K. H., & Petren, K. (2008). Isolation and characterization of 12 polymorphic microsatellite markers in the tropical house gecko (*Hemidactylus mabouia*). Molecular Ecology Resources, 8(6), 1319–1321. https://doi.org/10.1111/j.1755-0998.2008.02270.x

Short, K. H., & Petren, K. (2011a). Fine-scale genetic structure arises during range expansion of an invasive gecko. PloS One, 6(10), e26258. https://doi.org/10.1371/journal.pone.0026258

Short, K. H., & Petren, K. (2011b). Multimodal dispersal during the range expansion of the tropical house gecko *Hemidactylus mabouia*. Ecology and Evolution, 1(2), 181–190. https://doi.org/10.1002/ece3.18

Short, K. H., & Petren, K. (2011c). Rapid species displacement during the invasion of Florida by the tropical house gecko *Hemidactylus mabouia*. Biological Invasions, 14(6), 1177–1186. https://doi.org/10.1007/s10530-011-0147-z

Slavevoyages Development Team. (2018). Slavevoyages: The Trans-Atlantic Slave Trade Database.

Team, Q. D. (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Telles, F. B. S., Militão, C. M., Bergallo, H. G., & Rocha, C. F. D. (2015). Invasion of the alien gecko *Hemidactylus mabouia* (Moureau de Jonnès, 1818) in a natural habitat at Praia do Sul Biological Reserve, Ilha Grande, RJ, Brazil. Brazilian Journal of Biology, 75(3), 768–770. https://doi.org/10.1590/1519-6984.19614

Townsend, J. H., & Krysko, K. L. (2002). The distribution of *Hemidactylus* (Sauria : Gekkonidae) in northern peninsular Florida. Florida Scientist, 66, 204–208.

Tsutsui, N. D., Suarez, a V, Holway, D. a, & Case, T. J. (2000). Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences of the United States of America, 97(11), 5948–5953. https://doi.org/10.1073/pnas.100110397

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. Ecology Letters, 11(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Ujvari, B., Dowton, M., & Madsen, T. (2008). Population genetic structure, gene flow and sex-biased dispersal in frillneck lizards (Chlamydosaurus kingii). Molecular Ecology, 17(15), 3557–3564. https://doi.org/10.1111/j.1365-294X.2008.03849.x

Urquhart, J., Wang, Y., & Fu, J. (2009). Historical vicariance and male-mediated gene flow in the toad-headed lizards Phrynocephalus przewalskii. Molecular Ecology, 18(17), 3714–3729. https://doi.org/10.1111/j.1365-294X.2009.04310.x

Vanzolini, P. E. (1968). Lagartos brasileiros da família Gekkonidae (Sauria). Arquivos de Zoologia, 17(1), 1–84.

Wagner, P., Köhler, J., Schmitz, A., & Böhme, W. (2008). The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. Journal of Biogeography, 35(8), 1349–1361. https://doi.org/10.1111/j.1365-2699.2008.01883.x

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van Der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. Science, 332(6035), 1273–1277. https://doi.org/10.1126/science.1197479

Weterings, R., Barbetti, M., & Buckley, H. L. (2019). Hypothesis: Do invasive house geckos exacerbate dengue fever epidemics? Biological Invasions, 21(12), 3533–3543. https://doi.org/10.1007/s10530-019-02066-x

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., … Zimmermann, N. E. (2008). Effects of sample size on the performance of species distribution models. Diversity and Distributions, 14(5), 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Wood, J. P., Beer, S. D., Campbell, T. S., & Page, R. B. (2018). Insights into the introduction history and population genetic dynamics of the Argentine black-and-white tegu (Salvator merianae) in Florida. Genetica, 146(6), 443–459. https://doi.org/10.1007/s10709-018-0040-0